Legacy phosphorus and ecosystem memory control future water quality in a eutrophic lake

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Abstract

Lake water clarity, phytoplankton biomass, and hypolimnetic oxygen concentration are metrics of water quality that are highly degraded in eutrophic systems. Eutrophication is linked to legacy nutrients stored in catchment soils and in lake sediments. Long lags in water quality improvement under scenarios of nutrient load reduction to lakes indicate an apparent ecosystem memory tied to the interactions between water biogeochemistry and lake sediment nutrients. To investigate how nutrient legacies and ecosystem memory control lake water quality dynamics, we coupled nutrient cycling and lake metabolism in a model to recreate long-term water quality of a eutrophic lake (Lake Mendota, Wisconsin, USA). We modeled long-term recovery of water quality under scenarios of nutrient load reduction and found that the rates and patterns of water quality improvement depended on changes in phosphorus (P) and organic carbon storage in the water column and sediments. Through scenarios of water quality improvement, we showed that water quality improvement due to water column flushing, followed by a much longer rates of storage pools – an initial and rapid water quality improvement due to water column flushing, followed by a much longer and slower improvement as sediment P pools were slowly reduced. Water clarity, phytoplankton biomass, and hypolimnetic dissolved oxygen differed in their time responses. Water clarity and algal biomass improved within years of nutrient reductions, but hypolimnetic oxygen took decades to improve. Even with reduced catchment loading, recovery of Lake Mendota to a mesotrophic state may require decades due to nutrient legacies and long ecosystem memory.

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10	Key Points:
11 12	• Legacy phosphorus in lake sediments controls long term lake water quality response to nutrient remediation.
13 14	• Coupled cycles of nutrients, physics, and metabolism explain ecosystem memory of lake phosphorus, water clarity, and oxygen habitat.
15 16 17	• Improvement in lake water quality to pristine levels will require decades of commitment to nutrient load reductions.

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23 memory tied to the interactions between water biogeochemistry and lake sediment nutrients. To

investigate how nutrient legacies and ecosystem memory control lake water quality dynamics,
 we coupled nutrient cycling and lake metabolism in a model to recreate long-term water quality

of a eutrophic lake (Lake Mendota, Wisconsin, USA). We modeled long-term recovery of water

quality under scenarios of nutrient load reduction and found that the rates and patterns of water

quality improvement depended on changes in phosphorus (P) and organic carbon storage in the

29 water column and sediments. Through scenarios of water quality improvement, we showed that

30 water quality variables have distinct phases of change determined by the turnover rates of storage

31 pools – an initial and rapid water quality improvement due to water column flushing, followed

by a much longer and slower improvement as sediment P pools were slowly reduced. Water

clarity, phytoplankton biomass, and hypolimnetic dissolved oxygen differed in their time

responses. Water clarity and algal biomass improved within years of nutrient reductions, but

35 hypolimnetic oxygen took decades to improve. Even with reduced catchment loading, recovery

of Lake Mendota to a mesotrophic state may require decades due to nutrient legacies and long

- 37 ecosystem memory.
- 38

39 Plain Language Summary

40 Lake water quality, as measured by the concentration of algae near the lake surface, the clarity of the water, and the availability of dissolved oxygen to support organisms, is greatly reduced in 41 lakes with nutrient pollution from phosphorus. In Lake Mendota, Wisconsin, phosphorus applied 42 to the surrounding landscape for more than a century has accumulated in catchment soils and in 43 the lake water column and sediments (i.e., "legacy phosphorus"), leading to poor water quality. 44 To investigate how water quality in Lake Mendota might respond to nutrient pollution reduction, 45 we used computer models to simulate the elimination of phosphorus inputs from the catchment 46 and track water quality change. Phosphorus in the lake water column initially decreased quickly, 47 due to water column flushing, but then decreased very slowly due to release of legacy 48 phosphorus from lake sediments. Water quality recovery lagged that of phosphorus, indicating an 49

inherent "ecosystem memory" for past phosphorus levels. Ecosystem memory was due to

51 biological activity that remained elevated, even when phosphorus was declining in the water

column. With nutrient inputs to the lake eliminated, recovery of algae concentration and water

53 clarity to pristine conditions required decades, and a return to a fully oxygenated condition

- 54 required a century.
- 55

56 **1 Introduction**

- 57 The quality of surface freshwater underpins sustainable futures for the planet (Folke et al., 2020;
- Lee & Diop, 2009); however, water quality deterioration has been alarmingly persistent
- 59 (Damania et al., 2019; Oliver et al., 2017). Human activities have greatly exacerbated lake
- 60 eutrophication, or excess nutrient enrichment, which drives toxic phytoplankton blooms, reduced
- 61 water clarity, and bottom water anoxia (Smith & Schindler, 2009). Eutrophication is associated
- with nutrient loads to lakes (Schindler et al., 2016), especially watershed nitrogen (N) and
 phosphorus (P) export from lake catchments (Carpenter & Bennett, 2011). Water quality in lakes
- has shown troubling resistance to improvement, despite recognition of the problem and
- 65 management action intended to reduce nutrient loads (Jenny et al., 2016; Søndergaard et al.,
- 66 2007).
- 67 Slow recovery of lake water quality is due, in part, to the legacy of nutrient application in lake
- catchments (Chen et al., 2018). Here, we refer to nutrient legacies following (K. Van Meter et
- al., 2018), specifically referring to the excess N and P accumulated in catchment terrestrial soils
- due to decades of agriculture and other land use (Bennett et al., 1999; Sabo et al., 2021). For
- 71 many catchments, the effect of this nutrient legacy is eutrophication in downstream lake
- ⁷² ecosystems (Bennett et al., 1999; Keatley et al., 2011; K. J. Van Meter et al., 2021). Although
- 73 catchment-scale nutrient management programs have led to reduced nutrient export to lakes in
- some cases (Sharpley et al., 2019), lakes can be slow to recover from eutrophication (McCrackin stal 2017), due in part to loggery mutricate accumulated in lake acdiments (Japanesen et al.
- rs et al., 2017), due in part to legacy nutrients accumulated in lake sediments (Jeppesen et al., 2005)
- 76 2005).
- 77 Ecosystem memory in lakes may contribute to slow recovery from eutrophication. Here, we
- define ecosystem memory (a la Ogle et al., 2015) as the influence of past ecosystem states on the
- rates and patterns of future responses to change. In lakes, many processes may contribute to
- 80 ecosystem memory and associated responses to nutrient load reductions, such as slow flushing in
- 81 lakes with long hydrologic residence times (Hotchkiss et al., 2018), internal loading of nutrients
- 82 from large sediment pools (Carleton & Lee, n.d.; Søndergaard et al., 2007), and biological
- feedback mechanisms that promote persistently high algal biomass, despite decreasing nutrient
- 84 loads (Scheffer et al., 2001). While specific biophysical processes may be well described, it 85 remains a challenge to understand how their interactions control water quality metrics that
- remains a challenge to understand how their interactions control water quality metrics that emerge at the ecosystem scale, such as seasonal patterns of phytoplankton biomass, water clarity,
- and formation of deep-water anoxia.
- Lake metabolism provides a framework for investigating ecosystem memory by linking changes
- in nutrient concentration to biophysical processes that can be expressed as ecosystem-scale water
- 90 quality metrics over different time scales. While lake metabolism can be generalized as the
- balance of primary production and respiration (Odum, 1956; Staehr et al., 2010), its
- 92 implementation in analytical models often includes physical and biological processes that
- 93 quantify both metabolic processes and ecosystem states relevant to water quality (Ladwig et al.,
- 94 2022; Winslow et al., 2016). For example, elevated epilimnetic nutrients stimulate primary
- 95 production (i.e., autochthony), which reduces water clarity through phytoplankton-associated
- turbidity (Smith, 1982). Autochthonous organic matter supports high microbial respiration,
- which leads to consumption of available oxygen in deeper waters of thermally stratified
- 98 (Matzinger et al., 2010; Müller et al., 2012). Allochthonous organic matter also contributes to

- lake metabolism (Hanson et al., 2003) and is generally considered a more recalcitrant and
- 100 persistent source of organic carbon that contributes to long-term change in water quality metrics
- 101 (Kothawala et al., 2014). Metabolism models that consider both autochthonous and
- allochthonous organic matter sources and cycling can recreate both short-term and long-term
- ecosystem dynamics (Hoellein et al., 2013). By linking physical, nutrient, and organic carbon
- 104 cycles, metabolism models may also provide a mechanistic basis for the role of ecosystem
- 105 memory in eutrophication recovery.

106 We investigated how linked cycles of nutrients and lake metabolism control the time scale of

- 107 water quality responses to reduced nutrient loads projected for Lake Mendota (Wisconsin, USA).
- 108 We used 20 years of observational data to calibrate a physical-biogeochemical model and
- 109 recreate annual dynamics of three water quality metrics, which are water column P
- 110 concentrations, water clarity (as a function of dissolved and particulate organic carbon), and
- 111 hypolimnetic dissolved oxygen (DO) depletion. Through a scenario of long-term nutrient
- reduction, we quantified how P legacies in the lake influence the responses of water quality
- metrics, highlighting the role of long-term ecosystem memory. While we were interested in
- water quality recovery, we were equally interested in the internal feedbacks that alter the time
- scales of change for water quality to address the questions: How do P cycles and lake
- 116 metabolism interact to determine the time scales of change for water clarity and summer anoxia?
- How long is the legacy of historical P loading from the catchment to the lake on future water
- 118 quality conditions?

119 **2 Materials and Methods**

120 Our over-arching goal was to link sediment and water column nutrient and organic matter cycles for the purpose of investigating how seasonal water quality metrics change over decades to 121 centuries. While there are excellent examples of coupling sediment to water processes (Paraska 122 et al., 2014), we needed an approach that allowed us to model lake metabolism at the ecosystem 123 scale and that included general sediment properties, such as area, depth and P and organic carbon 124 (OC) pool sizes. Following the recent work by Carleton and Lee (2023), who used a relatively 125 simple model to recreate long-term P change in lakes and their sediments, we focus on simplicity 126 and flexibility, recognizing that our approach enables future scaling to build additional 127 complexity and application. We also placed high importance on recreating both seasonal and 128 129 long-term dynamics in addressing how a lake responds to nutrient load reduction. Seasonal dynamics are important because water quality impairment, such as algal blooms and 130 hypolimnetic anoxia, are generally summer phenomena in north temperate lakes. Long-term 131 dynamics (decades to centuries) are important because of the persistence of nutrient legacies in 132 lakes. We relied on high quality long-term data to inform the design of the model and calibrated 133 it for predicting water quality. We used the calibrated model to run scenarios of water quality 134 recovery, in which external nutrient loads to the lake were reduced. 135

136 2.1 Study system

137 Our study system was Lake Mendota, which is a eutrophic lake located in south-central

- 138 Wisconsin, USA. The lake's surface area is 39.61 km^2 , with a maximum and mean depth of 25 m
- and 12.8 m, respectively. The lake has a dimictic mixing regime and typically is stratified during

140 most of April-October. Lake Mendota is a drainage lake with an average water residence time of

141 4.3 years (Lathrop & Carpenter, 2014).

Lake Mendota and its catchment have a long history of human use. While people have lived near 142 Lake Mendota for thousands of years, eutrophication likely occurred over a relatively short time 143 period during the late 1800s to early 1900s, due to agricultural intensification, followed by 144 urbanization (Brock, 1985; Lathrop, 2007). For our study, we assumed that Lake Mendota was 145 either mesotrophic or oligotrophic in its water quality prior to European settlement, based on 146 sediment cores (Brock, 1985). Currently, the lake is eutrophic and its catchment is predominantly 147 urban and agricultural, with very high N and P biomass in catchment soils (Bennett et al., 1999; 148 Lathrop, 2007). As a result of decades of high N export from the catchment to the lake, the lake 149 tends to be P-limited (Lathrop, 2007), and thus we focused on P dynamics when modeling the 150 nutrient legacies of the lake. 151

152 2.2 Models linking physics, phosphorus, organic carbon, and dissolved oxygen

153 We used a time-dynamic approach to model lake water quality and linked the three lake water

154 quality cycles of interest – P, OC, and DO, all within the context of lake hydrodynamics (Fig. 1).

155 We used this model to generate daily metrics of water quality, which are water column P

concentrations, water clarity (as a function of dissolved and particulate OC), and hypolimnetic

DO depletion. To study long-term changes in water quality, we tracked ecosystem states in both the water column and sediments. Explicitly linking cycles of P, OC, and DO enabled us to study

how changes in external loads led to changes in major lake pools and subsequent changes in

160 seasonal water quality metrics.

161 Model details are provided in supplemental information (Tables S1-S3). The process-based

162 implementation of thermodynamics was adapted from our previous work on pond thermal

structure (Albright et al., 2022), lake metabolism modeling (Carey et al., 2018), and lake

164 phosphorus modeling (Hanson et al., 2020). The model is 1-D in the vertical dimension, with

three compartments modeled simultaneously using a box-modeling approach – water column

epilimnion and hypolimnion, and active sediments (Fig. 1). Each compartment is treated as fully

167 mixed.

168 The lake physical model solves the energy budget and mixing dynamics on an hourly time step 169 and produces 1 m vertical resolution temperature output. The lake physical model follows an

integral energy approach for heat transport and solves vertical diffusion using an implicit scheme

(see model formulations in Albright et al., 2022; note that we neglected the effects of

172 macrophytes on energy attenuation in the current study). Water clarity, updated daily by the 173 metabolism model, informs attenuation of short-wave radiation in the physical model. Hourly

temperature output by the physical model is averaged to daily values, and sequentially linked to

the water quality calculations. Thermal strata are calculated from the vertical temperature

gradient. Strata volume and areal contact with sediments are calculated daily from the

thermocline depth and lake hypsometry. In our application of the physical model output in the

metabolism model, each thermal layer was considered fully mixed, and mean layer temperature

179 was calculated from the layer's volume weighted average.



Figure 1. The lake model has three compartments: epilimnion, hypolimnion (when the lake is 182 thermally stratified), and active sediments. Boxes are state variables. DIC shown for reference 183 and is not modeled. Arrows are fluxes or biogeochemical transformations. Modeled state 184 variables are: phosphorus (P); in the sediments, P is divided between bound (P_B) and unbound 185 (P_U) forms; dissolved oxygen (DO); particulate and dissolved organic carbon (POC and DOC, 186 respectively) in two forms, labile (*OC_L) and recalcitrant (*OC_R). Three fluxes control 187 ecosystem inputs and outputs for P and OC (blue arrows) - load, export, and burial. Movement 188 of state variables between compartments indicated by black arrows. Metabolic processes are 189 NPP (green) and R (red). The dashed green arrow indicates that NPP is not a sink for P. P efflux 190 from the sediments is represented as recycling of P_U and release of P_B. Settling and rebinding 191 return P to the sediments. All state variables are subject to entrainment as the thermocline depth 192 changes. Numbers in parentheses refer to model equations (Table S1). 193

195 The metabolism model includes pools (i.e., state variables) of total phosphorus (P), organic

196 carbon (OC), and dissolved oxygen (DO) (Fig. 1; Table SI X). OC pools include particulate

197 (POC) and dissolved (DOC) fractions and labile (POC_L , DOC_L) and recalcitrant (POC_R , DOC_R) 198 forms. The model information is provided in detail in the SI, and summarized here. Pools are

tracked separately for the epilimnion and the hypolimnion. We assume allochthony is recalcitrant

and autochthony is labile. The model also includes an "active sediment layer," which has pools

201 for labile and recalcitrant POC and pools for tightly bound P (P_B) and loosely bound (including

202 organic) P, which we simplified to "unbound" (P_U). At a conceptual level, our overall approach

has similarities that of Carleton and Lee (2023) on P cycling in lakes. We highlight in the SI

some key similarities and differences between their work and ours, and we use the findings of
 Carleton and Lee (2023) and references therein in evaluating the long-term behavior of our

206 model.

207 The lake sediments are divided into an upper active zone above a permanent burial zone. The

active zone has POC_R , POC_L , P_U , and P_B , each of which interacts with the water column and is

subject to permanent burial. Sources of sediment $POC_{R,L}$ are settling from the water column.

210 Sinks for $POC_{R,L}$ include mineralization to inorganic carbon and permanent burial. Sources for

sediment P are settling (P_U) and rebinding (P_B) from the water column. Sinks for $P_{U,B}$ include

recycling of P_U back into the water column, release of P_B back into the water column under

anoxic conditions, and permanent burial of $P_{U,B}$. The details of rates and how they vary by

temperature and oxic condition are provided in the SI. Permanent burial of P and OC is determined by the accumulation of lake acciments. A acciment accumulation rate of 1.0 mm y^{-1}

determined by the accumulation of lake sediments. A sediment accumulation rate of 1.0 mm y^{-1} is assumed for Lake Mendota, unless otherwise stated in a scenario. Permanent burial of P and

OC is simply the product of the mass of each of the active sediment constituents and the ratio of

the sedimentation rate and active sediment depth. For example, under the above conditions,

permanent burial of POC would be $POC_{Sed} * 0.001 \text{ m y}^{-1} / 0.1 \text{ m} = POC_{Sed} * 0.01 \text{ y}^{-1}$. We

explore some of these assumptions in scenarios described below. See SI for more detailed

221 justification for sediment extent and dynamics.

222 2.3 Model calibration and sensitivity analysis

223 The model was manually calibrated to recreate observed ice cover onset and breakup, Secchi

depth, and volumetrically-weighted mean values for the epilimnion and hypolimnion for water

temperature, dissolved oxygen, total phosphorus, and dissolved organic carbon. Calibration was

based on the \sim 20 years of observational data from 1995-2015. Free parameters (Table S2) were

227 manually tuned to achieve visual correspondence between predictions and observations. Root

228 mean square error (RMSE), Nash–Sutcliffe model efficiency coefficient (NSE), and Kling-Gupta

229 Efficiency (KGE) are reported for the fit model over the calibration period.

230 We assumed that the calibrated model must approximate sediment core values of P. As described

previously, it was necessary to run the model for hundreds of years (repeating the 20 years of

driving data) to achieve sediment equilibrium for both P and OC. Because P recycling and

233 sediment respiration are a function of sediment P and OC pool sizes, a change in equilibrium of

the sediments affects water column predictions, requiring additional calibration. Thus,

calibration was an iterative process of selecting parameter values, running the model for

236 centuries to long-term equilibrium, and then checking for calibration. Although automated

optimization would likely yield more accurate predictions, the dominant sensitivities lie more in
 our assumptions regarding P pools and loads.

For the legacy scenarios described below, we did not have observational data for the Lake Mendota prior to western settlement. To test whether our calibrated model could reproduce oligotrophic and mesotrophic conditions (i.e., water quality conditions prior to western settlement), we assumed external P loads more typical of oligotrophic and mesotrophic lakes (Table S3). We ran the model for 300 years, repeating the use of 20 years of driver data, to allow the full system to reach dynamic equilibrium. We then compared water quality metrics with published indices for the different trophic states (Table S4).

246 2.4 Legacy scenarios

247 We ran three legacy scenarios to investigate the response of Lake Mendota to nutrient load

reductions (Table S3). In our base legacy scenario (Scenario 1), we assumed zero external load

of P for 120 years, repeating the same 20 years of hydrology and meteorology used in

calibration. We also assumed a 50% reduction in allochthonous OC load and a 50% reduction in

inert sediment load that determines P and OC burial rates. In Scenario 2, external P loads were

reduced to values typical of mesotrophic lakes, but other conditions were the same as in the base

scenario. In Scenario 3, permanent burial rate of sediment P was raised to values assumed for the

calibrated model, which provided for a faster water quality recovery than the base scenario.

255 We tracked all model states and rates through the three scenarios and noted when water quality

variables passed thresholds between trophic states (Table S4). We explored Lake Mendota's

257 memory to historical P loads by comparing the relative rates of change of water quality variables

with those of P in the sediments and water column over 120 y. Time series of variables were

smoothed with a forward/backward moving average filter (10 y) to eliminate interannual

variability due to climate and hydrology drivers, and then each time series was normalized to a

range of 0-1, with 1 and 0 representing their values at the beginning and end of a scenario,

respectively. With these normalized values, we calculated first differences for each variable and divided by, e.g., first differences for epilimnetic P. A value <1 indicated the variable was lagging

divided by, e.g., first differences for epilimnetic P. A value <1 indicated the variable was lagg
 (i.e. recovering more slowly than) epilimnetic P change, whereas a value >1 indicated the

variable was leading (i.e., recovering more quickly than) epilimnetic P change.

While we used the model to address several questions, we were most interested in understanding why lake water quality responds slowly to nutrient reductions and how Lake Mendota, as a test case, helps us interpret this phenomenon more generally. Thus, a precise estimate of when Lake

269 Mendota might reach an oligotrophic state in the future is less important than understanding how

270 lake processes interact to control the patterns of water quality change we might expect in

response to potential nutrient reductions. Through model scenarios, we demonstrate that the

272 general patterns of water quality change are robust to changes in key assumptions about the

273 model and about the lake.

274 **3 Limnological data and model driving data**

275 Limnological data for calibration were provided by the North Temperate Lakes Long Term

276 Ecological Research program and available in the Environmental Data Initiative repository

- 277 (Magnuson, John J et al., 2023). These data have been collected fortnightly or monthly,
- depending on the variable, since 1995 (Magnuson et al. 2006). Lake sediment core data were
- used to inform the sediment component of the model (Hurley et al., 1992; Walsh et al., 2019).

280 Data for driving the model included daily discharge, P and organic carbon (OC) loads, as well as

hourly meteorological data. Discharge was taken from Hanson et al. (2020); however, the entire

time series was linearly adjusted so that mean hydrologic residence time over the 20-year calibration period of the model was 4.3 years (Lathrop & Carpenter, 2014). Meteorological

forcing data were obtained from the second phase of the North American Land Data

Assimilation System (Xia et al., 2012). Meteorological variables used in this study included wind

- speed, air temperature, specific humidity, surface pressure, surface downward short- and
- longwave radiation, and total precipitation, which were used as boundary data for physical modeland metabolism model.
- 289

4 Results

4.1 Comparison of model predictions with observations

The model reproduced well the time dynamics of observed winter ice cover duration, as well as ice-off date (Fig. 2). Notable exceptions were 1998 and 2002, when the model over-predicted ice cover duration and ice-off date. The mean observed ice duration was 86 d (\pm 26, 1 SEM), and the mean ice-off day of year 86 (~March 27th), which compared well with the a modeled mean ice duration of 86 d, and modeled mean ice-off day of year 85 (~March 26th). On average, there was less variability among years in the model predictions than in the observations.

Physical and chemical dynamics of the epilimnion and hypolimnion compared well with the 298 observed data (Fig. 3A,B). The RMSE was 1.28 °C and 1.31 °C for the epilimnion and 299 hypolimnion, respectively (Table S5). For Secchi depth, predictions reproduced the observed 300 annual dynamics (Fig. 3D), although the RMSE was somewhat high at 2.15 m. Occasional high 301 Secchi values in the observational data were missed by the model. The annual DO cycle was 302 well reproduced for the epilimnion and hypolimnion (Fig. 3D,E), and RMSE values were 1.44 303 mg L^{-1} and 1.98 mg L^{-1} , respectively. Occasional very high epilimnetic DO values during winter 304 were missed by the model, and observed values well-below saturation later in summer were 305 missed. We suspect that low observed epilimnetic DO during summer were due to inclusion of 306 307 the upper half of the metalimnion in the calculation of average epilimnetic DO.

Total phosphorus annual dynamics were reproduced by the model (Fig. 4A,B). The RMSE

values for the epilimnion and hypolimnion were 51.6 μ g L⁻¹ and 183 μ g L⁻¹, respectively. In

310 general, the model underpredicted annual maxima early in the time series and over-predicted

annual maxima late in the time series. Low summer P values were reproduced well, which was

an outcome particularly relevant to summertime water quality predictions. The hypolimnetic P predictions matched observations until the end of the stratified period, at which time model

predictions increased dramatically. This was likely a consequence of a relatively low ratio of

hypolimnetic volume to sediment surface area, which results in higher hypolimnetic

316 concentrations.



Figure 2. Model results and observational data for lake ice cover for the calibration period. (A) Simulated and observed values for ice covered days each year. The year corresponds to the year

that ice-off occurred. (B) Simulated and observed values for ice-off day of year.



Figure 3. Model predictions (black line) and observations (red circles) for the full calibration period. Panels are (A) water temperature for the epilimnion, and (B) hypolimnion; (C) Secchi depth; (D) dissolved oxygen in the epilimnion, and (E) hypolimnion.





DOC predictions matched trends of the observations for both the epilimnion and hypolimnion (RMSE of 0.99 mg L⁻¹ and 0.98 mg L⁻¹, respectively). However, the model over-predicted DOC by about 1.5 mg L⁻¹ from about 2008-2013. We have sparse information on DOC loads, and model deviations from observations may be due to unmeasured changes in the driver data inflow concentrations.

- Goodness-of-fit showed mixed results, depending on the test and the state variable (Table S5).
- Although NSE was strongly positive for T and DO and slightly positive for Secchi depth, it was
- 337 negative for P and DOC. KGE, which is thought to be a more reliable statistic for environmental
- timeseries data (Gupta et al., 2009), was positive for all variables. However, KGE for DOC was
- near zero, suggesting our model for DOC only slightly outperformed a model based on the DOC
- 340 mean alone.

341 The test of the model using mesotrophic and oligotrophic P load scenarios produced expected

water quality behaviors (Figs. S1,S2). Phosphorus concentrations in the lake decreased to

mesotrophic and oligotrophic levels, with annual epilimnetic P ranging from 5-100 μ g L⁻¹ and 1-

5 μ g L⁻¹, respectively. DOC concentrations in the epilimnion also decreased to mesotrophic and oligotrophic levels, at approximately 4 mg L⁻¹ and 3 mg L⁻¹, respectively. Minimum summer

oligotrophic levels, at approximately 4 mg L^{-1} and 3 mg L^{-1} , respectively. Minimum summer Secchi depth increased to about 2.5 m and 5 m for mesotrophic and oligotrophic simulations,

respectively. For the mesotrophic simulation, duration of hypolimnetic anoxia decreased by

about 10 days y^{-1} ; whereas, in the oligotrophic simulation, anoxia no longer occurred.

349 4.2 Annual cycles of temperature, P, OC, and DO

350 The time dynamics of state variables underlying the water quality of Lake Mendota recreated the

351 expected annual limnological patterns through four distinct seasons. The winter ice-covered

period (Fig. 5A) had stable physical, chemical and biological conditions relative to other seasons,

353 with low but continuous P settling and P recycling (Fig. 6D). Winter productivity was low (Fig.

354 7D), resulting in relatively clear water (Fig. 7A). Cold water temperatures drove high annual DO

concentrations with oxygen at near saturation (Fig. 5A). Spring ice-off was a time of rapid

change, with high NPP and increasing settling of both POC (Fig. 7D,E,F) and P (Fig. 6D,F).

357 Spring catchment snowmelt and precipitation led to a rise in external P loads (Fig. 6D; Fig. 7D).

Decreasing epilimnetic DO was largely driven by changing temperature (Fig. 5A). Water clarity generally decreased in the spring, except during a distinct clear-water phase in late spring (Fig.

generally decreased in the spring, except during a distinct clear-water phase in late spring
 7A). Thermal stratification began in spring (Fig. 5C), along with a rapid decrease in

361 hypolimnetic DO (Fig. 5B).

Summer and autumn dynamics had high NPP and POC (algal biomass) (Fig. 7D), leading to 362 epilimnetic DO near or above saturation (due to high productivity), despite declining DO 363 solubility as temperatures warmed (Fig. 5A). Hypolimnetic DO decreased rapidly after the onset 364 of stable thermal stratification, and the hypolimnion became anoxic (Fig. 5B), except for 365 occasional influxes of DO due to short-term variability in the thermocline depth and entrainment 366 of DO-rich water from the epilimnion. High algal biomass resulted in low clarity (Fig. 7A). 367 Epilimnetic P decreased to its lowest annual values due to settling out of the epilimnion. 368 Hypolimnetic P became very high (Fig. 6A,B), due to recycling of P and release of P from the 369 sediments (Fig. 6E). Once the hypolimnion became anoxic, mineralization rate of organic P 370 slowed, and the dominant efflux of P from the sediments switched to release of bound P from the 371 active sediment layer (Fig. 6E,F). Autumn turnover triggered the mixing of hypolimnetic 372 nutrients into the entire water column. As P encountered oxic conditions in the surface waters, P 373 rebinding increased, and P settled into the sediments (Fig. 6D). Elevated nutrient concentrations 374 supported continued primary production into the autumn (Fig. 7D), although rates decreased 375 because of cooling temperatures and reduced irradiance prior to the onset of winter ice cover. 376





epilimnion and (B) hypolimnion, and (C) modeled thermocline depth. Periods of ice cover

shown in (A). Grey shaded periods represents thermal stratification.





Figure 6. Modeled total phosphorus (P) for 2005 and 2006. (A) P states for the epilimnion, (B)

hypolimnion, and (C) sediments. (D) P rates for the epilimnion, (E) hypolimnion, (F) sediments.

- 386 For rates, positive values are sources and negative values are sinks, with legends above or below
- zero, respectively. Entrainment not shown. Grey shaded periods represents thermal
- 388 stratification.



Figure 7. Modeled organic carbon and Secchi depth for 2005 and 2006. Lines for OC are

stacked. (A) Organic carbon states and Secchi depth for the epilimnion, (B) organic carbon states
 for the hypolimnion, and (C) sediments. (D) Organic carbon rates for the epilimnion, (E)

393 hypolimnion, (F) sediments. For rates, positive values are sources and negative values are sinks,

with legends above or below zero, respectively. Lines are not stacked for D-F. Inflow and

outflow are total organic carbon, settling is all forms of POC, and respiration includes both labile and refractory forms combined. Burial is all POC. Grey shaded areas represents thermal

397 stratification.

398 4.3 Major fluxes and storage

On an annual basis, most of the P in the water column originated from internal loading from the sediment. Internal P loading (Fig. 6D,E) was ~5.5 x that of the external load (0.8 gP m⁻² y⁻¹). Note that in Fig. 6D, the large flux of P from the hypolimnion to the epilimnion during fall mixis is not shown, but this accounts for the rapid epilimnetic P increase shown during mixis in Fig. 6A. The range of external versus internal loads was relatively narrow across the calibration period, in part because of our model assumptions for external loading, which did not account for changing P concentrations as a function of hydrologic flow.

Despite the seasonal variability in water column dynamics, permanent burial of P (Fig. 6F) and

407 OC (Fig. 7F) in the sediments appeared near constant through the year. This is because sediment 408 concentrations of these constituents are high relative to water column values and therefore have

409 low relative variability (Figs. 6C, 7C).

410 Annual autochthony (i.e., NPP) was much higher than allochthony (Fig. 7D). Although most of

the autochthony was respired (Fig. 7D-F), a substantial proportion was stored long term in the

sediments and buried (Fig. 7C,F), resulting in long term positive net ecosystem production

413 (NEP) for the lake.

414 4.4 Legacy scenarios

Improvement in water quality for Lake Mendota differed depending on the water quality metric

and scenario. For Scenario 1 (Fig. 8), in which external P loads were set to zero and OC and

sediment loads were reduced, epilimnetic P decreased rapidly in the first 20 years due to water

column flushing (Fig. 8A), followed by a long slow decrease that tracked decreasing

419 hypolimnetic and sediment P (Fig. 8B,C). For OC, the initial rapid decrease occurred for both the

epilimnion and the hypolimnion (Fig. 8D,E), because the autochthonous pool of OC was

421 produced by epilimnetic NPP. Over the 120 y simulation, sediment OC decreased to roughly half

of its original value (Fig. 8F). Secchi depth continually increased following decreases in OC

423 (Fig. 8G). Dissolved oxygen was the variable slowest to respond to reduced external loads.

Although sediment oxygen demand decreased linearly (Fig. 8H), the number of anoxic days

decreased slowly for about 50 years, and then decreased rapidly until about year 105, at which time anoxia no longer occurred (Fig. 8I). The annual range for P and POC decreased with the

decreasing mean value. For Secchi depth, the range decreased with increasing value.

- 428 Overall, the pathways to improved trophic states differed among variables after external loads
- 429 were set to zero (Fig. 9). Light extinction, which is inversely related to Secchi depth, and
- epilimnetic P passed the eutrophic-mesotrophic threshold between years 15-20 of the simulation.
 Epilimnetic P passed the mesotrophic-oligotrophic threshold at year ~50, while light extinction
- 431 Epilimnetic P passed the mesotrophic-oligotrophic threshold at year ~50, while light extinction 432 passed that threshold about 35 years later. The duration of anoxia showed a different pattern,
- 433 which was convex until about year 60 of the simulation. Although there was a steady decrease in
- 434 anoxia over time, anoxic days did not drop to mesotrophic levels until year ~95 of the simulation
- and did not drop to oligotrophic values (i.e., disappear) until about year ~ 105 .



Figure 8. Recovery of water quality metrics following cessation of external P inputs. Data are
smoothed annual means. Dashed lines indicate annual range. (A-C) Ecosystem total P. (D-E)
Total POC in the water column and (F) sediments. (G) Secchi depth, (H) Sediment oxygen
demand, and (I) anoxic days during.



Figure 9. (A) Response pathways for metrics of water quality. Water quality metrics normalized 444 to a range of 0-1, with high values representing initial conditions and zero representing values at 445 120 years following cessation of external P loads. Circles on Pepi, light extinction, and anoxic 446 days represent trophic thresholds, based on values before normalization. Earlier values are 447 eutrophic to mesotrophic thresholds, and later values are mesotrophic to oligotrophic thresholds. 448 Numbers in boxes are recovery phases. (B) Change in water quality metrics with respect to 449 change in mean surface P and (C) sediment P. Horizontal line at y=1 separates a lagged response 450 in water quality (<1) from an accelerated response (>1). 451

452 Scenarios 2 and 3 (Figs. S3, S4, S5, S6) showed the same general patterns as Scenario 1, but

with differing rates. For Scenario 2 (mesotrophic P loads), water quality values never passed the

threshold from eutrophic to mesotrophic. The duration of the scenario, set to 120 y, was simply

too short. In contrast, Scenario 3 (high inert sediment load and burial rate) demonstrated the

456 importance of higher burial rates in the sediment nutrient and carbon budgets. When burial rate

457 was high, water quality improvement occurred $\sim 20\%$ more quickly overall.

To quantify lags between changes in lake P and water quality responses, we calculated the

relative annual rates of change for variables over the simulation period (Fig. 9B,C). Until about

460 year 20, all metrics lagged (changed at a lower relative rate) changes in epilimnetic P

- concentrations (Fig. 9B). At 20 y, POC_{Epi} and sediment oxygen demand led (changed at a higher 461
- relative rate) P_{Epi}. Light extinction and anoxic days changed from lagging P_{Epi} to leading P_{Epi} at 462
- about year 50. When compared to sediment P (Fig. 9C), only sediment O₂ demand and anoxic 463
- days lagged P_{Sed} changes initially. Other metrics (P_{Epi}, POC_{Epi}, light extinction), which respond 464
- to water column flushing, led P_{Sed} until about year 20. All metrics, other than P_{Epi}, lagged P_{Sed} 465
- until about years 60-80. P_{Epi} continued to lag P_{Sed} through the end of the simulation. 466

5 Discussion 467

5.1 Legacies of eutrophication for Lake Mendota 468

The legacy of more than a century of high nutrient loads to Lake Mendota is degraded water 469

quality that persists for decades to longer than a century under the most aggressive nutrient 470 reduction scenario. Fundamentally, a century of water quality degradation requires a century (or 471

longer) of recovery. Although initial improvement in water clarity and epilimnetic P may occur 472

in a couple of decades, high internal nutrient loads will continue to fuel elevated primary

- 473 production for a century. The long and slow response of water quality to nutrient reduction has 474
- been shown empirically for other lakes (Jeppesen et al., 2005; Søndergaard et al., 2013). For 475
- Lake Mendota, we have demonstrated how nutrient cycling and lake metabolism interact to 476
- control how water quality responds to both the reduction of external loads and the long and slow 477
- depletion of sediment nutrient stocks. 478
- Phosphorus stored in the sediments of Lake Mendota controlled the bottom-up response of water 479
- quality to nutrient load reductions. At approximately 125 g P m⁻² of active sediment area, a 480
- typical sediment P density for eutrophic lakes (Carey & Rydin, 2011), the sediment pool has 481
- approximately two orders of magnitude more P than the annual average water column value of 482 \sim 1.0 g P m⁻². Given Lake Mendota's hydrologic residence time of \sim 4 years and typical water 483
- column P concentrations, only ~0.25 g P m⁻² at most can be flushed annually from the water 484
- column, assuming no additional external loads. Thus, a ~30% reduction in the sediment pool 485
- 486 needed for the lake to return to a mesotrophic state would take about 150 years through the process of flushing alone. These findings support previous work that eutrophication persists in 487
- lakes long-term, despite P remediation (Søndergaard et al., 2013, 2013). However, deposition of 488
- sediments that may bind P or bury it in sediments (Rothe et al., 2014) accelerates the recovery 489
- process, because permanent burial can be an important sink in the sediment P mass balance 490 (Carleton & Lee, n.d.). The high inert sediment load in Scenario 3 (Fig. S6) emphasizes the 491
- 492 importance of burial to sediment P reduction and subsequent water column improvement.
- 493
- 5.2 Ecosystem memory and surprises on the path to trophic state improvement

Ecosystem memory slowed the response of water quality to nutrient load reductions in Lake 494

- Mendota. Water clarity and DO improvement lagged the long, slow decline in sediment P 495
- 496 because of the coupled dynamics of P-cycling, metabolism, and DO. Our expectation was that all
- water quality metrics would improve following cessation of external loads in the legacy 497
- scenarios, even if the rate of improvement was slower than that of P in the water column. 498
- However, the rate of change in hypolimnetic anoxia initially remained nearly flat as the annual 499
- duration of hypolimnetic anoxia showed minimal improvement for nearly two decades (Fig. 9). 500
- In Scenario 2 (60% reduction in P load), which arguably would be a more likely "real-world" 501

scenario, the duration of anoxia actually became worse for the first two decades. This surprising

503 outcome was due to changes in the sediment OC mass balance. When allochthony was turned 504 off, sediment deposition decreased in our model, reducing permanent burial rates for P and OC.

- 504 off, sediment deposition decreased in our model, reducing permanent burial rates for P and OC. 505 For the first 1-2 decades of recovery, water column P was still at concentrations high enough to
- support high production of autochthonous POC (positive NEP), which kept the sediment OC
- 507 mass balance near neutral in Scenario 1 and positive (i.e., accumulation of sediment OC) in
- 508 Scenario 2. At about year 20 of recovery, sediment P diminished to the point where P recycled to
- the water column was lower, and NPP and POC were sufficiently reduced to tip the sediment
- 510 mass balance toward a reduction in POC. In general, consumption of hypolimnetic O_2 depends
- 511 on a number of factors, including lake morphometry (Steinsberger et al., 2020), climate
- variability (Ladwig et al., 2021; Snortheim et al., 2017), and water column stability (Ladwig et
- al., 2021), but chiefly the OC available as substrate for microbial respiration and the benthic flux
 of reduced substances (Müller et al., 2012). Once NEP in the water column became negative
- 515 (i.e., lower export of POC to the sediments), sediment O₂ demand and anoxic days diminished.
- 516 Linked cycles of P, OC, and DO produce nested lags in the response times of water quality
- 517 metrics to reduced nutrient loads and provide a mechanistic basis for ecosystem memory. The
- recovery to an improved trophic state of some water quality metrics can only occur following
- substantial changes in other nutrient or carbon pools. For example, elimination of hypolimnetic
- anoxia requires depletion of the OC available for respiration, and depletion of OC lags recovery
- of P by several decades because of the influence of P on autochthony and NEP (i.e., lake
- 522 metabolism). Lake metabolism is sensitive to long-term lake changes (e.g. Richardson et al.
- 523 2017), highlighting its utility for tracking coupled biological and chemical water quality
- responses to external loading.
- 525 Differing lags of recovery explain why different water quality metrics pass inter-trophic 526 thresholds at different times (Fig. 9). During recovery in Scenario 1, water clarity, based on POC
- 527 concentration (i.e., algal biomass in this model), lags P recovery by about 30 years, and
- 528 hypolimnetic oxygen lags water clarity by about 20 years. Thus, transitioning to an oligotrophic
- state can vary in time from about 50-100 years, depending on the water quality metric.
- 530 Nonetheless, the sequence of responses from decreasing P to improved oxic condition pass
- through a set of predictable phases, described below.
- 5.3 Phases of water quality improvement
- 533 Our scenarios reveal five distinct phases of water quality improvement (Fig. 9). The phases are
- identified visually, based on changes in water quality metrics relative to P_{Epi} (Fig. 9B), which is
- more easily measured in lakes than sediment P. The first phase is water column flushing, which
- corresponds to a rapid decrease in solutes as external loads of P and OC are eliminated and
- reduced, respectively. In phase 2, water quality metrics lag changes in P_{Epi} . In phase 3,
- improvement in water quality metrics accelerates relative to P_{Epi} and then decelerates in phase 4
- as all variables approach a new dynamic equilibrium in the oligotrophic state. In phase 5, water
- quality metrics have reached their oligotrophic values.
- 541 The long time period needed for transitions across these five phases provides context for
- 542 localized ecosystem behavior that otherwise might appear puzzling within the time frame of
- short-term monitoring programs. Any initial rapid improvement in water quality will stall

following water column flushing. Further improvement in water quality will proceed more

slowly than declining P_{Epi} (i.e., values <1 in Fig. 9B) for decades. Eventually, water quality will

improve more rapidly than P_{Epi} (i.e., values >1 in Fig. 9B) until the system reaches its improved

trophic state. In Lake Mendota, these phases would play out over decades and could be observed

548 only through long-term monitoring. We expect that this behavior likely would be applicable to 549 other eutrophic lakes with similar external loading history, although this remains unknown and

- other eutrophic lakes with similar external loading history, although this remains unknown and motivates future work. Altogether, a long view that incorporates ecosystem memory is required
- to understand localized ecosystem behavior during remediation of degraded water quality.

552 5.4 Caveats

Two assumptions in our model regarding sediment P pools are especially worthy of further 553 554 consideration for analyzing Mendota patterns and scaling these results to other lakes. First, the model sets sediment P binding capacity at 1 mg P per gram dry sediment, based on empirical 555 measures of sediment total P concentrations in Lake Mendota (Hoffman et al., 2013). Although 556 this static threshold works well in the model, the reality of sediment P sorption capacity is far 557 558 more complex and may depend on factors such as changes in particle size and mineralogy of deposited sediments (Stone & English, 1993). Along with hypolimnetic dissolved oxygen status, 559 the binding capacity parameter determines the rate at which P may re-bind to the mineral P pool 560 in the sediments and influences the balance of sediment P retention versus release. As such, the 561 model would benefit from further exploration of this parameter, including options for dynamic P 562

563 binding capacity over time.

564 Second, the model focuses solely on redox-sensitive P minerals (iron- and manganese-bound P) 565 in the bound sediment P pool. This focus is supported by empirical evidence of the importance of

anoxic internal P loading in Lake Mendota (Hoffman et al., 2013). However, mineral sediment P

567 may be associated with other metals, such as aluminum and calcium, which are generally

considered less mobile than redox-sensitive P forms (Orihel et al., 2017). Conversely, co-

569 precipitation of soluble phosphorus with calcite may be a pathway for P burial in Lake Mendota.

570 Paleolimnological evidence from Lake Mendota suggests that calcite whiting events and co-

571 precipitation may be an important process for removing soluble P from the water column and 572 permanently burying it in the sediments (Walsh et al., 2019). The model would benefit from

further exploration of linked calcium and P cycles in Lake Mendota.

Additionally, application of the modeling approach to other waterbodies may require

575 consideration of legacy N pools and cycling. We focused our assessment of nutrient cycling on P

due to evidence of P limitation in Lake Mendota (Lathrop, 2007) as well as numerous case

577 studies of P control eliciting desirable water quality responses (Schindler et al., 2016). This

assumption was supported by good model performance compared to the long-term observational

data. However, model application to N-limited waterbodies will require consideration of N

cycling as legacy N loads likely play an important role in long-term lake functioning in these

581 systems.

582 6 Conclusions

583 Repairing ecosystems usually requires more time and effort than damaging them (Jones et al.,

584 2018), in part due to long ecosystem memory. Lake Mendota was eutrophied over a relatively

- short time period probably less than 100 years and has likely had an anoxic hypolimnion as far
- back as the early 1900s (Lathrop, 2007). Our simulations indicate a return to pre-European
- settlement conditions using external P reduction alone will take decades, if not centuries.
- 588 Interaction of cycles in Lake Mendota underlie that long memory, leading to long delays
- between external P load reduction and water quality improvement, because available P must be
- reduced sufficiently to tip the ecosystem OC balance toward net mineralization rather than net accumulation. Only then can microbes begin to consume the organic matter of past decades and
- slowly eliminate the substrate that fuels anoxia. This takes time and the will of a society to
- undergo a multi-generational remediation of a precious water resource.

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- 600

601 **Open Research**

- All data and software for this project are open and freely available through Zenodo (Hanson,
- 603 2023). Data and software are lincenced as Creative Commons Attribution 4.0 International.
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