Macrophyte-hydrodynamic interactions mediate stratification and dissolved oxygen dynamics in ponds

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ABSTRACT

Small waterbodies are sensitive to stressors such as eutrophication and heatwaves; however, interactions between macrophytes and hydrodynamics may mediate the effects of compounding stressors. Leveraging an ecosystem experiment and hydrodynamic model, we evaluated how macrophyte biomass, thermal structure, and dissolved oxygen (DO) responded to the interaction of episodic nutrient loading and periods of high temperatures in two temperate ponds. In one pond we experimentally added pulses of nutrients, simulating storm-driven loading (the other pond served as an unmanipulated reference). Following the first nutrient pulse both ponds experienced a 5-day period of high surface water temperatures. Macrophytes in the nutrient addition pond began to senescence mid-summer due to phytoplankton shading from the nutrient addition and heat stress while macrophytes in the reference pond followed expected seasonal patterns, senescing in early autumn. Field observations and model results indicate that macrophytes structured the thermal environment through vertical attenuation of turbulent kinetic energy and light. Macrophytes reduced the vertical extent of water column warming during the heat event by 0.25-0.5 m and maintained cooler bottom temperatures (up to 2.5 °C cooler) throughout the summer, suggesting that macrophytes may buffer small waterbodies from heatwaves. Seasonal patterns in DO saturation also followed trends in macrophyte biomass; however, during the heat event, DO saturation fell sharply (-22.4 to 50.4 %) in both ponds and remained depressed through the remainder of the summer. This experiment and modeling exercise demonstrated that macrophyte influence on turbulent flows and light are pivotal in mediating how small waterbodies respond to compounding stressors.
INTRODUCTION

Small lakes and ponds are the most abundant lentic ecosystems worldwide and sites of critical importance for freshwater biodiversity and biogeochemical cycles (Scheffer et al. 2006; Cole et al. 2007; Messager et al. 2016). Small waterbodies are active components of regional- and global-scale carbon cycling, both as sites of burial and storage (Wilkinson et al. 2018; Taylor et al. 2019) and as sources of atmospheric carbon dioxide and methane (Holgerson and Raymond 2016; Peacock et al. 2021). Small lakes and ponds enhance local and regional biodiversity, due in part to abundant macrophytes (Van Geest et al. 2003). Robust macrophyte communities support greater diversity of other taxa by providing food resources and habitat structure (Williams et al. 2004; Scheffer et al. 2006). In addition to these biotic interactions, macrophytes play a pivotal role in the ecosystem structure and function of small waterbodies. Interactions between hydrodynamics and the physical structure of macrophyte beds influence turbulent mixing, water column thermal structure, and sediment stability as well as whole-lake productivity and nutrient cycling (Carpenter and Lodge 1986; Scheffer et al. 1993; Licci et al. 2019). Despite the prevalence and importance of small, vegetated lakes and ponds, these ecosystems remain understudied (Downing 2010; Biggs et al. 2017), particularly with regards to the role of macrophyte-hydrodynamic interactions in mediating ecosystem response to stressors.

The characteristic morphometry of small waterbodies makes these ecosystems more susceptible to stressors. For example, limited water volume and shallow mean depth reduce both dilution potential and thermal inertia making small waterbodies sensitive to nutrient loading and intense heatwaves (Biggs et al. 2017; Woolway et al. 2021a; Polazzo et al. 2022). As a result, eutrophication and aquatic heatwaves may act as compounding stressors for small lakes and ponds. Aquatic heatwaves are periods of sustained high surface water temperatures relative to
local and seasonal baseline conditions (Hobday et al. 2016; Tassone et al. 2021; Woolway et al. 2021a). The frequency, duration, and intensity of aquatic heatwaves have increased over the past century as a result of anthropogenic climate change, a trend which is anticipated to continue, even under low green-house-gas-emissions scenarios (Oliver et al. 2018; Woolway et al. 2021a, Woolway et al. 2022). Aquatic heatwaves may lower dissolved oxygen (DO) concentrations directly through reduced gas solubility in warmer waters and indirectly through increased ecosystem respiration (Tassone et al. 2021). Low DO concentrations and thermal stress have been linked to coral bleaching, declines in kelp forests, and mass seagrass mortality in marine systems (Wernberg et al. 2016; Hughes et al. 2017; Strydom et al. 2020). Although heatwaves are well-studied in coastal and marine systems, research on the effects of heatwaves in lakes and ponds is relatively nascent (Woolway et al. 2021a; Woolway et al. 2022). As such, it remains unclear how aquatic heatwaves affect the structure and function of lentic ecosystems, especially small, vegetated waterbodies.

Though aquatic heatwaves are projected to be more severe in small, shallow waterbodies (Woolway et al. 2021a), if present, macrophytes may buffer small lakes and ponds from extreme temperatures by restricting vertical heat transfer. Canopy-forming macrophyte beds attenuate incoming solar radiation and dissipate wind-driven turbulence, thus limiting the depth of heat transport and creating a shallow mixed surface layer separated from cooler bottom waters (Herb and Stefan 2004; Andersen et al. 2017a; Sand-Jensen et al. 2019). In short, macrophytes induce thermal stratification in small waterbodies, which may isolate bottom waters from rising surface temperatures during an aquatic heatwave. Stratification is also expected to restrict dissolved gas transport and may produce a vertically heterogenous chemical environment within macrophyte beds (Andersen et al. 2017b; Vilas et al. 2017). As a result, macrophyte structure could also
influence how DO responds to aquatic heatwaves. Rising surface water temperatures during a
heatwave are expected to lower DO concentrations; however, in maintaining cooler bottom water
temperatures, macrophyte-induced stratification may dampen the effects of a heatwave on gas
solubility and DO depletion. Altogether, macrophytes play a key role in the thermal structure and
DO environment of small waterbodies, potentially mediating the effect of temporary, external
stressors on these ecosystems’ structure and function. However, an explicit evaluation of how
macrophyte-hydrodynamic interactions may alter ecosystem response to stressors is lacking.
This is especially true for lakes and ponds as research on macrophyte-flow interactions has
largely focused on coastal and lotic systems (e.g., Fonseca et al. 2019; Tseng and Tinoco 2022).

While macrophytes influence ecosystem structure and function in small waterbodies,
environmental conditions also affect macrophytes. The abundance and growth of macrophytes in
small waterbodies is driven by temperature and the availability of light and nutrients (Carpenter
and Lodge 1986; Phillips et al. 2016), making them sensitive to environmental stressors such as
nutrient loading and heatwaves (Wu et al. 2021). Warmer water temperatures can enhance
macrophyte growth (Olesen and Madsen 2001, Bertani et al. 2016; Hansson et al. 2020);
however, high temperatures may also induce heat stress, impeding reproduction (Li et al. 2017)
or prompting senescence (Hao et al. 2018). Similarly, nutrient loading may have either a positive
or negative effect on macrophyte growth. Although macrophytes can benefit from enhanced
nutrient availability through foliar uptake (DeMarte and Hartman 1974; Twilley et al. 1977),
nutrient loading can also increase algal biomass and subsequently reduce light availability
through shading (Scheffer et al. 1993; Short et al. 1995). The effect of shading from
phytoplankton-associated turbidity is expected to vary across macrophyte growth forms, as
submersed species are more vulnerable to light limitation than emergent or floating-leaf species
While the individual responses of macrophytes to nutrient enrichment and heat stress have been established, it remains unclear how macrophytes respond to simultaneous, compounding stressors and what the consequences are for the thermal and chemical structure of small lentic ecosystems.

We experimentally evaluated the interacting effects of episodic external nutrient loading and an extreme heat event on macrophyte biomass and the subsequent changes in the physicochemical environment in two shallow, vegetated ponds. Specifically, we monitored spatiotemporal variation in water column thermal structure, DO profiles, and macrophyte biomass and canopy height in each pond and over the course of a growing season. We experimentally pulsed one of the ponds with nutrients to simulate a typical storm-driven external loading event, while the other pond served as a reference. Both ponds experienced a mid-summer heat event following the first experimental nutrient pulse. In the absence of severe environmental stressors, the phenology of the macrophyte communities in these temperate ponds follows a pattern of spring emergence from over-wintering rhizomes, growth throughout the summer, and then senescence of the leaves and stems in early autumn. However, we hypothesized that the combined stress of the nutrient addition and heat event in the experimentally eutrophied pond would induce early macrophyte senescence due to increased shading from phytoplankton and heat stress, thus reducing macrophyte biomass and subsequently altering the temperature and DO gradients in the water column. To further test the mechanistic relationship between macrophytes and pond hydrodynamics, we applied a hydrodynamic model for one-dimensional heat transport in vegetated ponds and simulated pond response to a heat event across a range of macrophyte biomass and canopy height.
Leveraging our ecosystem experiment and hydrodynamic model, our first research objective was to quantify macrophyte response to the compounding stressors of nutrient enrichment and an extreme heat event as well as the subsequent response of pond thermal structure and DO concentrations. We then explained the observed responses by focusing on the reciprocal relationship between macrophytes and pond hydrodynamics. Specifically, we asked (Q1) How do macrophyte biomass and canopy height influence pond thermal structure, and does macrophyte presence control vertical heat transfer during a heat event? (Q2) How does spatiotemporal variation in DO relate to macrophyte biomass and canopy height, and does macrophyte presence alter the DO response to a heat event? We anticipated that greater macrophyte biomass and canopy height would be associated with stronger thermal stratification and greater differences in DO between surface and bottom waters. We also hypothesized that macrophyte presence would maintain cool water habitat and stable DO concentrations during a heat event. Through the combination of our experiment, observations, and numerical modeling, we found that macrophyte structure can be a source of spatial and seasonal variation in the thermal and chemical environments of shallow waterbodies.

METHODS

Study Site and Field Measurements

We studied how macrophyte structure influences spatiotemporal variation in both the thermal and DO environments of small waterbodies using two ponds at the Iowa State University Horticulture Research Station (42.110005, -93.580454) during the summer of 2020. The ponds are rectangular, relatively small (surface area 400 m² at the water line; Figure 1), and shallow (maximum depth 2 m and mean depth 0.8 m), with simple, bowl-shaped bathymetries. These
waterbodies fit morphometric and functional definitions of ponds (Richardson et al. 2022). Water balance is driven solely from precipitation and evaporation as there are no surface inflows or outflows and the ponds are lined with bentonite to prevent groundwater interactions. As there is effectively no watershed for these ponds, we effectively controlled all external inputs of nutrients. The ponds were initially filled with water from the research station’s irrigation reservoir to seed natural phytoplankton and zooplankton communities. Early in the spring the ponds were stocked with yellow perch (*Perca flavescens*) and bluegill (*Lepomis macrochirus*) at roughly 20 kg ha\(^{-1}\) for both species, which is within the range of densities for temperate waterbodies (Carlander 1977; Schneider 1999). The macrophyte community in both ponds was composed of longleaf pond weed (*Potamogeton nodosus*; hereafter “floating-leaf”) and leafy pondweed (*Potamogeton foliosus*; hereafter “submerged”).

External nutrient loading typical of large storm events was simulated by adding nitrogen and phosphorus to one of the ponds (hereafter “nutrient addition pond”) twice over the course of the summer. Nitrogen was added as ammonium nitrate (NH\(_4\)NO\(_3\)), and phosphorus was added as sodium phosphate monobasic dihydrate ((NaH\(_2\)PO\(_4\)•(H\(_2\)O)\(_2\)) in a ratio of 24N:1P. The first nutrient addition (day of year, DOY, 176) raised the mass of phosphorus in the pond by 3 percent, and the second addition (DOY 211) raised the mass by 5 percent. These increases are consistent with the expected nutrient loading from a large storm event in an agricultural landscape (Vanni et al. 2001; Lürling et al. 2018). Nutrients were not added to the other pond (hereafter “reference pond”). To assess and compare the effects of the nutrient additions on algal biomass, we measured chlorophyll-\(a\) concentrations daily at the deep site of each pond (Figure 1) using the Total Algae sensor as a part of the YSI ProDSS multiparameter sonde (Yellow Springs Instruments, Yellow Springs, Ohio USA). The sensor logged continuously and was slowly
lowered through the water column. Surface concentrations of chlorophyll-\textit{a} were averaged over 0.3 m depth in the water column. To minimize drift, the sensor was calibrated regularly against laboratory standards.

To monitor thermal structure and dynamics across the ponds, we deployed vertical strings of high frequency temperature sensors (HOBO 8K Pendant Temperature Data Logger) at three sites, aligned from the deep (2 m) to shallow (1.5 m) ends of each pond (Figure 1). Temperature loggers were distributed throughout the water column every 0.25 m until 1.5 m deep and then every 0.5 to the bottom. Water temperature was logged every 30 minutes from May to August (DOY 143-233). We also took high frequency measurements of surface water DO concentration and saturation at the deep site of both ponds (miniDOT Clear Logger; logging every 30 minutes).

In order to quantify the three-dimensional DO environment, manual profiles of DO concentration, DO saturation, and water temperature were taken weekly (13 sampling events total) on a grid of 18 sites across each study pond using a kayak (Figure 1). Measurements were taken in the late morning, between 10:00AM and 12:00PM. A continuous profile of DO was logged at each site as the YSI ProDSS multiparameter sonde was slowly lowered through the water column.

We quantified variation in macrophyte structure over space and time by monitoring community composition, canopy height, and biomass from May to August (DOY 143-233) across the study ponds. Species presence-absence and canopy height were measured weekly at the three sites established from the deep to shallow ends of the ponds (Figure 1). Canopy height was measured as the distance from the sediment-water interface to the top of the canopy. Water depth was also measured at these points so that canopy height could be expressed as a proportion of the water column. Macrophyte dry biomass was sampled every other week (6 sampling events
Profiles were always taken before biomass was sampled. To collect a biomass sample, a two-side rake was lowered to the bottom and used to remove submersed and floating-leaf macrophytes from an approximately 0.4 m² area (Mikulyuk et al., 2011). All the above-sediment tissue was collected from the rake to determine dry biomass. Samples were dried at 60°C to a constant mass before weighing.

Hydrodynamic Modeling

In order to explore the mechanisms by which changes in macrophyte biomass and canopy height influence pond thermal structure, we applied a one-dimensional hydrodynamic model for vegetated waterbodies. Our model builds upon the one-dimensional, integral energy model by Herb and Stefan (2004) for heat transport in lakes with submersed macrophytes. Macrophytes are incorporated into the model through two key parameters: a light extinction coefficient due to macrophyte biomass shading and a term for turbulent kinetic energy dissipation by macrophytes based on their surface area and drag. Our contributions to the original model include adding convective overturn to address density instabilities over the diurnal cycles, a dynamic macrophyte growth and senescence boundary condition over time, dynamic light attenuation coefficient for water based on daily Secchi depth field data, and coding the model for use through open-source software (R; see Appendix S1 for more details on model algorithms and additional citations).

For boundary conditions, the model requires an initial water temperature profile, timeseries of meteorological drivers (air temperature, relative humidity, air pressure, wind speed, and short-wave radiation), and waterbody hypsography (depth-area relationship). We determined
the hypsography of the study ponds through manual calculations based off depth measurements from the profiles taken at 18 sites across each pond. We obtained the necessary meteorological data at an hourly timestep from a weather station located approximately 550 meters from the study ponds and maintained by the Iowa State University Soil Moisture Network (Iowa Environmental Mesonet, ISU Soil Moisture Network 2021). The initial temperature profile was supplied from a single reading from the temperature chain located at the deep site of the reference pond (Figure 1). Macrophyte data were incorporated into the model through weekly measurements of canopy height at the deep site of the reference pond as well as biomass density measurements taken every two weeks. Biomass density standardizes macrophyte biomass to the volume of water sampled (g m\(^{-3}\)). We used the average biomass density from the two sampling sites closest to the deep site temperature sensors, in the southern region of the pond.

The model was run on a 1-hour timestep from late May-August (DOY 143-241; 99 days total). The observed, high frequency water temperature profiles from the deep site of the reference pond were used to calibrate 9 model parameters (Table S1) and assess model fit (quantified as root mean square error, RMSE). Once the model was sufficiently calibrated to the full duration of the observed field data, we manipulated the input macrophyte data to simulate the effect of different macrophyte biomass and canopy dynamics on thermal structure (Table S2). Specifically, we tested a scenario with no macrophytes present in the pond compared to macrophyte biomass and canopy heights that were measured in the reference pond. All modeling analyses were completed in R version 4.1.2 (R Core Team 2021) using the gotmtools (https://github.com/aemon-j/gotmtools), rLakeAnalyzer (Winslow et al. 2019), lubridate (Garrett and Wickham 2011), and tidyverse (Wickham et al. 2019) packages.
Our delineation of extreme heat events in the experimental ponds was informed by the definition developed for marine heatwaves (Hobday et al. 2016) and applied more recently to estuaries (Tassone et al. 2021) and lakes (Woolway et al. 2021a). Following this definition, an aquatic heatwave occurs when daily mean surface water temperatures exceed the seasonal 90th percentile threshold for at least 5 days, without dropping below that threshold for 2 or more days. Since we did not have long-term data on summer water temperatures in the experimental ponds, we could not use this formal definition. Therefore, we elected to use temperature monitoring data for the study period only, but a more stringent definition of a heat event threshold (i.e., 95th percentile) for the same extended period (5 days). To determine the 95th percentile surface water temperature for each pond, we used temperature loggers placed at 0 and 0.25 m at the middle at deep sites. For each site, we averaged the readings from these surface loggers, calculated a daily mean, and then averaged values from the middle and deep sites. These steps produced a daily mean surface water temperature for each pond, which we used to calculate the 95th percentile threshold. We then identified any days in which the daily mean surface water temperature exceeded this threshold. A period with at least five days above this threshold was classified as a sustained aquatic heat event (hereafter, “heat event”).

To visualize pond thermal structure from our high frequency water temperature data, we used a linear interpolation to estimate temperature for depths at which we either did not place sensors (1.75m deep for both ponds) or for depths at which sensors ceased to function during the summer (1m at the middle and deep sites of the nutrient addition pond, 0.25-0.75m at the shallow site of the nutrient addition pond, and 0.25m at the middle site of the reference pond). The interpolated values were used solely for visualization. Only empirical measurements of
water temperature were used in the model and to calculate indices of pond thermal structure (i.e.,
thermocline depth and Lake Number). Lake Number is a ratio that compares the internal stability
of the water column to external wind stress across the waterbody surface, so it can be used to
determine the strength of stratification and likely response to observed wind stress (Robertson et
al. 1990). Thermocline depth and Lake Number were calculated using the rLakeAnalyzer
package. (Winslow et al. 2019). We defined surface water temperature as the average from the 0
and 0.25m sensors. We used the deepest sensors (2m at the middle and deep sites, 1.5m at the
shallow sites) for measurements of bottom water temperature.

In order to compare macrophyte biomass between the study ponds, we calculated the
mean macrophyte biomass across 18 sampling sites for each sampling event. However, we
weighted this average so that sampling sites around the perimeter of the pond (n=14) had the
same weight was sites in the interior or the pond (n=4; Figure 1) so that the mean value would
not be biased by water depth. Weighted, pond-averaged macrophyte biomass values were used to
plot seasonal changes and explore the relationship between biomass and water column thermal
stability. We also standardized macrophyte canopy height as a percent of the water column depth
for each sampling site and event to aid comparisons between shallow and deeper sites.

To analyze the manual DO profiles, we first determined that there were no instances of
mid-depth DO maximum for any sites or sampling events. The vertical distribution of DO
saturation was either uniform, highest in the surface waters, or highest in the bottom waters
depending on the site and time of year (Figure S1). Therefore, we focused on DO dynamics in
the surface and bottom layers of ponds by averaging values from 0-0.25 m and 0.25 m from the
sediment-water interface respectively. Surface and bottom water DO values were used to explore
temporal variation, calculate the difference between surface and bottom DO, and quantify
variation over space and time. We used coefficients of variation to quantify temporal and spatial variation in surface and bottom water DO saturation. Specifically, spatial variation was defined as the coefficient of variation for DO for each sampling day within each pond, so variation was due to differences among the 18 sampling sites (Figure 1), standardized by the pond-mean for that day. Temporal variation was calculated based on the coefficient of variation in DO for each sampling site, so variation was due to differences in DO over time, standardized by the summer mean DO saturation for that site.

A generalized additive model (GAM) was used to smooth the daily time series of chlorophyll concentrations and weekly time series of DO saturation to visually highlight differences in trends over time between the nutrient addition and reference pond. All statistical analyses were completed in R version 4.1.2 (R Core Team 2021) using the mgcv (Wood 2017), rLakeAnalyzer (Winslow et al. 2019), lubridate (Garrett and Wickham 2011), and tidyverse (Wickham et al. 2019) packages.

RESULTS

Environmental Stressors and Macrophyte Response

Chlorophyll-\(a\) concentrations were variable in both ponds throughout the experiment, but there was a clear increase in chlorophyll-\(a\) following the sequential additions of nutrients in the experimental pond (Figure 2A). Early in the season, chlorophyll-\(a\) concentrations were low in the reference pond, likely due to high Daphnia sp. biomass (Butts et al., in prep). Following this early clear-water phase and prior to the experimental nutrient additions, chlorophyll-\(a\) concentrations were similarly low in both ponds (DOY 160). Nutrient additions on DOY 176 and 211 resulted in chlorophyll-\(a\) concentrations 2-3 times higher in the nutrient amended pond.
compared to the reference pond. Heightened chlorophyll-\(a\) concentrations in the nutrient addition pond are indicative of higher algal biomass and thus phytoplankton-associated turbidity, likely resulting in reduced light availability in the nutrient addition pond.

Both ponds experienced a heat event from DOY 185-190 (Figure 2B). During this period, mean daily surface water temperatures exceeded the seasonal 95\(^{th}\) percentile in each pond (greater than 29.8 °C in the nutrient addition pond and 30.6 °C in the reference pond). Maximum daily surface water temperatures ranged from 34.5-37.1 °C in the nutrient addition pond and 33.7-38.6 °C in the reference pond during the heat event. Although both ponds had brief periods of high surface water temperatures at other points throughout the summer, DOY 185-190 was the only sustained period of high surface water temperatures (\(\geq\) 5 days). The heat event began 9 days after the first nutrient pulse, creating multiple stressors (i.e., reduced light availability and prolonged heat stress) for macrophytes in the nutrient addition pond.

Surface DO saturation was variable over the study period, at times differing between the two study ponds (Figure 2C). Early in the summer, both ponds were supersaturated with DO, and mean surface saturation was similar between the ponds before the initial nutrient addition. In the reference pond, DO remained fairly stable until the heat event (DOY 185-190), after which DO saturation declined and generally remained below saturation for the remainder of the study period. In contrast, mean surface DO saturation in the nutrient addition pond declined immediately following the first nutrient addition (DOY 176) and remained below saturation for the rest of the summer.

Spatiotemporal patterns in macrophyte biomass differed between the ponds and macrophyte growth forms (Figure 2D, 3). The floating-leaf species was largely limited to a ring around the shallower edges of the ponds where the floating leaves could easily reach the surface.
The submerged species was present across a range of depths but reached the highest biomass in the deeper, central region of each pond. In the reference pond, macrophytes followed expected phenology with increasing biomass through late summer and then senescence of both growth forms beginning in early autumn (Figure 2D, 3). The heat event did not affect macrophyte biomass or assembly in the reference pond. However, in the nutrient addition pond, submerged macrophytes growing in 1.75 to 2 m of water began to senesce following the initial nutrient addition and heat event such that no plants were present in the deepest areas of the nutrient addition pond 9 days (DOY 199) after the heat event and the middle site of the pond 23 days (DOY 213) after the heat event ended (Figure 3). Early senescence of submersed macrophytes in the nutrient addition pond resulted in rapid declines in both biomass (Figure 2D) and canopy height (Figure 4). Both submersed and floating-leaf plants persisted in shallow water around the edge of the pond through the end of the summer.

Spatiotemporal Variation in Pond Thermal Structure
Both ponds experienced intermittent thermal stratification during the study period and similar spatial patterns of stratification from shallow to deep ends of the pond (Figure 4). Early in the summer, both ponds were cool and isothermal. As surface waters began to warm, the middle and deep sites of both ponds began to stratify while the shallow sites remained fairly well-mixed. At the center of the ponds, a stable thermocline between 1-1.5 m depth was observed in the reference pond between DOY 155-161, and almost constantly between DOY 168-210 (Figure S2A), while the thermocline in the nutrient addition pond was more intermittent (DOY 157-159, 170-174, and 178-192; Figure S2B). When present, pond thermoclines cooled and deepened slightly (0.05-0.1 m) during the night, indicating nighttime convective cooling and
mixing in the surface layer. During periods of thermal stratification, differences between surface and bottom water temperatures ranged from 4.3 to 11.5 °C (mean 8.1°C) in the reference pond and 4.5 to 10.2 °C (mean 7.3 °C) in the nutrient addition pond.

Similarities in pond thermal structure occurred during times of similar macrophyte coverage, either early or late in the season (Figure 4). For example, both ponds experienced a strong mixing event in late summer (DOY 216-220), driven by cooler air temperatures and higher wind speeds (Figure 5) and facilitated by declining macrophyte structure (Figure 4). Similar meteorological conditions occurred earlier in the summer and resulted in some water cooling (e.g., DOY 164, 175); however, the ponds did not mix as fully during these events, likely due to the macrophyte structure present in both ponds in early summer (Figure 4). Similarities in pond thermal structure in relation to extrinsic factors (i.e., wind speed) are further demonstrated by similar lake number values for both ponds over the study period (Figure S3).

Although overall seasonal patterns in thermal structure were similar between the ponds, there were brief dissimilarities, related to differences in the timing of macrophyte senescence (Figure 4). There was a prolonged period of stable thermal stratification from DOY 180-210 in the reference pond, with only brief instability between DOY 198-199. A stable thermocline set-up in the nutrient addition pond around the same time (DOY 178); however, stratification began to break down approximately 18 days earlier (DOY 192) than in the reference pond (Figure S2). The timing of destratification in the nutrient addition pond coincides with declines in macrophyte biomass (Figure 3) and canopy height (Figure 4) in the center of the pond. Destratification in the reference pond also followed patterns of biomass senescence and loss of canopy height, although this did not occur until later in the summer in this pond. In both ponds, there was strong temporal coherence between the timing of destratification and macrophyte senescence, driven by the...
compounding stress of eutrophication and a heat event in the nutrient addition pond and typical
seasonal senescence in the reference pond. The declines in canopy cover and biomass were
associated with increased thermal mixing and warmer bottom water temperatures, especially in
the nutrient addition pond.

During the aquatic heat event (DOY 185-190), both ponds experienced a similar increase
in surface water temperatures (Figure 2B, Figure 4). However, there was a stark difference in the
response of bottom water temperatures at the deep and middle sites between the ponds (Figure
S4). During the heat event, bottom water temperature remained consistent at both the deep and
middle sites of the reference pond. The daily mean bottom water temperature increased by only
0.2 °C at both sites. In contrast, bottom water temperatures in the nutrient addition pond did
respond to the heat event, increasing by 1.3 °C and 1.4 °C at the deep and middle sites,
respectively. At the shallow site in both ponds bottom water temperatures increased 1-1.3 °C
during the heat event, suggesting an interaction with water depth. The different response of
bottom water temperature to the heat event related to differences in macrophyte biomass between
the two ponds. At the time of the heat event, macrophyte biomass (Figure 2D) and canopy height
(Figure 4) were greater in the reference pond because submersed macrophytes in the center of
the nutrient addition pond began to senesce following the first nutrient pulse (DOY 176; Figure
3). Overall, bottom waters in the nutrient addition pond warmed over the course of the heatwave
while cooler bottom water temperatures were maintained in the reference pond, despite
significant warming in the surface layers.

Spatiotemporal Variation in Dissolved Oxygen
In both ponds, DO varied across sites, vertically in the water column, and over time. Weekly DO profiles captured broad seasonal trends in surface DO saturation as similar temporal patterns were observed between weekly and high-frequency values (Figure 2C, S5A). Surface waters were supersaturated with DO early in the summer in both ponds (Figure S5A). In the reference pond, mean pond surface DO declined through DOY 170, remained fairly stable, and then declined again during the heat event (DOY 185-190). In the nutrient addition pond, surface DO saturation was similar to the reference pond before the nutrient addition. Surface DO then decreased after the nutrient addition and through the heat event. Over a one-week period during and after the heat event (DOY 186-192), DO saturation fell 22.4% and 50.4% in the nutrient addition and reference ponds, respectively. After the heat event, surface DO in both ponds was generally below saturation, with increased instances of DO saturation below 25%. Bottom water DO saturation mirrored the seasonal pattern in surface DO (Figure S5B). For both ponds the difference in DO saturation between surface and bottom waters was most pronounced early in the season (reference pond range -87.1 to 23.3%; nutrient addition pond range -56.8 to 58.8%). Surface and bottom water DO saturation became more similar throughout the summer, especially following the heat event (reference pond range -2.1 to 17.0%; nutrient addition pond range -0.3 to 12.2%; Figure S5C).

For both surface and bottom water DO saturation, temporal variation on a seasonal scale was greater than spatial variation across the ponds (Table 1). The coefficient of variation at a given site in the pond over time was 3.6-5.2 times greater than the variation among sites on a given sampling day. The magnitude of temporal versus spatial variation was similar between ponds. Seasonal patterns in DO saturation followed some trends with declining macrophyte
biomass following the nutrient addition associated with lower DO; however, the heat event had the most pronounced effect on seasonal DO patterns (Figure 6).

Mechanisms of Macrophyte Control of Pond Hydrodynamics

We used a one-dimensional hydrodynamic model to illuminate the mechanistic relationship between macrophytes and pond thermal structure and test how macrophyte presence mediates the degree to which bottom water temperatures warm in response to a heat event. We based our model on the deep site of the reference pond. The model projections were consistent with the observed temperature profiles (mean RMSE 1.67 °C across 8 discrete depths; Figure S6). Error was greatest in the surface waters (0 m; RMSE 2.47 °C), where the model underpredicted water temperature and did not capture the full range of observed diel oscillations, especially early in the summer. Error was lower in the bottom waters of the pond (1.25-2 m). The model underpredicted water temperature early in the summer but then showed good agreement with the observed temperatures (RMSE range 1.05-1.52 °C). Overall, the model captured the magnitude and seasonal trends of temperature throughout the water column.

We applied the hydrodynamic model to quantify differences in pond thermal structure under contrasting scenarios of macrophyte presence (Figure 7). Specifically, we tested a scenario in which there were no macrophytes present (i.e., canopy height and biomass density were set to zero over the study period) and compared the results to the model output for the reference pond when the observed macrophyte data were used (Table S2). Under the scenario where macrophytes were present, the model predicted strong stratification during the period of peak macrophyte biomass and canopy height in the middle of the summer and cool bottom water temperatures throughout the study period (Figure 7A). In contrast, under the scenario in which
macrophytes were entirely absent from the pond, the model predicted complete water column mixing and much warmer temperatures throughout the water column, especially following the aquatic heat event (Figure 7B). When macrophytes were present, the increase in bottom water temperatures over the course of the aquatic heat event was negligible (0.01 °C), and bottom temperatures then remained below 25 °C for the remainder of the summer (maximum temperature 23.3 °C; Figure 7A, C). However, the no-macrophyte scenario resulted in a 1.92 °C increase in bottom water temperatures during the heat event and much higher maximum water temperatures later in the summer (33.4 °C; Figure 7B, C). The model simulations demonstrate that macrophyte structure increases thermal stratification and promotes cooler bottom water temperatures, even during an extreme heat event.

**DISCUSSION**

We leveraged an ecosystem experiment and complimentary hydrodynamic model to test macrophyte response to compounding stressors (i.e., stochastic external nutrient loading and extreme heat events) and evaluate the consequences of stress-induced macrophyte senescence for the physicochemical environment in two shallow, vegetated ponds. The type and severity of environmental stressors differed between the study ponds, producing distinct temporal patterns in macrophyte assembly and coverage. In the reference pond, both submersed and floating-leaf macrophytes followed the expected phenology of spring emergence, summer growth, and then senescence beginning in late summer. This natural phenology may be attributed to the lack of severe physiological stressors in the reference pond. Although this pond did experience a heat event, dense macrophyte beds limited the depth of water column warming and maintained stable bottom water temperatures. In contrast, submersed macrophytes in the nutrient addition pond
began to senesce in mid-summer after the first experimental nutrient pulse and continuing after the heat event. This early senescence was dominated by submersed macrophytes in the deeper, central region of pond, suggesting that light limitation from phytoplankton shading was a contributing stressor (Scheffer et al. 1993; Short et al. 1995; Phillips et al. 2016). Light limitation may have been exacerbated by heat stress, which was likely more acute in the nutrient addition pond as declining macrophyte biomass following the nutrient pulse allowed temperatures to rise throughout the water column rather than just the surface layers. Early senescence of submersed macrophytes in the nutrient addition pond as a result of compounding stressors altered the thermal environment and DO saturation in relation to the reference pond.

Thermal Structure

On a seasonal scale, we observed strong temporal coherence between macrophyte growth and senescence and pond thermal structure. Both ponds began to experience intermittent thermal stratification in early summer, once macrophytes had grown to fill the majority of the water column. This threshold is consistent with the expectation that canopy-forming macrophyte beds may induce diurnal stratification once they occupy at least 50 percent of the water column (Vilas et al. 2017). By mid-summer we observed strong thermal stratification, characterized by large differences (around 10°C) between surface and bottom water temperatures, comparable to stratification in other small, vegetated ponds (Andersen et al. 2017a; Vilas et al. 2017). However, in other studies, macrophyte-induced stratification followed diel cycles, with daytime stratification and nighttime overturn due to convective mixing (Martinsen et al. 2019; Sand-Jensen et al. 2019), which can move through macrophyte structure more readily than external turbulent mixing (Herb and Stefan 2005; Andersen et al. 2017b). Although we observed
nighttime convective cooling and mixing in the surface of the ponds during periods of 
macrophyte-induced stratification, convective cooling did not mix the entire water column. 
Stable thermal stratification began to break down in both study ponds during macrophyte 
senescence. Declining macrophyte canopy height and biomass removed structural barriers that 
had previously attenuated incoming solar radiation and dissipated wind-driven turbulent mixing 
(Herb and Stefan 2004), allowing the warm, mixed surface layer to deepen and eventually mix 
the entire water column. However, the timing of both destratification and macrophyte senescence 
differed between the study ponds, driven by compounding stressors in the nutrient addition pond 
and typical seasonal senescence in the reference pond. In the nutrient addition pond consistent 
water column mixing began when macrophyte biomass and canopy height in the center of the 
pond began to decline in response to phytoplankton-shading following the experimental nutrient 
pulse and the heat event.

Macrophyte presence mediated how pond thermal structure responded to an extreme heat 
event by restricting vertical heat transfer and maintaining cooler bottom water temperatures. 
Both study ponds saw high surface water temperatures during the heat event. However, as 
anticipated, the depth of water column warming and overall change in bottom water temperature 
differed between the ponds as a result of differences in macrophyte coverage. At the time of the 
heat event, macrophyte canopy height and biomass were rapidly declining in center of the 
nutrient addition pond due to phytoplankton-shading. In the reference pond, macrophyte biomass 
was still increasing and the canopy reached to fill over 75 percent of the water column. During 
the heat event, a layer of cooler water between 0.25 and 0.5 m thick remained in the reference 
pond, with only subtle increases in daily mean temperature (+0.2 °C). In contrast, the nutrient 
addition pond saw increasing water temperatures throughout the water column, including a 1.3°C
increase in daily mean temperatures in the deepest waters of the pond over the 5-day heat event.

Given the observed differences between the study ponds, it is very likely that macrophyte structure played a pivotal role in mediating the depth and degree of water column warming during the aquatic heat event. Nevertheless, thermal structure in small waterbodies arises from complex interactions between waterbody features and external forces (Herb and Stefan 2004; Branco and Torgersen 2009). In order to explicitly test the mechanisms underpinning the differences we saw between the study ponds and evaluate the role of macrophytes, we used a hydrodynamic model for heat transport in vegetated waterbodies and simulated water column thermal structure during a heat event under contrasting scenarios of macrophyte density.

The model results support our field observations and demonstrate that macrophytes structure the thermal environment in shallow ponds through vertical attenuation of both light and turbulent kinetic energy. Simulations of seasonal patterns in pond thermal structure under variable macrophyte density revealed that macrophyte presence reduces the depth and degree of water column warming both during and after an aquatic heat event and maintains cooler bottom water temperatures throughout the course of the summer. Our experimental observations and model simulations provide evidence that macrophytes may buffer small waterbodies from brief aquatic heatwaves, at least with the vertical extent of warming in the water column. As aquatic heatwaves become more widespread and frequent, heatwaves in small waterbodies are expected to be shorter but more intense compared to larger waters (i.e., due to lower thermal inertia; Woolway et al. 2021a; Polazzo et al. 2021; Woolway et al. 2022). Our findings suggest that macrophytes can mediate the intensity of brief aquatic heatwaves in small lakes and ponds. As such, managing for robust macrophyte communities is a potential tool for mitigating heatwave
effects in small waterbodies and promoting thermal heterogeneity to support other aquatic organisms (Carpenter and Lodge 1986; Till et al. 2019).

Our hydrodynamic model enhances a conceptual and analytical framework for incorporating biological structure into one-dimensional heat transport models (Herb and Stefan 2004). Overall, there was good agreement between the model predictions and the observed temperature profiles. The largest discrepancies between the model output and field data occurred in early summer when the model underpredicted temperature. The early summer period coincides with rapid growth in macrophyte biomass and canopy height. It is possible that the temporal resolution of our field data during this time was insufficient to accurately capture biological dynamics in the pond for the model input. Canopy height was measured weekly while biomass was collected every two weeks. More frequent observations could have fit the macrophyte input data closer to conditions captured by the high frequency temperature profiles. Additionally, other one-dimensional heat transport models (i.e., Simstrat, GOTM, GLM) have been shown to have greater error during extreme meteorological events, including atmospheric heatwaves (Mesman et al. 2020). This tendency could explain some of the disparities between model output and field data during a brief period of high air temperatures around DOY 155, reflected in rapid increases in water temperature in the first 1.25 m of the profile. Our model would benefit from additional testing across a variety of vegetated waterbodies to inform best practices for applying this approach in other waters. However, our findings indicate that macrophytes should be incorporated into hydrodynamic models for vegetated systems, and our modeling approach provides an example of how to do so.

Dissolved Oxygen
Within both study ponds, DO saturation varied on a seasonal scale and responded to the experimental nutrient pulse as well as the heat event. We had anticipated greater spatial variation in DO saturation within each pond as a result of macrophyte-induced thermal stratification. This expectation was based on evidence of steep vertical gradients of DO and dissolved inorganic carbon in other shallow, vegetated waterbodies (Andersen et al. 2017a; Vilas et al. 2017). However, most of the DO profiles were uniform with depth, suggesting that the balance of processes releasing and consuming oxygen (e.g., gross primary production versus respiration) were similar throughout the ponds or that DO was able to diffuse readily throughout the water column. Temporal patterns in surface and bottom water DO saturation were connected to the compounding environmental stressors, beginning with the initial experimental nutrient addition. Following the first nutrient pulse, DO remained stable in the reference pond but declined below 100 percent saturation in the experimental pond. We might have expected to see increased DO after the nutrient addition as a result of enhanced phytoplankton production, but the observed decline in DO suggests that ecosystem respiration was stimulated by the added nutrients, outweighing any increases in gross primary production. Stress-induced macrophyte senescence likely contributed to this pattern through reduced macrophyte photosynthesis and dramatic increases in macrophyte necromass, the decomposition of which would consume oxygen. Although we observed differences in DO saturation between the ponds after the nutrient addition, the most pronounced temporal shift in DO occurring following the heat event. During the heat event, DO saturation fell sharply in both ponds and remained depressed through the remainder of the study period. We had expected macrophyte structure to maintain stable DO saturation in the bottom waters of the reference pond; however, both ponds responded similarly, regardless of the differences in macrophyte coverage and thermal structure. Our
observations support findings from freshwater and marine systems that aquatic heatwaves are associated with declines in DO due to reduced gas solubility and increased respiration rates (Ali et al. 2016; Brauko et al. 2020; Tassone et al. 2021). Reduced DO availability has consequences for nutrient and carbon cycling as well as greenhouse gas production. For example, anoxia within the sediment profile can mobilize phosphorus from redox-sensitive minerals (i.e., anaerobic internal phosphorus loading; Orihel et al. 2017). Anoxic conditions in the sediments also promote denitrification and methanogenesis, two microbial processes that can produce potent greenhouse gases (i.e., nitrous oxide and methane respectively; Fonseca et al. 2017; Ming et al. 2022). Both denitrification and methanogenesis require organic carbon substrate, which was augmented by macrophyte necromass in the nutrient addition pond (Boon et al. 1995; Bastviken et al. 2005; Deng et al. 2020). Although both ponds likely experienced shifts in other elemental cycles as a result of reduced DO saturation during the aquatic heatwave, the consequences for greenhouse gas production were likely more pronounced in the nutrient addition pond due to early macrophyte senescence increasing organic matter inputs to the sediments. This difference between the study ponds highlights the complex interactions that may arise from compounding stressors in lentic ecosystems.

**Conclusions**

Aquatic heatwaves are becoming more frequent and are likely to co-occur with chlorophyll-a maxima in lakes and ponds (i.e., algal blooms; Woolway et al. 2021b). As such, there is a growing need to understand and forecast how lentic ecosystems will respond to compound, extreme events. Our findings illuminate the role that macrophyte-hydrodynamic interactions play in mediating ecosystem response to multiple stressors. Overall, dense
macrophyte structure can buffer small waterbodies from brief aquatic heat events by restricting vertical heat transport. However, declines in DO saturation are expected during heat events, regardless of macrophyte coverage. Our findings also reinforce that small lakes and ponds are vulnerable to nutrient loading and temperature extremes. Given the prevalence and importance of small waterbodies for biodiversity and biogeochemical processing, it is essential that we continue to build our mechanistic understanding of the effects of compound, extreme events in these ecosystems and the role that macrophytes can play in ameliorating stressors.

Acknowledgements

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Data Availability Statement

The data supporting the conclusions and the analysis code are available in the Github repository https://github.com/AlbrightE/pond_physics_2022. Following manuscript acceptance, the Github
repository will be archived on Zenodo, and the data will be published on the Environmental Data Initiative’s online repository under a Creative Commons Attribution license (CC-BY).
REFERENCES


Table 1. Temporal versus spatial variation in DO Saturation

<table>
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<th>Spatial Variation in DO Saturation</th>
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<td></td>
<td></td>
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<td>CV (%) Range</td>
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<td>Reference</td>
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<td>20.2 – 34.4</td>
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<td>Nutrient Addition</td>
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<td>20.6 – 28.8</td>
</tr>
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<td>Reference</td>
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<td>24.1 – 45.6</td>
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<td></td>
<td>Nutrient Addition</td>
<td>26.8</td>
<td>22.1 – 40.3</td>
</tr>
</tbody>
</table>

Figure 1. Spatial and temporal resolution of measured variables and sample site locations.
Figure 2. (A) Timeseries of surface chlorophyll-a concentrations. Values from each pond were GAM-fit to highlight temporal trends. The asterisks next to the effective degrees of freedom.
(edf) correspond to the estimated p-value, with *** denoting $p < 0.001$. (B) Timeseries of mean daily surface (0-0.25 m) water temperature. Surface sensors at the deep and middle sites were used for these pond averages. The 95\textsuperscript{th} percentile surface water temperature thresholds are noted in horizontal lines for the nutrient addition (29.8°C) and reference (30.6°C) ponds. (C) High frequency surface dissolved oxygen (DO) saturation at the deep site of each pond over the study period. The daily mean is plotted in a darker line. The horizontal grey line marks 100 percent saturation. (D) Time series of mean macrophyte biomass in each pond. Error bars mark the standard error of the mean. Across all panels, dashed lines mark the timing of nutrient additions (DOY 176, 211) and the grey box highlights the aquatic heat event (DOY 185-190).

\textbf{Figure 3.} Spatial and temporal variation in macrophyte dry biomass and community composition. Biomass was sampled during the aquatic heat event (DOY 185-190), as noted by the thicker, red pond outline on DOY 186. Dashed lines mark nutrient additions on DOY 176 and 211.
Figure 4. Spatial and temporal variation in macrophyte canopy height and temperature profiles. Canopy height is plotted as a percent of the water column height. Black, horizontal lines mark an aquatic heat event from DOY 185-190. High frequency water temperature loggers were placed every 0.25 m of the water column up to 1.5 m and then every 0.5 m to the bottom. Temperature values at 1.75 m were interpolated for the sake of visualization. Several surface sensors (0-0.5 m) from the shallow site of the nutrient addition pond lost power following DOY 215 (grey box). An initial canopy height measurement is missing from the nutrient addition pond because the water was not sufficiently clear to see and measure the top of the canopy. The canopy height was less than 1 m or 50-75% of the water column at this time.
Figure 5. Air temperature (A) and windspeed (B) over the study period. Daily mean values are plotted in thicker lines over the hourly time series.
Figure 6. Spatiotemporal variation in bottom water dissolved oxygen (DO) saturation. Sampling sites are ordered approximately from the deepest to most shallow locations. The pond-averaged biomass values are plotted above. Error bars represent the standard error of the mean.
Figure 7. Model simulation results contrasting a no macrophyte scenario with the observed macrophyte coverage from the reference pond. Predicted temperature profiles with (A) observed macrophyte biomass and canopy height versus (B) no macrophytes present in the reference pond. Black, horizontal lines mark an aquatic heat event (DOY 185-190). (C) Timeseries of predicted daily mean bottom water (2m) temperatures with no macrophytes versus observed macrophyte biomass and canopy height.
Appendix S1

Macrophyte-hydrodynamic interactions mediate stratification and dissolved oxygen dynamics in ponds

Ellen A. Albright¹,², Robert Ladwig², and Grace M. Wilkinson¹,²

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Introduction

The appendix contains additional methods text detailing the algorithms and approach for the hydrodynamic model as well as an overview of calibrated model parameters (Table S1) and simulation input data for testing heat event response under variable macrophyte scenarios (Table S2). Model fit is illustrated in Figure S6.

Figure S1 provides an example of individual dissolved oxygen (DO) saturation profiles to illustrate there was no evidence of mid-depth DO maxima. We provide time series of estimated thermocline depth (Figure S2) and Lake Number (Figure S3) for each pond as well as time series of bottom water temperatures at each sampling site on each pond (Figure S4). We further provide supplementary visualizations for our DO data, specifically time series of surface and bottom water DO saturation and the difference between surface and bottom water DO (Figure S5).
Model Equations and Approach

Model description

A one-dimensional, integral energy model was developed to simulate the temperature, heat flux and stratification dynamics in small, vegetated ponds. Model algorithms are based on the MINLAKE model (Ford and Stefan 1980; Riley and Stefan 1988; Herb and Stefan 2004).

Heat transport is implemented through the one-dimensional temperature diffusion equation:

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left( K_z \frac{\partial T}{\partial t} \right) + \frac{H(z)}{\rho_w c_p} + \frac{H_{geo}(z)}{\rho_w c_p}$$

where $K_z$ is the vertical turbulent diffusion coefficient, $H$ is internal heat generation due to incoming solar radiation, $\rho_w$ is water density, $c_p$ is specific heat content of water, and $H_{geo}$ is internal geothermal heat generation.

Internal heat generation is implemented as:

$$H(z) = (1 - \alpha) I_s \exp(-(k_d + k_m)z)$$

where $\alpha$ is the water albedo, $I_s$ is total incident short-wave radiation, and $k_d$ is a light attenuation coefficient and $k_m$ is the light attenuation coefficient due to macrophyte biomass.

For the upper, surface boundary condition we assume a Neumann type for the temperature diffusion equation:

$$H_{net} = \rho_w c_p \left( K_z \frac{\partial T}{\partial t} \right)$$

where $H_{net}$ is the net heat flux exchange between atmosphere and water column:

$$H_{net} = H_{lw} + H_{lwr} + H_v + H_c$$

where $H_{lw}$ is the incoming long-wave radiation, $H_{lwr}$ is emitted radiation from the water column, $H_v$ is the latent heat flux, and $H_c$ is the sensible heat flux. Implementations to estimate the respective heat fluxes were taken from Livingstone and Imboden (1989) and Goudsmit et al.
Latent and sensible heat fluxes were calculated using the atmospheric stability algorithms from Verburg and Antenucci (2010). The lower, sediment boundary condition was prescribed as:

\[ K_z \frac{dT}{dt} = 0 \]  

The model algorithm is modularized into three components: (a) heat generation from boundary conditions and vertical diffusion, (b) turbulent mixing up to the mixed layer depth, and (c) convective overturn to account for density instabilities.

(a) Heat generation from boundary conditions and vertical diffusion

In the first step the heat fluxes \( H \) and \( H_{geo} \) are applied over the vertical water column. The atmospheric heat flux, \( H_{net} \), is applied to the surface layer. Simultaneously, vertical turbulent diffusion between adjacent grid cells is calculated. Here, we applied the implicit Crank-Nicholson scheme. The vertical turbulent diffusion coefficient \( K_z \) is calculated based on the empirical equations by Hondzo and Stefan (1993) for lakes in Minnesota as a function of the buoyancy frequency:

\[ K_z = a_k (N^2)^{-0.43} \]

where \( a_k \) is an empirical factor accounting for the surface area of the lake \( A_s \):

\[ a_k = 0.00706(A_s)^{0.56} \]

and \( N^2 \) is the squared buoyancy frequency:

\[ N^2 = \frac{g}{\rho_w} \frac{\partial \rho_w}{\partial z} \]

Values of \( N^2 \) less than \( 7.0 \times 10^{-5} \text{ s}^{-2} \) were set to \( 7.0 \times 10^{-5} \text{ s}^{-2} \).

(b) Mixed layer depth

In the third step, we quantified the depth where the amount of external kinetic energy by wind shear stress equals the internal potential energy of the water column. Up to this mixed layer
depth, $z_{ml}$, adjacent layers are subsequently mixed to account for a wind shear stress acting over the vertical water column. Here, the kinetic energy $KE$ is described as:

(Eq. 9) \[ KE = \tau u^* \Delta t \]

where $\tau$ is the surface turbulent shear stress, and $u^*$ is the surface shear velocity, which was calculated from wind velocity as:

(Eq. 10) \[ u^* = \sqrt{\frac{C_{10} \rho_a}{\rho_w}} U_2 \]

where $C_{10}$ is the wind stress coefficient dependent on the measured wind speed $U_2$ at 2 m height above the water surface, and $\rho_a$ is the density of air, respectively (Herb and Stefan, 2005).

The dissipation of turbulent kinetic energy (DKE) by macrophytes is incorporated as:

(Eq. 11) \[ DKE_z = (\rho_w \hat{a} C_d)(u^*)^3 \Delta z \Delta t \]

where $\hat{a}$ is the ratio of plant surface area per unit volume water and $C_d$ is the plant form drag coefficient.

The potential energy of the water column for each layer over the depth is calculated as:

(Eq. 12) \[ PE_z = g Z_z (Z_{z+1} - Z_{cv}) \Delta \rho \]

where $g$ is gravitational acceleration, $Z_{cv}$ is the center of volume depth, and $\Delta \rho$ is a density change from the current layer to the next layer below.

The mixed layer depth $z_{ml}$ is calculated by incrementally increasing the comparison between the difference of total kinetic energy $KE$ to the dissipation of KE by macrophytes, and the internal potential energy $PE$ as:

(Eq. 14) \[ z_{ml} \rightarrow PE_{z+1} > (KE - DKE_z) \]

(c) Convective overturn
In the fourth step, any density instabilities over the vertical water column are mixed with a first stable layer below an unstable layer. Here, we applied an area weighed mean of temperature between adjacent layers to calculate the temperature of the mixed layer.

**Appendix References**


**Table S1. Calibrated model parameter values**

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<th>Description</th>
<th>Value</th>
<th>Parameterization</th>
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<td>$C_d$</td>
<td>Wind momentum drag</td>
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<td>$K_m$</td>
<td>Macrophyte light extinction coefficient</td>
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<td>$C_d_{\text{plant}}$</td>
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**Table S2. Input macrophyte data for model simulations**

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**Figure S1.** Examples of individual dissolved oxygen (DO) saturation profiles near deep sites. Profiles are color-coded by the DOY of the sampling event. These profiles were taken in the deeper, central region of the ponds. The vertical grey line highlights 100 percent saturation.

**Figure S2.** Estimated thermocline depth by pond. Periods of a stable thermocline for the reference (A) and nutrient addition (B) ponds are noted in the grey shaded boxes. Nutrient additions are noted with dashed black lines. Estimated thermocline values oscillating rapidly between the near surface and bottom waters were not considered time of stable stratification.
Figure S3. Time series of Lake Number for the reference (A) and nutrient addition (B) ponds. A value of one (horizontal dashed line) indicates that the internal stability of the water column is balanced with wind stress. Values greater than one indicate that the water column is strongly stratified while values less than one mean that stratification is weak compared to wind shear stress.
Figure S4. Bottom water temperature time series across sampling sites. The grey box marks an aquatic heat event from DOY 185-190. Yellow dashed lines indicate the nutrient additions on DOY 176 and 211.

Figure S5. Time series of surface and bottom water dissolved oxygen (DO) saturation and the difference between the two. (A) Surface water DO saturation, (B) bottom water DO saturation, and (B) the difference between surface and bottom water DO saturation is based on weekly profiles at 18 sites across each pond. Negative values of delta-DO indicate greater DO saturation in the bottom waters while positive values mean DO is higher in the surface layer. Values from each pond were GAM-fit to highlight temporal trends. The asterisks next to the effective degrees of freedom (edf) correspond to the estimated p-value, with *** denoting p < 0.001. Across both panels, dashed yellow lines mark the timing of nutrient additions and the grey box highlights the aquatic heat event.
Figure S6. Model fit at discrete depths in the reference pond. Predicted water temperatures from the hydrodynamic model are plotted against the observed temperatures at the same depths. The root mean square error (RMSE, °C) are noted in the top right corner of each panel.