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## RESEARCH LETTER

**Key Points:**
- Shallow and small waterbodies have high but variable rates of gross primary production and respiration
- Depth plays a large role in metabolism rates
- Shallow waterbodies are some of the most productive freshwater ecosystems, with implications for carbon cycling and ecosystem dynamics

# Freshwater Biogeochemical Hotspots: High Primary Production and Ecosystem Respiration in Shallow Waterbodies

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**Abstract**  Ponds, wetlands, and shallow lakes (collectively "shallow waterbodies") are among the most biogeochemically active freshwater ecosystems. Measurements of gross primary production (GPP), respiration (R), and net ecosystem production (NEP) are rare in shallow waterbodies compared to larger and deeper lakes, which can bias our understanding of lentic ecosystem processes. In this study, we calculated GPP, R, and NEP in 26 small, shallow waterbodies across temperate North America and Europe. We observed high rates of GPP (mean 8.4 g $O_2$ m$^{-3}$ d$^{-1}$) and R (mean $-9.1$ g $O_2$ m$^{-3}$ d$^{-1}$), while NEP varied from net heterotrophic to autotrophic. Metabolism rates were affected by depth and aquatic vegetation cover, and the shallowest waterbodies had the highest GPP, R, and the most variable NEP. The shallow waterbodies from this study had considerably higher metabolism rates compared to deeper lakes, stressing the importance of these systems as highly productive biogeochemical hotspots.

**Plain Language Summary**  Ecosystem metabolism is an important metric for understanding how an ecosystem uses and transforms energy and materials. In aquatic ecosystems, ecosystem metabolism is most often calculated by measuring oxygen. Oxygen is produced by aquatic plants and algae through photosynthesis, and oxygen is consumed by bacteria and other organisms through aerobic respiration. Oxygen production and consumption (metabolism) indicate how organic matter is flowing through the ecosystem, and whether an aquatic system is predominantly respiring (indicating it is a carbon source), or photosynthesizing (indicating it is a carbon sink). Metabolism rates in freshwater lakes scale with surface area and depth, but there are few metabolism rates calculated from oxygen measurements in shallow waterbodies. Ponds, wetlands, and shallow lakes are the most abundant freshwater systems on Earth and may function differently from larger lakes. In this study, we show that shallow systems are incredibly productive, with some of the highest rates of metabolism among aquatic ecosystems, and that depth is one of the most important factors affecting metabolism rates.

## 1. Introduction

Ponds, shallow lakes, and wetlands (collectively "shallow waterbodies") are biogeochemical hotspots with high variability (Bansal et al., 2023; Cheng & Basu, 2017; Downing, 2010; Holgerson & Raymond, 2016). To better understand why shallow waterbodies have high rates of biogeochemical activities, we need large-scale, multi-site studies to assess how ecosystem functions scale across size and depth gradients (e.g., Cheng et al., 2023; Hansen et al., 2018; Qin et al., 2020; Richardson et al., 2022). An important measure of ecosystem function is ecosystem metabolism, an integrative measure of aquatic primary production and aerobic respiration of organic carbon. Ecosystem metabolism includes rates of gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP), and describes whether waterbodies are ultimately autotrophic (GPP > R) or heterotrophic (GPP < R).

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Ecosystem metabolism in lakes varies due to both waterbody size and depth, indicating that understudied shallow waterbodies may have different functional responses to environmental drivers than well-studied larger lakes (Brylinsky & Mann, 1973; Staehr et al., 2012). For example, volumetric GPP typically decreases with increasing lake size and depth (Duarte & Kalff, 1989), yet there can also be high variability among both small and shallow waterbodies (Hornbach et al., 2017, 2020; Martinsen et al., 2017; Richardson et al., 2022; Staehr et al., 2012). Similarly, most shallow waterbodies have high, but variable R, often leading to net heterotrophic conditions (Hagerthey et al., 2010; Hoellein et al., 2013). Heterotrophy is likely driven by increased coupling between the sediments and water column as well as a strong edge effect, which increases terrestrial carbon entering these waterbodies (Holgerson, 2015; Rubbo et al., 2006). Yet, the low number of metabolism studies in small or shallow waterbodies precludes a more comprehensive understanding of freshwater metabolism.

Water depth may mechanistically change metabolism in shallow waterbodies. Specifically, benthic processes can affect the entire water column in shallower systems, and therefore lead to higher rates of open-water R (Staehr et al., 2012). Similarly, shallow depths promote growth of submerged and emergent plants, which contribute to metabolism through photosynthesis, providing labile carbon for respiration, providing physical structures for epiphytes, and altering the light environment (Bortolotti et al., 2019; Burkholder & Wetzel, 1989; Hornbach et al., 2020; Martinsen et al., 2017; Rabaey et al., 2021). Macrophyte production can occur either inside or outside of the water column depending on plant growth forms (e.g., submerged vs. emergent), thus affecting the measurement of GPP (Hagerthey et al., 2010; Sand-Jensen et al., 2019). Shallow waterbodies are also prone to water column anoxia when R greatly exceeds GPP, for example, due to terrestrial inputs of organic carbon or water column drawdown (Martinsen et al., 2019), or when macrophytes shade the lower parts of the water column (Andersen, Kragh, & Sand-Jensen, 2017; Rabaey & Cotner, 2022).

In this study, we aimed to (a) quantify ecosystem metabolism (GPP, R, and NEP) across a range of shallow waterbodies, (b) partition background R from R closely tied to GPP (c) identify drivers of GPP, R, and NEP in these systems, and (d) assess how metabolism differs across shallow waterbody types (i.e., ponds, wetlands, shallow lakes). We predicted that shallow waterbodies are net heterotrophic with higher rates of GPP and R than most aquatic systems. Further, we expected that metabolism rates would be most affected by water column depth, waterbody surface area, and macrophyte coverage and type.

## 2. Methods

### 2.1. Field Sampling

We sampled 35 freshwater shallow (maximum depth < 4.8 m) and relatively small (surface area < 17 ha) waterbodies, mostly located across temperate North America with one site in Europe (Figure S1 in Supporting Information S1). All waterbodies fell under definitions of ponds (maximum depth < 5 m, surface area < 5 ha), shallow lakes (<5 m, >5 ha), or wetlands (<5 m, >30% emergent vegetation cover) described in Richardson et al. (2022). The wetlands in this study all had an open water location where sensors were placed, surrounded by vegetation that comprised over 30% of the basin. Sampling took place during the open water period between 2010 and 2022, with only one season of data used for each waterbody. To calculate ecosystem metabolism, we measured near-surface dissolved oxygen (DO) and water temperature using high-frequency sensors (Table S1 in Supporting Information S1). Photosynthetically active radiation (PAR) was measured either on site (16 waterbodies) or at nearby meteorological stations. Physical, chemical, and biological characteristics (hereafter "waterbody characteristics") were measured at least once during the study period (Table S2 in Supporting Information S1).

### 2.2. Metabolism Modeling

To estimate volumetric GPP, R, and NEP, we fit ecosystem metabolism models using the DO, PAR, and temperature data with the maximum likelihood method in the *LakeMetabolizer* R package (Winslow et al., 2016). We used a simple metabolism model that assumed a fully mixed water column and assumed a constant $k_{600}$ value to estimate the gas exchange coefficient ($k$). We used a constant $k_{600}$ value of 0.654 m day$^{-1}$, as this was the average $k_{600}$ estimated for 30 small waterbodies (surface area < 10 ha) via floating chambers or gas tracers (Holgerson et al., 2017).

We compared this simple model to three more complex models: one that used wind to estimate $k$ (Vachon & Prairie, 2013), one that used water column thermistors to calculate the mixing depth ($z_{mix}$), and one that used both wind-derived $k$ and temperature-derived $z_{mix}$. Even though shallow systems can often stratify intermittently (Andersen, Sand-Jensen, et al., 2017; Holgerson, Richardson, et al., 2022) and $k_{600}$ values can vary across systems (Holgerson et al., 2017), the simple model was similar to the more complex models in both goodness of fit and estimated metabolism values (Text S1, Table S3, Figures S2 and S3 in Supporting Information S1). Therefore, all further analyses used the simplest model to maximize the number of included waterbodies as only a subset had onsite wind data required to estimate $k$ (19 waterbodies) or thermistor data required to estimate $z_{mix}$ (12 waterbodies).

### 2.3. Drivers of Model Fit

For each daily model fit on each waterbody, we visually inspected the observed and modeled DO curves along with DO residuals, PAR, and fit statistics (e.g., residual sums of squares). Following Richardson et al. (2017), each daily fit was inspected by at least three team members independently to determine if the model fit was "good" or "bad" (see Text S1–S3; Figure S4 in Supporting Information S1), with impossible values ($R > 0$, GPP < 0) automatically deemed as bad model fits.

We then assessed relationships between waterbody characteristics and model fit at the daily scale, including daily $\Delta$DO (difference between DO at sunrise and DO at sunset), daily duration of anoxia (<1 mg L$^{-1}$ DO), mean daily PAR, and mean daily temperature, as well as waterbody characteristics with the proportion of good model fit days for each of the 35 waterbodies. For all comparisons, we only included data from the summer period (21 June–22 September) to reduce seasonality among waterbodies with different sampling periods, and all waterbodies were required to have >14 days of data (regardless of good or bad model fits) within this period. To relate daily model fits (good vs. bad) across all waterbodies to possible drivers, we used a binomial generalized linear mixed-effects model with a logit link function using the *lme4* package in R (Bates et al., 2015). To compare site-level drivers, the proportion of good model fit days was regressed against waterbody characteristics using a linear model or a log-linear model, with the best model being chosen by Akaike Information Criterion for small sample sizes (AICc).

After testing drivers of model fit, we further split the data to only include waterbodies with >14 days of good model fits within the summer period. This resulted in 26 of the total 35 initially eligible waterbodies, which we used for the remainder of analyses.

### 2.4. Calculating Background Metabolism

We fit regression models to describe the relationship between volumetric rates of R and GPP in each waterbody to estimate coupling between GPP and R ($\beta_1$) and calculate background respiration (R$_{background}$; $\beta_0$) (Text S2 in Supporting Information S1). R$_{background}$ represents the respiration of less-labile organic material that decomposes slowly and is more stable through time, including allochthonous (externally derived) organic matter, recalcitrant autochthonous organic matter, and in situ senescence of macrophytes (Solomon et al., 2013). We compared the R$_{background}$ with coupling parameters using semi-log transformed regression. We determined if differences in R$_{background}$ across waterbodies related to waterbody characteristics using a classification and regression tree (CART) analysis using the rpart package in R (Therneau & Atkinson, 2022).

### 2.5. Drivers of Metabolism and Waterbody Comparisons

To assess daily drivers of metabolism, we used a linear mixed-effects model to regress daily rates against daily variables using the *lme4* package in R (Bates et al., 2015). For site-level drivers, we regressed mean rates of GPP, R, and NEP (waterbody mean) against waterbody characteristics. As GPP cannot be negative, and R cannot be positive, we compared a simple linear model and an exponential model (asymptote at 0) for GPP and R versus waterbody characteristics and chose the best model based on AICc. For NEP, we compared a linear model as well as a second-order polynomial model.

To put our results in context, we compared our data to three previous syntheses of aquatic ecosystem metabolism: Hoellein et al. (2013), Holgerson, Hovel, et al. (2022), and Richardson et al. (2022). We removed repeated data across the three data sets and used waterbody surface area and maximum depth to classify waterbodies as in Richardson et al. (2022) as ponds, shallow lakes, small lakes (>5 m, <5 ha), lakes (>5 m, >5 ha), and wetlands.
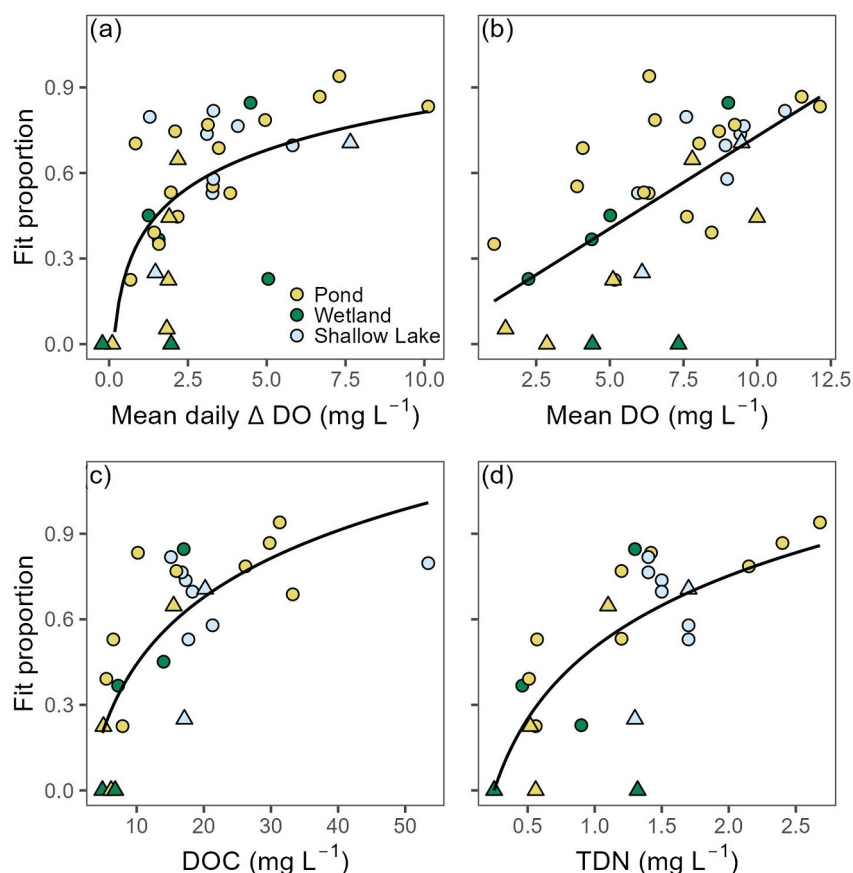
**Figure 1.** Proportion of good metabolism model fit days per shallow waterbody (Fit proportion) versus (a) mean daily change in dissolved oxygen ($\Delta$DO) from sunrise to sunset ($R^2 = 0.39$, $p < 0.001$), (b) mean DO ($R^2 = 0.44$, $p < 0.001$), (c) dissolved organic carbon (DOC) concentrations ($R^2 = 0.57$, $p < 0.001$), and (d) total dissolved nitrogen (TDN) concentrations ($R^2 = 0.52$, $p < 0.001$). Circles represent the 26 waterbodies that were used in subsequent analyses, triangles represent the 9 waterbodies that did not have enough good metabolism fits to analyze further. Model parameter estimates are given in Table S4 in Supporting Information S1.

To make our results comparable, we scaled our volumetric rates to areal rates using 66% of the maximum depth for each waterbody which was the mean mixing depth of waterbodies where mixing data were available ($n = 12$). We then compared areal GPP, R, and NEP across these five aquatic waterbody types using non-parametric Kruskal-Wallis tests with Wilcoxon post-hoc comparisons (Hochberg p-value adjustment) if at least one median was different. For all analyses, we used R statistical software (R 4.4.2, R Core Team 2022).

## 3. Results

### 3.1. Drivers of Model Fit

The proportion of good model fits for the 35 waterbodies ranged from 4% to 100% of days (mean 59%). Within waterbodies, the probability that each day was a good or bad model fit was related to the daily duration of anoxia and the daily $\Delta$DO (Figure S5 in Supporting Information S1). Across waterbodies, higher proportions of good fit days were related to higher mean daily $\Delta$DO, mean DO concentrations, and dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) concentrations (Figure 1).

### 3.2. Drivers of GPP, R, and NEP

Mean volumetric rates (g $O_2$ m$^{-3}$ d$^{-1}$) averaged by waterbody ranged by an order of magnitude for GPP (1.1–24.0; mean 8.4), R (−1.3 to −28.0; mean −9.1), and NEP (−5.0 to 3.6; mean −0.6). Daily rates were as high as 38 g $O_2$ m$^{-3}$ d$^{-1}$ for GPP and −43 g $O_2$ m$^{-3}$ d$^{-1}$ for R (Figure 2). Mean NEP was negative in 15 waterbodies and
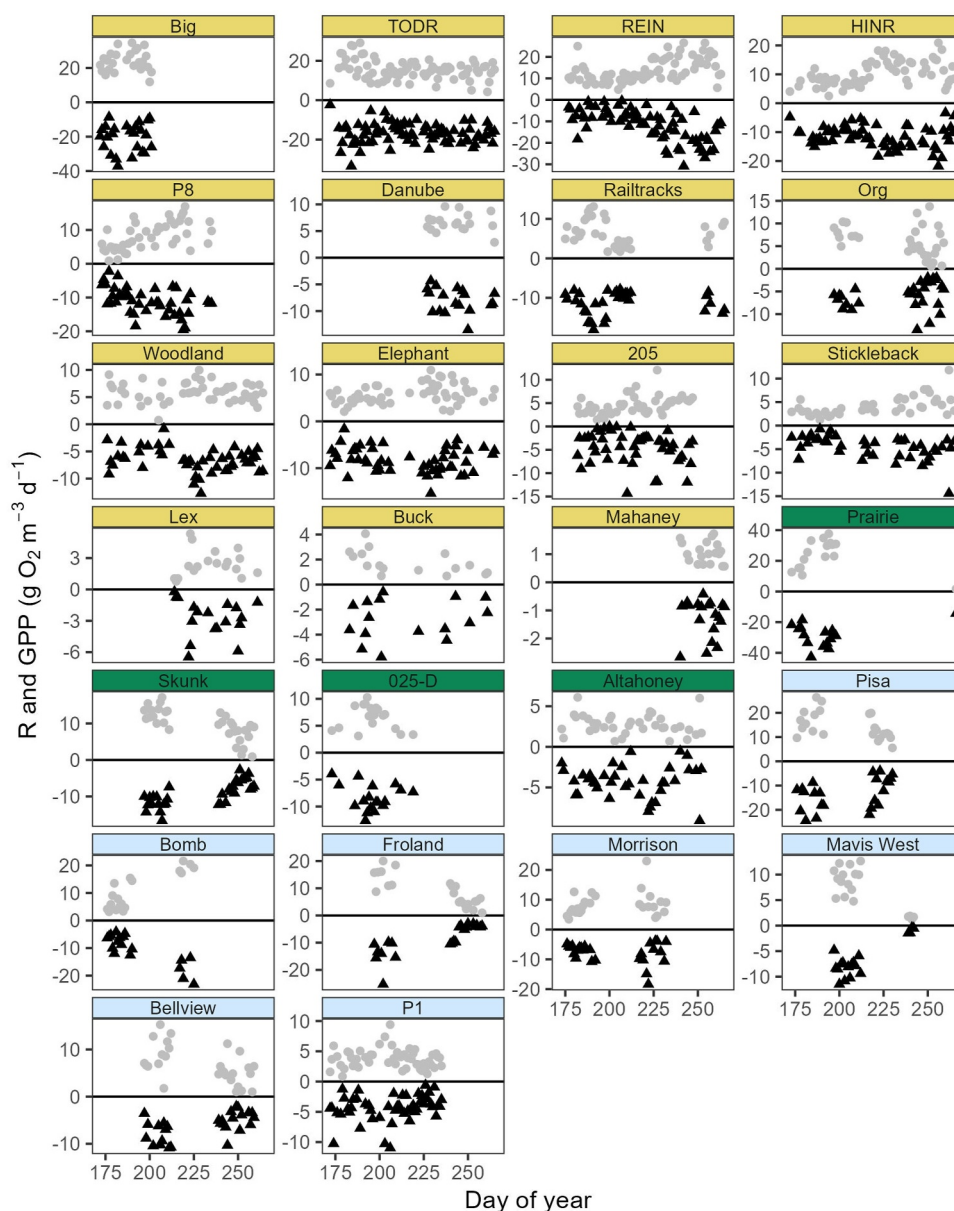
**Figure 2.** Daily volumetric gross primary production (GPP; gray circles) and respiration (R; black triangles) for the 26 shallow waterbodies. Panels are colored by waterbody type, ponds (yellow), wetlands (green), and shallow lakes (blue). Note the y-axis differs across waterbodies. Gaps in the data are times when data was unavailable, or when metabolism values were removed due to poor model fits. Refer to Table S2 in Supporting Information S1 for site descriptions.

positive in 11, though for 9 waterbodies with a positive mean NEP and 2 waterbodies with negative mean NEP the 95% confidence interval included 0.

When relating mean waterbody metabolism to waterbody characteristics, the magnitude of GPP and R exponentially decreased with increasing maximum depth, especially for waterbodies <2 m deep (Figures 3a and 3d). GPP and R did not relate to waterbody surface area, whereas NEP significantly increased with increasing surface area (Figure 3h). Both the most positive and most negative NEP were observed in the shallowest waterbodies, with less variability in NEP amongst larger (>5 ha) and deeper (>2 m) waterbodies. The magnitude of GPP and R increased with increasing emergent vegetation cover (Figures 3c and 3f), though this was driven by one wetland with high (80%) emergent cover. NEP had a unimodal relationship with emergent cover, with intermediate amounts of emergent cover equating to a positive NEP, while NEP was negative where emergent vegetation was
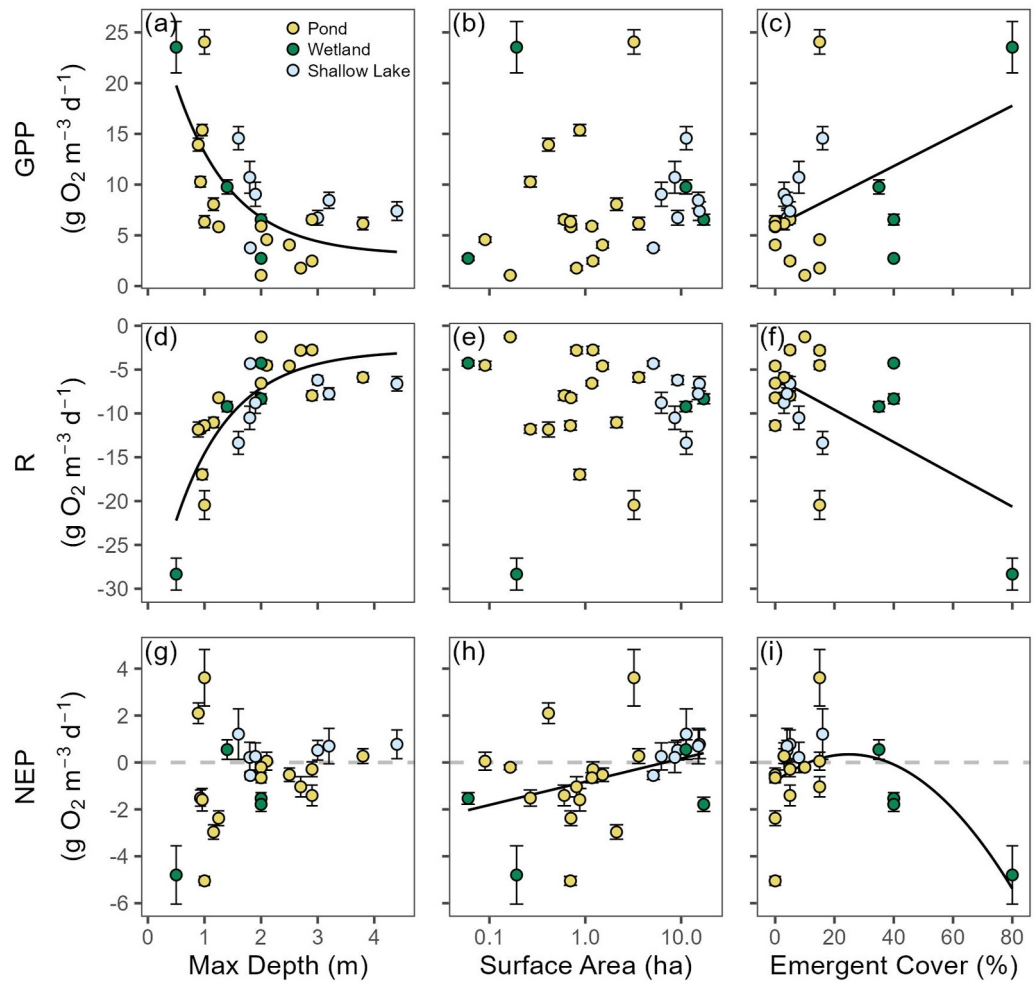
**Figure 3.** Relationships of volumetric gross primary production (GPP), respiration (R), and net ecosystem production (NEP) with maximum depth, surface area, and emergent vegetation cover in shallow waterbodies. Each point is the mean rate, error bars represent $\pm 1$ SE. Trend lines represent significant relationships, including (a) GPP versus Max depth ($R^2 = 0.51$, $p < 0.001$), (c) GPP versus emergent vegetation cover ($R^2 = 0.23$, $p = 0.029$), (d) R versus Max depth ($R^2 = 0.68$, $p < 0.001$), (f) R versus emergent vegetation cover ($R^2 = 0.34$, $p < 0.0053$), (h) NEP versus surface area ($R^2 = 0.15$, $p = 0.050$), (i) NEP versus emergent vegetation cover ($R^2 = 0.37$, $p < 0.016$). Twenty-one waterbodies had data for emergent cover (c, f, i), and only one waterbody had high emergent cover (over 40%). With this 80% emergent cover point removed, relationships in (c) and (f) are no longer significant, while (i) remains significant. Model parameter estimates are given in Table S4 in Supporting Information S1.

either low or very high. No other waterbody characteristics (e.g., nutrients, chl $a$) were significantly correlated with mean waterbody GPP, R, and NEP (Figure S6 in Supporting Information S1). Daily rates of NEP were most strongly correlated with the mean daily DO concentration and the density gradient across the water column (Figure S7 in Supporting Information S1).

### 3.3. Background Respiration Drivers

Coupling of R to GPP was strong in more than half of the waterbodies (15 out of 26), indicated by coupling not being significantly different than $-1$ ($-1$ indicating perfect R-GPP coupling, Figure S9 in Supporting Information S1). $R_{background}$ was <0 in the majority of systems (15 out of 26, Figure S10 in Supporting Information S1), indicating the importance of allochthonous or less-labile organic matter metabolism. $R_{background}$ was minimal (less negative) where R-GPP coupling was most negative (Figure 4a, $R_{background} = -e^{4.0+4.7*\beta 1} + 0.21$, $p < 0.001$, $F_{1,22} = 14.7$), suggesting that autochthonous labile carbon production exceeded allochthonous contributions in those waterbodies. Maximum depth was the only predictor of $R_{background}$ from the pruned regression tree
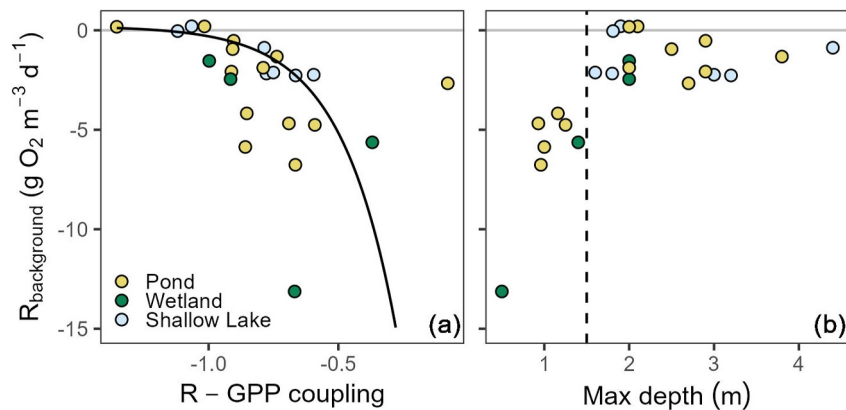
**Figure 4.** Background respiration ($R_{background}$) related to (a) the coupling between respiration (R) and gross primary production (GPP) where a value closer to −1 indicates strong coupling of respiration and photosynthesis and (b) maximum depth of the waterbody, where a regression tree identified a split (vertical dashed line) with higher $R_{background}$ in waterbodies shallower than 1.5 m maximum depth.

(Figure 4b) with a split at 1.5 m maximum depth. Median $R_{background}$ was −5.6 g $O_2$ m$^{-3}$ d$^{-1}$ in sites with <1.5 m maximum depth and −1.5 g $O_2$ m$^{-3}$ d$^{-1}$ sites with >1.5 m maximum depth.

### 3.4. Comparing Ecosystem Metabolism Across Waterbody Types

When aggregated with areal metabolism rates reviewed in Hoellein et al. (2013), the waterbodies from this study have among the highest metabolism rates measured in freshwater ecosystems (Figure 5a). When excluding streams and adding additional published lentic metabolism rates, we found that ponds and wetlands were on the highest end of areal metabolism measured relative to lakes (Figure 5b). Small lakes had significantly lower areal GPP (Kruskal-Wallis: $\chi^2 = 30.7$, df = 4, $p < 0.001$) and R ($\chi^2 = 21.0$, df = 4, $p < 0.001$) than all other waterbodies (ponds, wetlands, shallow lakes, and lakes). Areal NEP differed among the five waterbody types (Figure 5c, Kruskal-Wallis: $\chi^2 = 25.4$, df = 4, $p < 0.001$). Lakes had the highest NEP and were balanced between GPP and R;
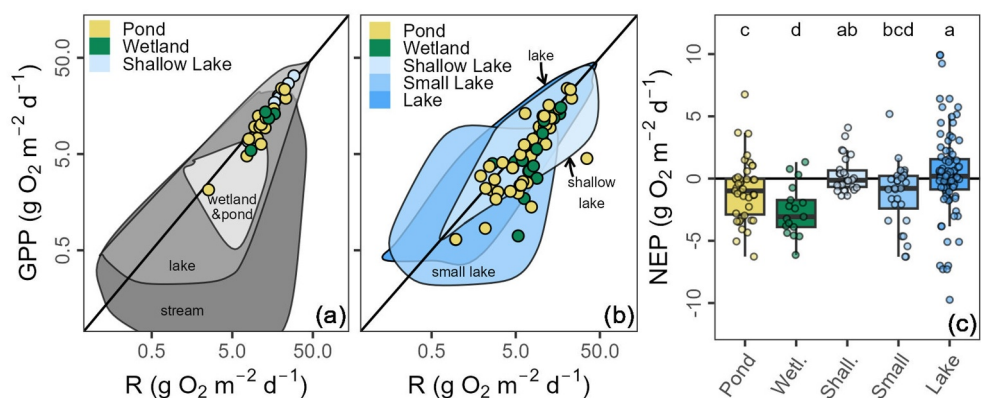


**Figure 5.** (a) Areal gross primary production (GPP) and respiration (R) from this study (filled circles), separated out by pond, wetland, and shallow lake overlaid with a recreated Hoellein et al. (2013) Fig. 1c in greyscale. (b) All pond and wetland metabolism rates from this study and literature (filled circles) overlaid over the extent of all lakes, small lakes, and shallow lakes from both this study and published values including reclassifying ecosystem types from Hoellein et al. (2013). Note the log scale GPP and R axes in panels (a) and (b); R is presented as positive to match Hoellein et al. (2013). (c) Areal net ecosystem production (NEP; g $O_2$ m$^{-2}$ d$^{-1}$) from this study and the literature across five waterbody types: Pond (mean ± sd = −1.6 ± 5.1), Wetland (Wetl.) (−2.6 ± 2.1), shallow lake (Shall.) (−0.4 ± 3.9), small lake (Small) (−1.3 ± 2.6), and Lake (0.4 ± 3.5). One shallow lake (NEP = −18.5) was excluded from the graph for ease of viewing but was included in the statistical analysis. Letters in panel (c) indicate groups of similar NEP values from post-hoc pairwise Wilcoxon tests. Box plots depict the minimum, first quartile, median, third quartile, and maximum, overlain with each individual point.

but there were both autotrophic and heterotrophic waterbodies (Figure 5c). The most heterotrophic waterbodies were wetlands, followed by ponds and small lakes (Figure 5c).

## 4. Discussion

We found that open-water metabolism rates corresponded strongly to waterbody size and maximum depth with ponds, shallow lakes, and wetlands differing in ecosystem metabolism compared to larger lakes (Figure 5). Specifically, the shallowest waterbodies had the highest volumetric rates of GPP and R, and were the most variable in terms of NEP; we also found that net heterotrophy increased with decreasing surface area (Figure 3). Overall, the rates of GPP and R of the 26 waterbodies in our study are some of the highest reported among freshwater ecosystems.

### 4.1. Drivers of Metabolism in Shallow Waterbodies

While depth and surface area have been strongly correlated in previous studies of lake metabolism (Staehr et al., 2012), depth and area were not correlated in our study ($R = 0.22$, $p = 0.21$), allowing us to disentangle their individual effects. Despite all waterbodies being <5 m deep, depth strongly predicted ecosystem metabolism and $R_{background}$; however, surface area only predicted NEP. Larger waterbodies had more positive NEP, possibly due to a smaller edge effect that could reduce shading from forest canopy and reduce allochthonous nutrients and DOC inputs per water volume. In contrast to surface area, depth directly predicted R and GPP. The shallowest systems (<1.5 m maximum depth) had the greatest R, $R_{background}$, and R-GPP decoupling, indicating a greater role of allochthonous or more recalcitrant organic matter similar to lakes (e.g., del Giorgio & Williams, 2005; Solomon et al., 2013). Benthic-pelagic coupling is stronger in shallow waterbodies, which allows for sediment respiration to have a stronger effect on open-water metabolism (Richardson et al., 2022; Staehr et al., 2012) and $R_{background}$. The importance of stronger benthic-pelagic coupling in shallow systems is further supported by our finding that waterbodies with stronger stratification had higher NEP (Figure S7 in Supporting Information S1) as stratification would weaken the impact that sediment R has on epilimnetic metabolism.

Depth also predicted GPP, which is likely because shallow waterbodies can have light penetration throughout the entire water column, allowing GPP by both phytoplankton and submerged macrophytes. With adequate light, nutrient-rich sediments can boost GPP, perhaps explaining why our shallowest systems had some of the highest rates of open-water GPP. The magnitude and variability of open-water GPP and NEP may also be explained by aquatic macrophytes, including submerged (Brothers et al., 2013; Rabaey et al., 2021), floating (Allende & Fontanarrosa, 2023; Rabaey & Cotner, 2022), and emergent plants, which contrasts phytoplankton-driven GPP in deeper systems. Submerged macrophytes can increase GPP through photosynthesis and by providing substrata for epiphytes (Burkholder & Wetzel, 1989), and can also increase R when macrophyte beds are dense (Theus et al., 2023). While submerged macrophyte production and respiration affect DO, emergent macrophytes have limited direct impact on water-column GPP with photosynthesis occurring above the water-air interface. However, they can contribute to both open-water and sediment R by releasing carbon and fueling heterotrophic decomposition (Barko et al., 1991). We found that waterbodies with higher emergent vegetation coverage (i.e., freshwater wetlands) had greater R and lower NEP, though largely driven by one waterbody with 80% emergent coverage. As wetlands are highly variable in hydrology, vegetation, and soil properties, more research should explore how different plant communities influence ecosystem metabolism. Furthermore, our research suggests that traditional indicators of trophic status (e.g., nutrients, chl a, secchi depth) which often predict GPP in lakes (e.g., Hoellein et al., 2013) may not apply for shallow waterbodies (Figure S6 in Supporting Information S1).

### 4.2. Using Open-Water Metabolism Models in Small Waterbodies

Using the open-water metabolism technique (Hanson et al., 2003; Odum, 1956) in shallow waterbodies captures an integrated measure of pelagic and benthic metabolism, but comes with limitations. Specifically, we were unable to model metabolism for 48% of days across our 35 initial waterbodies (Table S3 in Supporting Information S1), a challenge consistent with other studies of shallow waterbody metabolism (Martinsen et al., 2019). Poor model fits were related to hypoxia or limited diel DO changes (Figure 1, Figure S5 in Supporting Information S1) as many waterbodies went anoxic for days or weeks during the summer period. Anoxia does not necessarily signify low productivity; rather high respiration rates can mask high productivity rates in shallow waters (e.g., Holgerson, Post, & Skelly, 2016), though this may still bias our results by removing days with large

respiration rates. When biologically-driven DO changes are small, physical processes (i.e., wind, nighttime mixing, groundwater inputs) can have a larger relative effect that cannot be accounted for by simplified models of gas exchange, a phenomenon seen in ponds (Holgerson, Zappa, & Raymond, 2016) and oligotrophic lakes (Brothers et al., 2017; Richardson et al., 2017). For example, we observed that waterbodies undersaturated in DO frequently exhibited nighttime or early morning reaeration, likely driven by convective cooling increasing turbulence and DO exchange (Holgerson, Zappa, & Raymond, 2016; Figure S4b in Supporting Information S1). Overall, we need to better integrate variable oxygen regimes into metabolism models for shallow waterbodies, which may require improved field and modeling methods, such as eddy covariance (e.g., Berg et al., 2022), using bottle assays to artificially add DO during anoxic conditions, or approaches that monitor both DO and dissolved $CO_2$ (e.g., Vachon et al., 2020).

### 4.3. Conclusion

Small, shallow waterbodies are among the most productive of all freshwater ecosystems (Wetzel, 2001; Figure 5). Specifically, shallow systems appear to be functionally distinct from larger, deeper lakes (Richardson et al., 2022) due to shallow depths promoting strong benthic-pelagic coupling, greater heterotrophy, and greater diversity of aquatic primary producers. These high metabolic rates in shallow systems are likely significant on a global scale. For instance, if we assume that small waterbodies <10 ha have an average depth of 2.6 m and global volume of 1,780 km$^3$ (13% of all lakes by surface area, Cael et al., 2017) and that half of annual GPP and R occurs during the summer (Text S3 in Supporting Information S1), we estimate that these small and shallow waterbodies have global rates of 1.3 Pg yr$^{-1}$ GPP and 1.4 Pg yr$^{-1}$ R, which is more than half of estimates for global rates of GPP and R from all freshwater lentic and lotic ecosystems (Maranger et al., 2018). Therefore, our findings support that shallow waterbodies are some of the most biogeochemically active systems on the planet (Bansal et al., 2023; Cheng & Basu, 2017; Downing et al., 2008; Holgerson & Raymond, 2016; Schmadel et al., 2019; Wetzel, 2001).

## Data Availability Statement

Data is available in the Environmental Data Initiative (EDI) Repository (Rabaey et al., 2024). Data collected by the U.S. Geological Survey (P8, P1) can be found at Bansal et al. (2021).

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