Key Points:
- Winter data have rarely been included in lake metabolism studies, limiting our understanding of how ice affects metabolism estimates
- Annual metabolism estimates were similar across 6 years with widely varying ice cover
- Water chemistry explained variability in daily gross primary production, but not respiration or net ecosystem production, over 6 years

Variability in Ice Cover Does Not Affect Annual Metabolism Estimates in a Small Eutrophic Reservoir

Dexter W. Howard[1] , Jennifer A. Brentrup[2] , David C. Richardson[3] , Abigail S. L. Lewis[1] , Freya E. Olsson[1] , and Cayelan C. Carey[1]

[1]Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA, [2]Minnesota Pollution Control Agency, Saint Paul, MN, USA, [3]Biology Department, SUNY New Paltz, New Paltz, NY, USA

Abstract Temperate reservoirs and lakes worldwide are experiencing decreases in ice cover, which will likely alter the net balance of gross primary production (GPP) and respiration (R) in these ecosystems. However, most metabolism studies to date have focused on summer dynamics, thereby excluding winter dynamics from annual metabolism budgets. To address this gap, we analyzed 6 years of year-round high-frequency dissolved oxygen data to estimate daily rates of net ecosystem production (NEP), GPP, and R in a eutrophic, dimictic reservoir that has intermittent ice cover. Over 6 years, the reservoir exhibited slight heterotrophy during both summer and winter. We found winter and summer metabolism rates to be similar: summer NEP had a median rate of -0.06 mg O_2 L^{-1} day^{-1} (range: -15.86 to 3.20 mg O_2 L^{-1} day^{-1}), while median winter NEP was -0.02 mg O_2 L^{-1} day^{-1} (range: -8.19 to 0.53 mg O_2 L^{-1} day^{-1}). Despite large differences in the duration of ice cover among years, there were minimal differences in NEP among winters. Overall, the inclusion of winter data had a limited effect on annual metabolism estimates in a eutrophic reservoir, likely due to short winter periods in this reservoir (ice durations 0–35 days), relative to higher-latitude lakes. Our work reveals a smaller difference between winter and summer NEP than in lakes with continuous ice cover. Ultimately, our work underscores the importance of studying full-year metabolism dynamics in a range of aquatic ecosystems to help anticipate the effects of declining ice cover across lakes worldwide.

Plain Language Summary Lakes and reservoirs around the world are experiencing decreases in ice cover duration, with many waterbodies starting to experience non-continuous ice cover throughout the winter. These changes in ice duration have the potential to influence carbon cycling, but to date few long-term studies have included winter data. We analyzed 6 years of minute-resolution oxygen data from a small reservoir that experiences non-continuous ice cover to estimate whether the surface water was a source or sink of carbon at daily, seasonal, and annual scales. We found that the reservoir was often a source of carbon to the atmosphere, regardless of whether data from winter were included. Our results differed from previous studies conducted in higher-latitude lakes that experience continuous ice cover throughout the winter, potentially due to the already-short duration of ice cover in this reservoir. As the duration of ice cover continues to decrease across lakes and reservoirs worldwide, our work highlights the need for studying how changing winter conditions—especially non-continuous ice cover—affects year-round carbon cycling.

1. Introduction

Changing climate and the shrinking duration of winter are altering the role of freshwater ecosystems in the global carbon cycle (IPCC, 2022), which can be quantified using functional ecosystem metrics (Brentrup et al., 2021; North et al., 2023; Palmer & Richardson, 2009). One commonly used functional metric is net ecosystem production (NEP), the balance of whole ecosystem gross primary production (GPP) and respiration (R), which can elucidate whether freshwaters are net sources or sinks of organic carbon. Negative NEP indicates heterotrophy, whereas positive NEP indicates ecosystem autotrophy (Lovett et al., 2006). Studies quantifying ecosystem metabolism rates (i.e., NEP, GPP, and R) have primarily focused on the metabolism of naturally-formed lakes in the summer months (e.g., Richardson et al., 2017; Solomon et al., 2013; but see Williamson et al., 2021), leaving substantial uncertainty as to how these rates vary among seasons and years in the face of climate change. Multiple studies in north temperate lakes have shown that winter metabolism rates are more heterotrophic than summer rates (Brentrup et al., 2021; North et al., 2023; Rabaey et al., 2021), and that the inclusion of winter rates in annual estimates can shift lakes from autotrophic to heterotrophic (Brentrup et al., 2021), highlighting the importance of monitoring lake and reservoir metabolism year-round.

Investigation: Dexter W. Howard, Jennifer A. Brentrup, David C. Richardson, Abigail S. L. Lewis, Freya E. Olsson, Cayelan C. Carey
Methodology: Dexter W. Howard, Jennifer A. Brentrup, David C. Richardson, Abigail S. L. Lewis, Freya E. Olsson, Cayelan C. Carey
Project administration: Dexter W. Howard, Cayelan C. Carey
Software: Dexter W. Howard, Jennifer A. Brentrup, David C. Richardson
Supervision: Cayelan C. Carey
Validation: Freya E. Olsson
Visualization: Dexter W. Howard, Jennifer A. Brentrup, David C. Richardson
Writing – original draft: Dexter W. Howard
Writing – review & editing: Dexter W. Howard, Jennifer A. Brentrup, David C. Richardson, Abigail S. L. Lewis, Freya E. Olsson, Cayelan C. Carey

Lakes and reservoirs can be net autotrophic or heterotrophic (Hanson et al., 2003; Hoellein et al., 2013), with shifts between autotrophy and heterotrophy occurring throughout the year (Brentrup et al., 2021; Rabaey et al., 2021). Some north temperate lakes with trophic states ranging from eutrophic to oligotrophic have been found to be autotrophic in summers but heterotrophic in winters (Brentrup et al., 2021; North et al., 2023; Rabaey et al., 2021), while other lakes in subtropical regions are autotrophic in both summer and winter (Hu et al., 2015). While these few studies demonstrate that intra-annual variation in metabolism can occur in at least some lakes, there is still much uncertainty in the prevalence, magnitude, and drivers of intra-annual variation in metabolism in freshwater ecosystems. Understanding intra-annual variation is important as previous work has found that inferring annual NEP from summer-only measurements can result in biased metabolism rates (Brentrup et al., 2021). Additionally, annual metabolism estimates can vary substantially year to year (Pace et al., 2021; Richardson et al., 2017), supporting the need for multi-year metabolism studies to better understand how NEP changes both within and among years.

Previous studies have shown that the environmental drivers of metabolism in naturally-formed lakes during the ice-free period vary across lakes (Solomon et al., 2013), within years (Brentrup et al., 2021; Hu et al., 2015), and among years (Oleksy et al., 2022; Richardson et al., 2017), but less is known about the drivers of metabolism in human-made reservoirs. For example, nutrient concentrations have been positively correlated with GPP and R across lakes (Solomon et al., 2013) and between years (Richardson et al., 2017), whereas local meteorology (Hu et al., 2015; Richardson et al., 2017), hydrology (Klug et al., 2012), and water temperature (Hu et al., 2015) have been found to be important drivers of intra-annual variation in metabolism. These important advances in our understanding of metabolism in naturally-formed lakes during the ice-free period (Hanson et al., 2003; Hu et al., 2015; Richardson et al., 2017; Solomon et al., 2013) set the stage for increasing our understanding of the drivers of year-round metabolism dynamics in human-made reservoirs, which are understudied relative to naturally-found lakes (Doubek & Carey, 2017). In reservoirs, which have shorter residence times and greater catchment to lake area ratios than naturally-formed lakes (Hayes et al., 2017), we expect hydrology to be an important driver of metabolism (Oleksy et al., 2022; Williamson et al., 2021), as shorter residence times will lead to more rapid turnover of nutrients and organic carbon that can stimulate R and GPP (Catalán et al., 2016; Hanson et al., 2003).

The presence of ice can affect winter metabolism estimates in lakes and reservoirs in contradictory ways, by either stimulating or repressing phytoplankton growth (Jewson et al., 2009). In some cases, similar or even higher levels of phytoplankton biomass can persist under-ice when compared to ice-free conditions, resulting in increased GPP (Hampton et al., 2017; Jewson et al., 2009; Twiss et al., 2012). However, under other conditions (e.g., opaque ice or snow cover), phytoplankton productivity may be limited, decreasing winter GPP and resulting in net heterotrophy (Jewson et al., 2009; Leppäranta et al., 2012; North et al., 2023). These variable responses highlight the need for characterizing metabolism during ice-covered periods as ice cover and thickness is decreasing on lakes worldwide (Magnuson et al., 2000; Sharma et al., 2021; Weyhenmeyer et al., 2022). However, estimating ice-covered metabolism rates remains a major challenge due to the logistical difficulties of winter data collection, especially in sites with intermittent ice that prevent safe conditions to sample and deploy sensors (Block et al., 2019). As a result, most winter metabolism studies have been conducted in naturally-formed lakes that experience continuous ice cover throughout the winter (e.g., Brentrup et al., 2021; Huang et al., 2021; Obertegger et al., 2017; Song et al., 2019). Consequently, research on intermittently ice-covered freshwater ecosystems is needed to improve our understanding of the role dynamic ice cover plays on annual metabolism rates as climate change increases the prevalence of winters in which north temperate waterbodies experience intermittent or even no ice cover (Sharma et al., 2019).

To improve our understanding of intra-annual and inter-annual variability in freshwater metabolism, we estimated 6 years of daily rates of GPP, R, and NEP using inverse modeling of high-frequency dissolved oxygen (DO) data in a eutrophic reservoir with variable and intermittent ice cover. These 6 years of data represent the longest continuous record of metabolism calculated from inverse modeling of high-frequency DO data, to the best of our knowledge. We used these metabolism estimates to answer: (a) What is the inter- and intra-annual variability of metabolism in a dimictic reservoir that exhibits intermittent ice conditions in winter? (b) How do estimates of winter metabolism affect annual metabolism estimates? and (c) What are the most important drivers of variability in metabolism? We first predicted higher R and lower GPP estimates in winter (vs. summer) months. Second, we expected that the inclusion of winter metabolism rates, especially in winters with extended ice cover duration, would lead to higher annual R estimates and shift annual NEP toward heterotrophy, compared to winters with a

shorter duration of ice cover. Finally, we expected that the magnitude of reservoir GPP and R estimates would be positively correlated with nutrient and carbon concentrations and with reservoir inflow rates.

2. Methods

2.1. Analysis Overview

To quantify the magnitude and drivers of intra- and inter-annual metabolism in a eutrophic reservoir, we modeled GPP, R, and NEP using high-frequency observational data, then used time series analysis to identify drivers of the metabolic rates at multiple time scales. First, we monitored DO and multiple environmental variables over the 6-year monitoring period (Section 2.3). Second, we used an inverse model (Section 2.4) with inputs of high-frequency DO, water temperature at multiple depths, photosynthetically active radiation (PAR), and wind speed (Section 2.3.1) to estimate GPP and R, from which we calculated NEP. Third, we classified seasons using multiple approaches to compare metabolism at different times of year (Section 2.3.3 and 2.5.2). Fourth, we quantified metabolism variability, differences in metabolism among seasons and years, and the importance of environmental drivers, including meteorology, water chemistry, and hydrology, on reservoir metabolism (Section 2.5).

2.2. Study Site

Falling Creek Reservoir (FCR) is a small eutrophic reservoir located in Vinton, Virginia, USA (37° 18′ 12″ N, 79° 50′ 14″ W; Figure 1a). FCR has a surface area of 0.12 km^2, a maximum depth of 9.3 m, a mean depth of 4 m, and a catchment to surface area ratio of 29:1 (Gerling et al., 2014; Howard et al., 2021). FCR is a drinking water source located in a primarily deciduous forested catchment and is owned and managed by the Western Virginia Water Authority. FCR is typically dimictic with summer thermal stratification usually occurring between March and October and intermittent ice cover between December and February (Carey & Breef-Pilz, 2022; Figure 1b). Throughout the monitoring period of 9 November 2015–28 February 2022, the water level in FCR was managed to be at full capacity, with only small fluctuations. Water residence time during the duration of the study had a median of 185 days (interquartile range of 56–512 days), following the calculation methods of Gerling et al. (2014). The reservoir is fed by one primary inflow, which contributes ∼95% of the water budget (Gerling et al., 2016).

2.3. Field Data Collection

2.3.1. High-Frequency Sensor Data Collection

A high-frequency optical DO sensor was deployed in the epilimnion at the deepest site in FCR to capture diel DO dynamics over the 2015–2022 monitoring period (Figure 1). From 9 November 2015 to 31 December 2018, an InsiteIG Model20 DO sensor (Insite Instrumentation Group, Slidell, LA, USA) measured DO concentration and water temperature every 15 min at 1 m below the surface (Carey, Howard, et al., 2023). From 29 August 2018 to 28 February 2022, a YSI EXO2 sonde (YSI Incorporated, Yellow Springs, OH, USA) measured DO and water temperature every 10 minutes at 1.6 m below the surface (Carey, Breef-Pilz, & Woelmer, 2023). The EXO2 was deployed at 1.6 m to correspond with a water outtake valve and was additionally equipped with chlorophyll-*a* and fluorescent dissolved organic matter sensors (Carey, Breef-Pilz, & Woelmer, 2023). To harmonize the DO data between the two sensors and calculate metabolism over a near-continuous period from 9 November 2015 to 28 February 2022, we compared the 5-month long period when both sensors were simultaneously deployed (August 2018 to January 2019), and applied a linear offset to the 1-m InsiteIG sensor data from the 1.6-m YSI DO sensor based off the median difference between sensor observations (see Text S1 and Figure S1 in Supporting Information S1 for details).

Water temperature profiles were collected at the deepest site of FCR with a suite of sensors during the monitoring period. From 9 November 2015 to 14 January 2018, a depth profile of water temperature was measured at 1-m intervals from 1 m below the surface to just above the sediments (9 m) every 10–15 min using HOBO thermistors (HOBO Pendant Temperature Data Logger, Bourne, MA, USA; Carey, Howard, et al., 2023). In July 2018, NexSens T-Node FR Thermistors (Fondriest Environmental Inc., Fairborn, OH, USA) were deployed at the same site at FCR and also monitored water temperature at 1-m intervals from the surface to the bottom of FCR every 10 min (Carey, Breef-Pilz, & Woelmer, 2023). We applied standardized gap-filling procedures to fill the
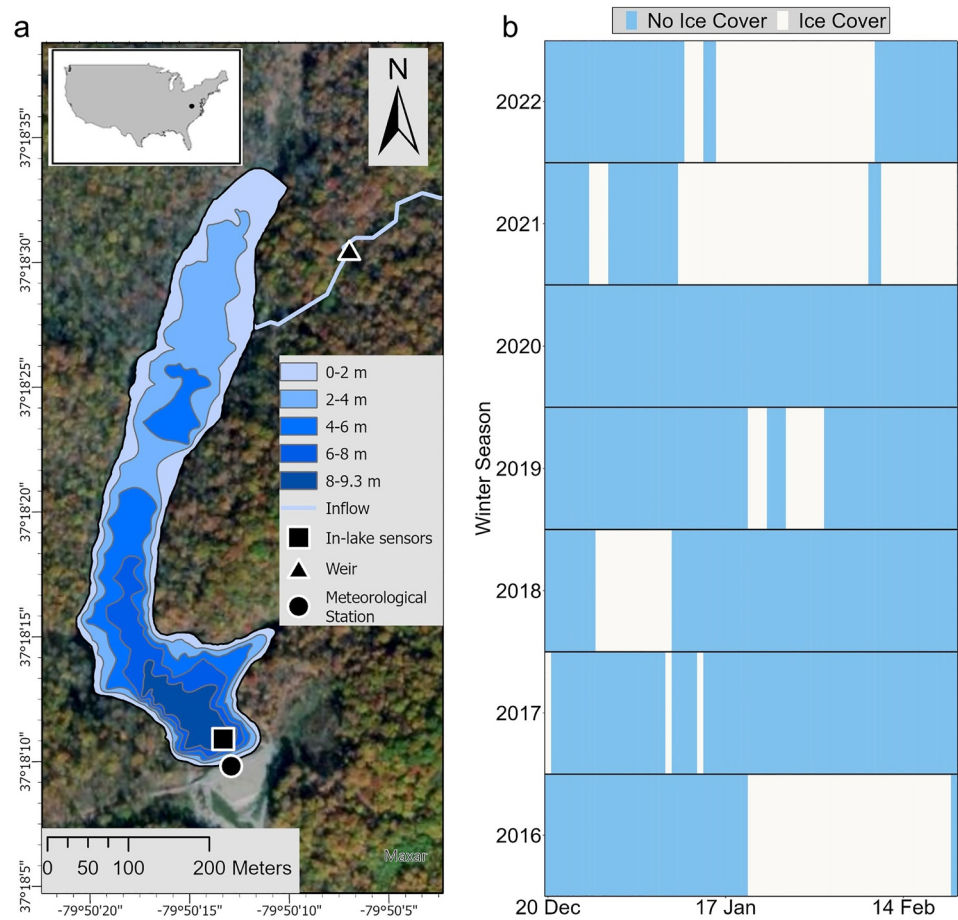
Figure 1. (a) Map of Falling Creek Reservoir (FCR) and its primary inflow stream, located in Vinton, Virginia, USA. The inset map depicts the location of the reservoir within the coterminous USA. The deep hole basin is the region of the reservoir encompassed between the latitudes of 37°18′10″ and 37°18′15″. (b) Time series of ice cover duration in FCR in each winter season of our study (operationally defined as 20 December–22 February, Section 2.5.2). White shading denotes ice-covered periods and light blue shading denotes ice-free periods. Ice cover at FCR was classified as the presence of ice covering greater than 50% of the deep hole basin of the reservoir.

continuous 5 months of missing values when no thermistors were deployed by using modeled temperature profiles (Carey, Hanson, et al., 2022) and interpolated manual weekly profiles (see Text S2 in Supporting Information S1).

A research-grade meteorological station (Campbell Scientific, Logan, UT, USA) was deployed on FCR's dam throughout the monitoring period (Figure 1) to collect one-minute resolution downwelling shortwave radiation, precipitation, air temperature, and wind speed measurements (see Carey & Breef-Pilz, 2023b for sensor specifications). We calculated PAR from downwelling shortwave radiation using the R *LakeMetabolizer* package (Winslow et al., 2016). PAR and wind speed data were averaged to 10 or 15-min resolution to match DO data used in the metabolism model (Section 2.4). Meteorological data had three gaps due to sensor maintenance ranging in duration from 16 to 77 days. We filled these gaps using downscaling corrections developed between observed meteorology and data from the North American Land Data Assimilation System-2 (NLDAS-2; Xia et al., 2012; Text S2, Figures S2 and S3 in Supporting Information S1). Reservoir inflow discharge was calculated every 15 minutes from the primary tributary to FCR (Figure 1) at a weir equipped with an INW Aquistar PT2X pressure sensor (INW, Kirkland, WA; see Carey & Breef-Pilz, 2023a for details).

2.3.2. Weekly Environmental Driver Sampling

In addition to high-frequency sensors, we collected weekly to monthly measurements of light and water chemistry to determine drivers of metabolism variability. Light attenuation was estimated using light extinction coefficients (K_d) from vertical PAR profiles collected at the deepest site of the reservoir using either a conductivity, temperature, and depth (CTD) profiler (SBE 19 plus CTD profiler, Seabird Electronics, Bellevue, WA, USA) or handheld PAR sensor (LiCor LI-192 underwater quantum sensor, LI-COR Biosciences, Lincoln, NE, USA) weekly from spring to fall and monthly through the winter (Carey, Lewis, & Breef-Pilz, 2023). When sensor data were not available, light attenuation was estimated from Secchi disk measurements at a weekly frequency from spring to fall and monthly through the winter (Carey, Breef-Pilz, et al., 2023). Light attenuation measured via the Secchi and PAR sensor profile methods gave similar K_d estimates (median K_d from sensors = 1.0 m^{-1}; median K_d from Secchi = 1.1 m^{-1}). We additionally calculated the derived mean daily mixed layer irradiance ($\bar{E}_{24}$), a measure of mean light experienced by phytoplankton, from K_d, mixed layer depth, and daily incident irradiance data ($\bar{E}_0$; Guildford et al., 2000; Pernica et al., 2017).

Throughout the monitoring period, we collected weekly (spring to fall) to monthly (winter) water samples at 1.6 m for dissolved organic carbon (DOC), nitrogen (total nitrogen (N), nitrate, and ammonium), and phosphorus (total phosphorus (P) and soluble reactive P). All N and P samples were analyzed colorimetrically using flow injection analysis on a Lachat Instruments XYZ Autosampler ASX 520 Series and QuikChem Series 8500 (Lachat ASX 520 Series, Lachat Instruments, Loveland, Colorado, USA; Carey, Wander, et al., 2023). DOC was analyzed using the persulfate catalytic method on a Total Organic Carbon Analyzer (TOCA) from OI Analytical from 2015 to 2016 (OI Analytical 1010 TOCA with 1051 autosampler, College Station, TX USA) and on a Vario TOC Cube from Elementar from 2016 to 2022 (vario TOC cube, Elementar Analysensysteme GmbH, Hanau, Germany; Carey, Wander, et al., 2023).

2.3.3. Ice Cover Monitoring

Ice cover at FCR was classified as the presence of ice covering greater than 50% of the deep hole basin of the reservoir (Figure 1), regardless of ice thickness, and was determined using three methods (Carey & Breef-Pilz, 2022). First, the presence of ice was assessed by visual observation from observers standing at the deep hole of the reservoir or from automated cameras (Carey & Breef-Pilz, 2022). If visual observations were not available, we next checked for the presence of inverse stratification via water temperature profiles, which was validated by looking for changes in upwelling shortwave radiation and albedo from the reservoir (Carey & Breef-Pilz, 2022). Finally, we looked for the depletion of DO at 9 m depth in FCR, using an InSitu RDO Pro-X Dissolved Oxygen Sensor (InSitu Inc., Fort Collins, CO, USA) deployed at the same site as the epilimnetic DO sondes (Carey, Breef-Pilz, & Woelmer, 2023). This sensor collected DO measurements every 10 minutes and was used to monitor for winter DO depletion, as hypolimnetic DO depletion is noticeable when ice cover duration exceeds one day (Carey & Breef-Pilz, 2022). When ice cover was present at FCR, the area surrounding the in-lake sensors (Figure 1a) was completely covered, providing reasonable assurance that any upstream atmospheric exchange of oxygen had a negligible effect on DO dynamics at our monitoring site.

2.4. Metabolism Model

Daily estimates of GPP and R were calculated using an open-water inverse modeling method that can account for ice-covered and ice-free periods (Hanson et al., 2008, as implemented by Brentrup et al., 2021). Model input data included epilimnetic DO concentrations, epilimnetic water temperature, water temperature profiles, wind speed at 10 m, and PAR. The open-water model is based on Equation 1 (Hanson et al., 2008; Odum, 1956), in which changes in DO concentration (dDO/dt) are calculated as:

$$\frac{dDO}{dt} = \text{GPP} - R + D \tag{1}$$

where D is atmospheric oxygen flux.

DO dynamics were then modeled every 10–15 min (depending on sensor frequency) following Equation 2 (Richardson et al., 2017; Solomon et al., 2013; Van de Bogert et al., 2007):

$$DO_{t+1} = DO_t + g \times I_t - r + D_t + \gamma_t \tag{2}$$

where DO_t and DO_{t+1} represent DO concentrations at times t and $t + 1$; g is the parameter describing the rate of photosynthesis per I_t; I_t is incoming PAR at time t; r is the parameter describing a mean rate of respiration; D_t is atmospheric flux of oxygen; and γ_t represents process error. I_t was not adjusted during periods of ice cover, as ice is typically thin and transparent at FCR (Figure S4 in Supporting Information S1).

Atmospheric flux of DO was modeled every 10–15 min following Equation 3 (Richardson et al., 2017; Solomon et al., 2013):

$$D_t = d_t \times (-k_t) \times (DO_t - S_t) / z_t \tag{3}$$

where k_t is the piston velocity of oxygen calculated using wind speed every 10 min (Cole & Caraco, 1998); S_t is the saturation concentration of DO based on water temperature and atmospheric pressure; z_t is the mixed layer depth calculated based on the water density gradient using water temperature profiles following Coloso et al. (2011); and d_t is a binary variable used to represent if the DO sonde was above or below z_t. A d_t of one indicates the DO sonde is above z_t and oxygen can exchange with the atmosphere, versus a d_t of 0 indicates the sonde is below z_t and oxygen cannot exchange with the atmosphere. Atmospheric flux was assumed to be zero during periods of ice cover following Brentrup et al. (2021).

GPP and R were modeled as parameters through the optimization of the metabolism model in Equation 2 using a Nelder-Mead optimization algorithm that reduces the negative log-likelihood of the error (γ_t) in Equation 2, following Solomon et al. (2013) and Richardson et al. (2017), and based on Hanson et al. (2008) and Van de Bogert et al. (2007). GPP and R were then scaled from 10 to 15 min rates to daily rates of GPP and R reported in mg O_2 L^{-1} day^{-1} (Richardson et al., 2017). We note that this model does not account for vertical diffusion of oxygen to epilimnion, which has the potential to influence R during fall mixing. However, we did not observe large changes in R during fall turnover, indicating that upwelling likely had a limited effect in our system (Figure S5 in Supporting Information S1).

2.5. Statistical Analyses

2.5.1. Q1: What Is the Inter- and Intra-Annual Variability of Metabolism in a Dimictic Reservoir?

To investigate inter-annual and intra-annual variation in metabolism rates, we compared metabolism between ice-free and ice-covered periods within the winter, among seasons in the year, and across years. We were able to fit estimates of GPP and R for 54% of the $n = 2,302$ total days in our time series when GPP and R were above ecologically meaningful rates of 0.001 mg O_2 L^{-1} day^{-1} (following Brentrup et al., 2021); values below those rates were set as NA. Our proportion of model fits was similar to another study with 1 year of data that compared ice-covered and ice-free metabolism (57% days acceptable fits; Brentrup et al., 2021). NEP was calculated for days with acceptable estimates of both GPP and R. Kruskal-Wallis rank sum tests were used to test for significant differences in mean GPP, R, and NEP rates across years and seasons (Hollander & Wolfe, 1973) using the *stats* package in R (R Core Team, 2023).

We compared intra and inter-annual variability by calculating the coefficient of variation (CV) for GPP, R, and NEP for the entire time series, across years and seasons, and for individual seasons and years (summary of metabolism estimates provided in Table S1 in Supporting Information S1). We applied the Levene's test to check for statistical differences among GPP, R, and NEP using the *car* package in R (Fox & Weisberg, 2019).

2.5.2. Q2: How Do Estimates of Winter Metabolism Affect Annual Metabolism Estimates?

There are many different ways to classify seasons in lakes and reservoirs (e.g., Gray et al., 2020; Jane et al., 2023; Pierson et al., 2011; Rabaey et al., 2021; Woolway et al., 2022); here, we focus on results generated using operational definitions for each season. We tested multiple seasonal classifications in our analysis, including the use of seasons defined by solar equinoxes/solstices and thermal stratification periods, and note that alternate season calculations did not affect our primary findings (Text S3, Table S2, and Figure S6 in Supporting Information S1). In our operational definition of winter in FCR, winter was the period starting on the earliest date of ice

cover recorded across all years of our study (20 December, observed in 2016, Figure 1b) and ending on the latest day of ice cover recorded across all years of our study (22 February, observed in 2021, Figure 1b). Winter seasons were then classified as the duration from 20 December of the previous calendar year through 22 February of a given year (e.g., Winter 2020 was classified as 20 December 2019–22 February 2020). This operational definition of winter was adapted from other studies studying lakes with continuous ice cover (Hampton et al., 2017; Pierson et al., 2011; Woolway et al., 2022).

Similar to winter, summer was defined as the period starting on the earliest first day of continuous summer thermal stratification recorded in any year of our study (9 March, observed in 2016) and ending on the latest day of summer stratification recorded in any year of our study (2 November, observed in 2021). This definition was chosen to correspond with other studies that operationally classify summer as the period of continuous thermal stratification (Jane et al., 2023; Ladwig et al., 2022). We used two metrics to determine the onset and end of summer stratification—both criteria had to be met for us to consider the reservoir stratified on a given date. First, we assessed whether the difference in water density between epilimnetic (1 m below the surface) and hypo-limnetic (1 m above the sediments) water was at least 0.1 kg m^{-3} (Woolway et al., 2021). Density is a robust and widespread metric of stratification, with multiple studies using 0.1 kg m^{-3} as a threshold to determine the presence of stratification (e.g., Andersen et al., 2017; Ladwig et al., 2021; Woolway et al., 2021). Second, we analyzed whether Schmidt stability was greater than 2% of the summer maximum stability. Schmidt stability is a common metric for determining the strength of stratification in lakes (Duka et al., 2021; Sahoo et al., 2016) and was calculated using the *rLakeAnalyzer* R package (Winslow et al., 2019) according to Idso (1973) using water temperature profiles and bathymetry of FCR (Carey, Lewis, et al., 2022). Calculating the percent of maximum Schmidt stability enables comparison to other lakes or reservoirs. Together, we defined summer stratification as beginning on the first day that both criteria were met for the subsequent 2 weeks, to remove spring and fall days when stratification was setting up or intermittent. Following this definition, summer stratification ended on the first day when the density difference was less than or equal to 0.1 kg m^{-3} and percent maximum Schmidt stability was less than 2%.

The spring mixed period occurred between the first day after winter ended (23 February) and the day before onset of summer stratification (8 March), and fall was considered the period between the day after the end of summer stratification (3 November) and the day before winter began (19 December). Altogether, we defined a lake-year to span from 20 December of the prior calendar year to 19 December of a given year to prevent the transition between years occurring mid-winter and disrupting ecologically-relevant within-season dynamics (i.e., the 2016 lake-year was 20 December 2015–19 December 2016).

We conducted non-paired Wilcoxon tests to compare ice-covered and ice-free periods during the winter and Kruskal-Wallis tests to compare across seasons using the *stats* package in R (R Core Team, 2023). Dunn post-hoc tests were used to determine statistical differences between seasonal means when Kruskal-Wallis results were significant using the *FSA* package in R (Ogle et al., 2023). To test the effect of including winter metabolism rates on annual estimates, we used a paired *t*-test comparing annual estimates of NEP that included and excluded winter rates.

2.5.3. Q3: What Are the Most Important Drivers of Variability in Metabolism?

To identify environmental drivers of metabolism, we developed autoregressive (AR) models for GPP, R, and NEP at daily timesteps. We collated daily data for air temperature, precipitation, fluorescent dissolved organic matter, chlorophyll-*a*, reservoir inflow discharge, TN, nitrate, ammonium, TP, soluble reactive phosphorus (SRP), DOC, Schmidt stability, K_d, and $\bar{E}_{24}$. We then developed correlation matrices to identify collinearity between potential environmental driver variables, defined as when two variables had a Spearman rank correlation of $r > 0.5$. For variables that had $r > 0.5$, we tested which of the correlated variables had a stronger correlation to the metabolism variable of interest based on univariate scatterplots and retained only the variable with a stronger correlation (following McClure et al., 2020).

After removing collinear variables, there were seven candidate variables for daily models of NEP (precipitation, TP, DOC, SRP, nitrate, ammonium, $\bar{E}_{24}$), GPP (precipitation, TP, TN, SRP, nitrate, ammonium, $\bar{E}_{24}$), and R (precipitation, TP, DOC, SRP, nitrate, ammonium, $\bar{E}_{24}$). We z-transformed predictors to enable comparison of the magnitude of coefficients in AR models. We then developed global models for each metabolism metric that included an AR1 lag term to account for temporal autocorrelation (Box & Pierce, 1970) and all possible
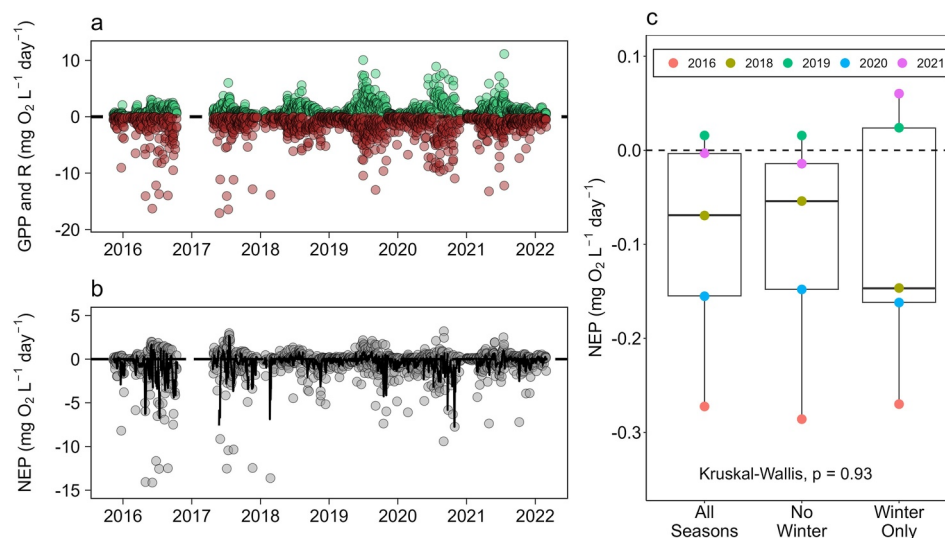
Figure 2. (a) Daily estimates of gross primary production (GPP; green points), respiration (R; brown points) in Falling Creek Reservoir from November 2015 through February 2022. (b) Daily estimates of net ecosystem production (NEP) (gray points) and 7-day moving average of NEP (black line). (c) Boxplots comparing annual median NEP calculated from daily estimates from all seasons; only spring, summer, and autumn (excluding winter); and only winter. The color of the points denotes different years. Metabolism estimates are not included for 2017 due to missing dissolved oxygen data.

combinations of the non-collinear predictor variables, and ranked models by AICc to determine which models best predicted metabolism rates using the *dredge* function in the *MuMIn* package in R (Bartoń, 2022). All analyses were conducted in R version 4.2.3 (R Core Team, 2023), with all code archived in a Zenodo repository (Howard et al., 2024).

3. Results

3.1. Q1: What Is the Inter- and Intra-Annual Variability of Metabolism in a Dimictic Reservoir?

The magnitude and variability in R, GPP, and NEP differed among variables when aggregated over the 6-year study (Figures 2 and 3). The absolute value of R was greater than GPP (Table 1), with a median R of -0.99 mg O_2 L^{-1} day^{-1} compared to 0.82 mg O_2 L^{-1} day^{-1} (Wilcoxon test $p < 0.001$). R was more variable than GPP (daily CVs of -1.29 and 1.05, respectively; Levene's test $p < 0.001$). NEP was near-zero or slightly negative in FCR (54% of days had negative NEP when NEP could be estimated, $n = 1243$), with a median daily rate of -0.05 ± 1.79 mg O_2 L^{-1} day^{-1} (Figures 2 and 3; Table 1), indicating that FCR was net heterotrophic across the study period. NEP was more variable than R throughout the study period (CV $= -3.85$; Levene's test $p < 0.001$) but was not more variable than GPP ($p = 0.08$).

FCR exhibited greater inter-annual variation in NEP than GPP and R throughout our study period (Figures 2 and 3). Across the 5 years with full data (i.e., 2015, 2017, and 2022 were excluded because they lacked estimates for all seasons), median annual NEP estimates ranged from -0.27 mg O_2 L^{-1} day^{-1} (in 2016) to 0.02 mg O_2 L^{-1} day^{-1} (in 2019), and were statistically different across years (Kruskal-Wallis H$_4$ = 16.7, $p = 0.002$; Figure S7, Table S3 in Supporting Information S1). Median annual GPP and R were not as variable as NEP across years (Figure S7 in Supporting Information S1), with GPP ranging from 0.80 to 0.95 mg O_2 L^{-1} day^{-1} and R ranging from -0.96 to -1.16 mg O_2 L^{-1} day^{-1} (Table S3 in Supporting Information S1). Neither GPP nor R were statistically different among years ($p = 0.22$ and $p = 0.16$, respectively). Variation in CV in distinct years also differed among metabolism rates, with annual NEP rates having the largest CV range (-6.63 to -2.40), while annual R and GPP rates had similar ranges of annual CV (-1.06 to -1.41 and 0.73 to 1.12, respectively; Table S3 in Supporting Information S1).

While NEP was highly variable between years (Figure S7 in Supporting Information S1), GPP and R exhibited higher variation across seasons (Figures 3 and 4), with median annual GPP and R estimates significantly different across seasons (Kruskal-Wallis H$_3$ = 12.1, $p = 0.01$; and H$_3$ = 9.9, $p = 0.02$; respectively; Figures 4a and 4b).
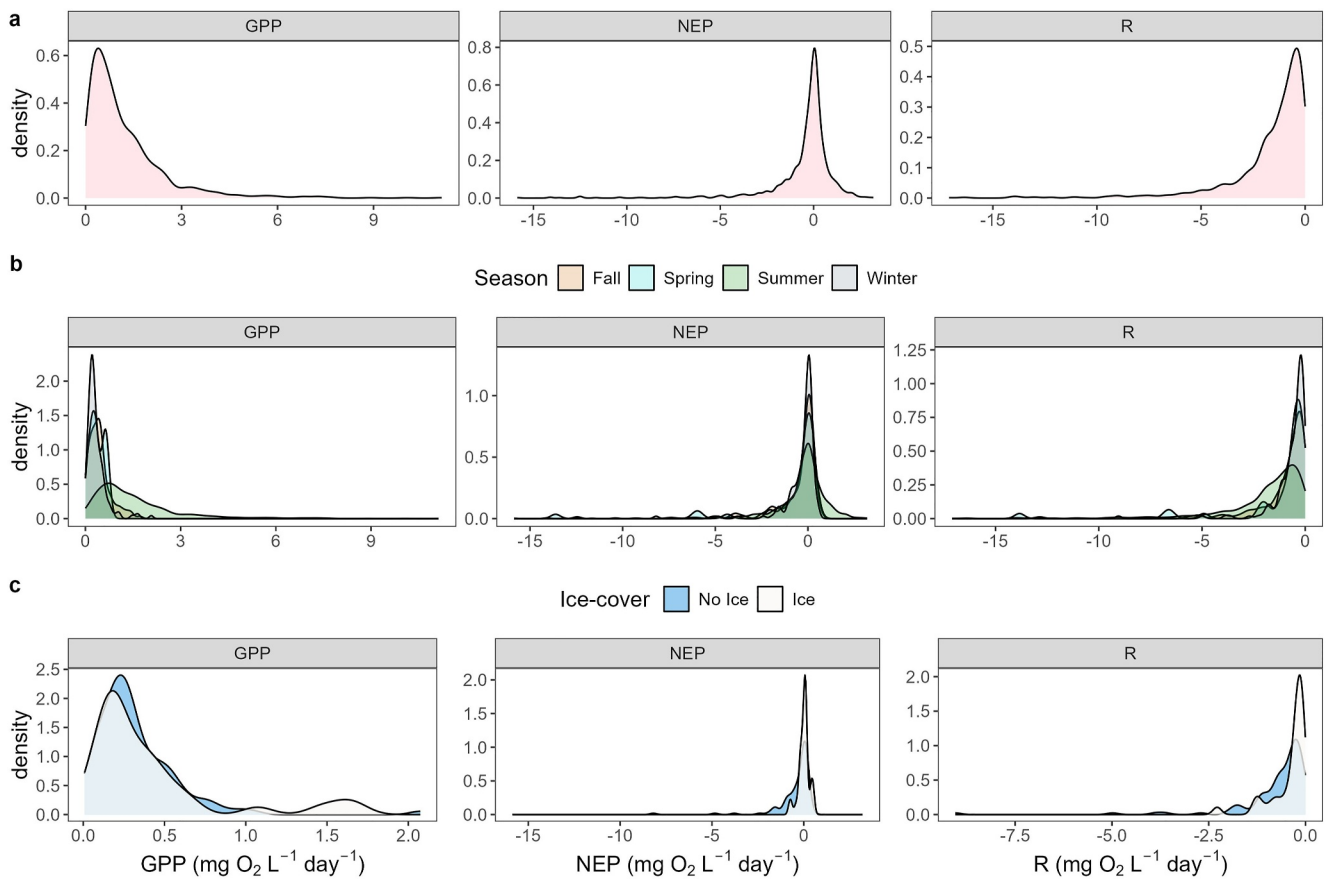
Figure 3. Distributions of gross primary production (GPP), net ecosystem production (NEP), and respiration (R) for (a) the entire time series, (b) for each season, and (c) in winter ice-covered and ice-free conditions. Note differences in the *x*- and *y*-axis ranges across panels.

GPP and R were greater in the summer than other seasons when aggregated across years (Table 1, Figures 4a and 4b). Winter had the lowest median annual rates of GPP and R among seasons (Table 1). NEP was not significantly different between seasons (Kruskal-Wallis $H_3 = 3.3$, $p = 0.34$; Table 1; Figure 4c).

Altogether, seasonal differences in median GPP were nearly six times higher than inter-annual differences (seasonal and inter-annual ranges = 0.89 and 0.15 mg O_2 L^{-1} day^{-1}, respectively; Table 1 and Table S3 in Supporting Information S1), and four times higher in median R (seasonal and inter-annual ranges = 0.91 and 0.20 mg O_2 L^{-1} day^{-1}, respectively; Table 1 and Table S3 in Supporting Information S1). In contrast, median NEP seasonal differences were nearly five times less than inter-annual variation (seasonal and inter-annual ranges = 0.06 and 0.29 mg O_2 L^{-1} day^{-1}, respectively; Table 1 and Table S3 in Supporting Information S1).

3.2. Q2: How Do Estimates of Winter Metabolism Affect Annual Metabolism Estimates?

FCR experienced intermittent ice cover in most years, with up to three separate periods of ice cover within a winter season. Ice cover duration ranged from 0 days (2020) to 35 days of ice (2016) across the six winters (Figure 1b). In 2017 and 2021, FCR exhibited three separate periods of ice cover throughout each winter, and in 2019 and 2022, two separate periods of ice cover occurred. In contrast, there was only one period of continuous ice cover in 2016 and 2018 (Figure 1b).

Patterns of winter GPP, R, and NEP were variable among years and durations of ice cover (Figure 5). Overall, the inclusion of winter NEP estimates did not have a statistically significant effect on annual NEP rates ($t_4 = -0.1$, $p = 0.93$; Figure 2b). Aggregated across all ice-covered and ice-free winter periods, NEP was not statistically different in any year except for in 2019, when NEP was higher on ice-covered days than ice-free days in the winter (Figure 6a). NEP was additionally not significantly different between ice-covered and ice-free days when

Table 1
Summary Table of Daily Gross Primary Production (GPP), R, and Net Ecosystem Production (NEP) ($mg\ O_2\ L^{-1}\ day^{-1}$) Estimates Aggregated Throughout Our Study Period

Metabolism rate	Full time series	Spring	Summer	Fall	All	Winter Ice-covered	Ice-free
NEP ($mg\ O_2$ $L^{-1}\ day^{-1}$)	−0.05 (−0.63 to 0.23)	−0.08 (−0.69 to 0.13)	−0.06 (−0.65 to 0.35)	−0.03 (−0.65 to 0.13)	−0.02 (−0.46 to 0.10)	0.03 (−0.13 to 0.13)	−0.09 (−0.59 to 0.09)
GPP ($mg\ O_2$ $L^{-1}\ day^{-1}$)	0.82 (0.39 to 1.60)	0.34 (0.22 to 0.59)	1.15 (0.65 to 1.92)	0.38 (0.20 to 0.54)	0.26 (0.17 to 0.42)	0.22 (0.16 to 0.44)	0.27 (0.18 to 0.42)
R ($mg\ O_2$ $L^{-1}\ day^{-1}$)	−0.99 (−2.00 to −0.42)	−0.46 (−0.98 to −0.22)	−1.26 (−2.32 to −0.60)	−0.51 (−1.15 to −0.23)	−0.36 (−0.77 to −0.18)	−0.21 (−0.46 to −0.12)	−0.40 (−0.80 to −0.23)

Note. Columns denote different time periods; values are medians with the interquartile range provided in parentheses for each study period. Ice-covered and ice-free periods are subset from the full winter season. Seasons are operationally defined based on summer stratification and ice cover, as detailed in Section 2.
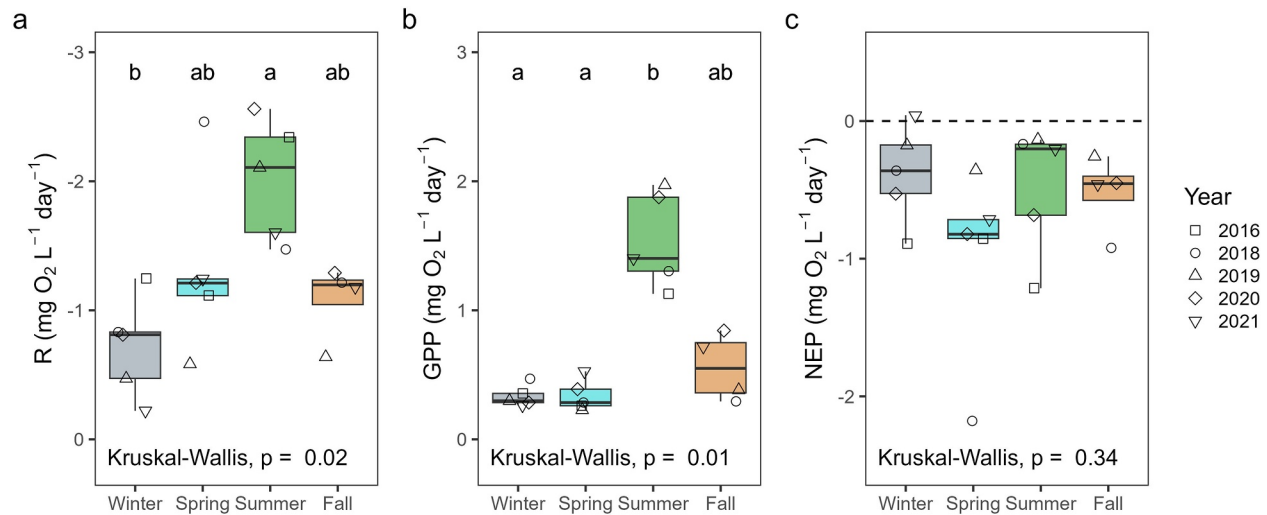
Figure 4. (a–c) Boxplots comparing median daily respiration (R), gross primary production (GPP), and net ecosystem production (NEP) estimates across seasons per year. 2015, 2017, and 2022 were not included since they did not have estimates for multiple seasons.

aggregated across years, though rates were slightly higher when ice-cover was present (Wilcoxon test $p = 0.07$; Figure 6b). R was only significantly different between ice-covered and ice-free days in winter 2016 (lower when ice-covered; Wilcoxon test $p = 0.03$). GPP was significantly different in 2016 and 2022, but the direction of effect differed between the two years (higher when ice-covered in 2022, lower in 2016; Wilcoxon test $p < 0.05$, Figure S8 in Supporting Information S1).

3.3. Q3: What Are the Most Important Drivers of Variability in Metabolism?

Water chemistry variables were consistently important drivers of daily GPP (Table 2), but there were no statistically significant models with environmental predictors of R or NEP. NEP was more strongly correlated to R (Spearman rho = 0.58, $p < 0.001$) than GPP (Spearman rho = 0.21, $p < 0.001$). The model fits varied across the

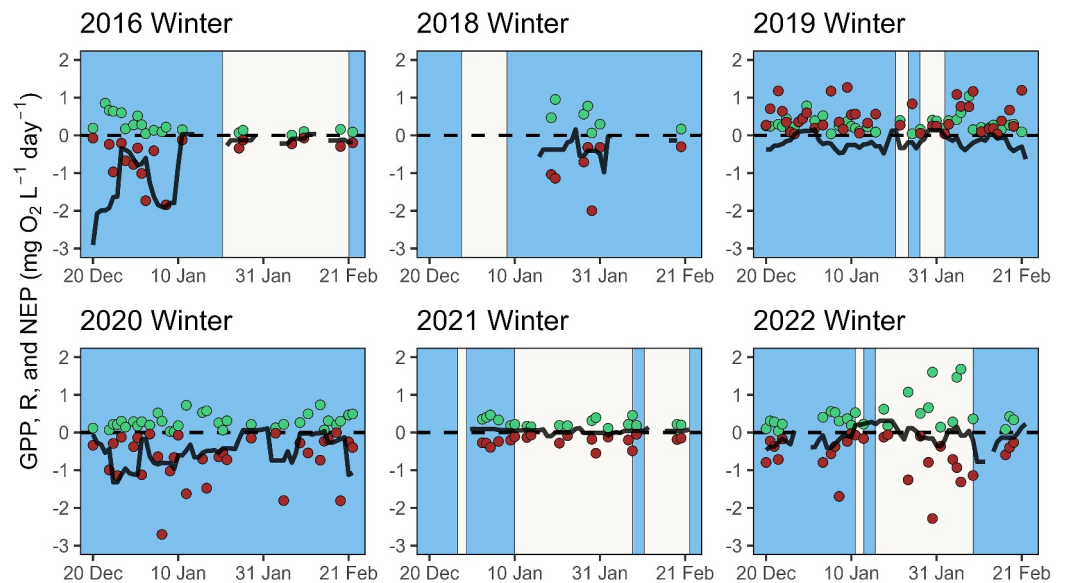

Figure 5. Daily estimates of gross primary production (GPP; green points), respiration (R; brown points), and 7-day rolling average of net ecosystem production (NEP; black line) in different winter seasons. Blue-shaded rectangles denote ice-free periods and white rectangles denote periods of ice cover. Metabolism estimates are excluded for winter 2017 due to missing dissolved oxygen data.
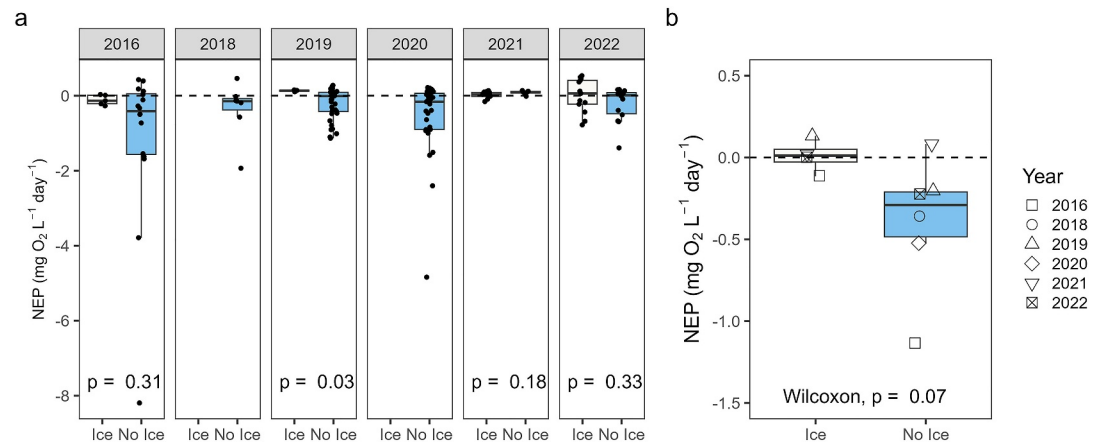
Figure 6. (a) Boxplots of daily net ecosystem production (NEP) rates for each winter season comparing days with ice cover (white) and days without ice cover (blue). (b) Boxplots comparing ice-covered and ice-free median daily NEP estimates per year. There were no winter NEP estimates in 2018 on days with ice cover, and winter 2020 had no days of ice cover.

metabolism metrics, with substantially more variation explained by our candidate environmental predictors for GPP ($R^2 = 0.55$–0.57), versus R and NEP ($R^2 = 0$; Table 2).

The top models predicting GPP had multiple environmental drivers (TN, SRP, ammonium, Precipitation, and $\bar{E}_{24}$), which were all included in more than one best-fitting model (Table 2). TN, SRP, and $\bar{E}_{24}$ were positively associated with GPP in all of these models, and ammonium and precipitation were negatively associated with GPP. Neither R or NEP had best-fitting models with environmental drivers, as the top model for both metabolism metrics only included the autoregressive lag term and had R^2 values of 0 (Table 2). We additionally tested the effects of water temperature on metabolism rates, but the inclusion of water temperature did not significantly alter our results in Table 2 (Table S4 in Supporting Information S1).

4. Discussion

We observed large variability in metabolism rates throughout 6 years in a small eutrophic reservoir. While ice cover duration varied substantially between years, annual metabolism estimates were similar between years (Figure 2c), and winter had similar rates of NEP to other seasons (Figure 4). NEP was generally higher on ice-covered days than ice-free days (Figure 6b), but this result was only statistically significant in winter 2019

Table 2
Best-Fitting (Within 2 AICc Units of the Top Model), Statistically Significant Autoregressive Models for Daily Gross Primary Production (GPP), R, and Net Ecosystem Production (NEP), Listed in Descending Order

Model	Equation	AICc	R^2	p
GPP	$GPP = 0.29(GPP_{t-1}) + 0.52(TN) + 0.23(\bar{E}_{24}) + 1.00$	114.7	0.55	<0.001
	$GPP = 0.28(GPP_{t-1}) + 0.50(TN) + 0.22(\bar{E}_{24}) + 0.10(SRP) + 1.02$	114.8	0.56	<0.001
	$GPP = 0.28(GPP_{t-1}) + 0.52(TN) + 0.21(\bar{E}_{24}) - 0.16(NH_4) + 0.12(SRP) + 1.01$	115.9	0.57	<0.001
	$GPP = 0.30(GPP_{t-1}) + 0.53(TN) + 0.22(\bar{E}_{24}) - 0.11(NH_4) + 1$	116.4	0.55	<0.001
	$GPP = 0.27(GPP_{t-1}) + 0.52(TN) + 0.21(\bar{E}_{24}) + 0.11(SRP) - 0.07(Precip) + 1.03$	116.4	0.57	<0.001
	$GPP = 0.28(GPP_{t-1}) + 0.53(TN) + 0.23(\bar{E}_{24}) - 0.06(Precip) + 1.02$	116.5	0.55	<0.001
R	$R = -0.02(R_{t-1}) - 1.5$	320.5	0.00	0.84
NEP	$NEP = -0.04(NEP_{t-1}) - 0.23$	314.9	0.00	0.61

Note. There were no statistically significant models for R and NEP, but we retained the base autoregressive models in the table for comparison. We tested the effects of seven candidate environmental drivers, which were z-transformed prior to analysis. GPP_{t-1}, NEP_{t-1}, and R_{t-1} are the one-day autoregressive lag terms in each metabolism model. The environmental drivers were: DOC = dissolved organic carbon, $\bar{E}_{24}$ = mean light experienced by phytoplankton, NH_4 = ammonium, NO_3 = nitrate, Precip = total daily precipitation, SRP = soluble reactive phosphorus, TN = total nitrogen, and TP = total phosphorus.

(Figure 6a). GPP and R, but not NEP, differed significantly between seasons, with highest rates in the summer (Figure 4), whereas NEP was the only metabolism rate with significant inter-annual variation (Figure S7 in Supporting Information S1). Water chemistry parameters were a significant driver of GPP, while R and NEP were not significantly predicted by any of the other candidate environmental drivers (Table 2). Below, we explore how our results inform our understanding of intra- and inter-annual metabolism in a reservoir with intermittent ice cover, as well as identify future directions for winter research.

4.1. Ice-Covered Metabolism Rates Compared to Ice-Free Metabolism

Contrary to our hypotheses, the inclusion of winter did not significantly alter annual NEP estimates (Figure 2c). Within the winter, ice-covered periods exhibited higher NEP than ice-free periods in 1 year (2019), which had intermediate ice coverage relative to the other years (Figures 5, Figure 6a), but it is possible that the duration of ice cover at FCR (0–35 days per year) was overall too short to have a substantial effect on annual estimates in our 6-year study. Assuming that additional days of ice cover would exhibit the median NEP rates observed when ice-cover was present in this study, a back-of-envelope calculation suggests that even an additional 100 days of ice per winter would not cause the inclusion of winter data to alter annual NEP estimates (Text S4, Table S5 in Supporting Information S1). Consequently, multiple months of ice cover per winter may be needed for winter dynamics to significantly affect annual metabolism rates in our study reservoir.

Similar NEP rates across seasons were contrary to our prediction that NEP would decrease under ice, as observed in a previous study (Brentrup et al., 2021). We expected that ice cover would lead to decreased primary production, resulting in greater R than GPP (Huang et al., 2021; Obertegger et al., 2017). Instead, our results indicate the opposite pattern, suggesting that ice-covered conditions promoted greater rates of primary production compared to ice-free conditions in the winter (especially in Winter 2022; Figure 6). High concentrations of phytoplankton under-ice have been observed in other studies (Leppäranta et al., 2012; Reinl et al., 2023), in which phytoplankton can use the ice surface as a substrate, promoting growth that may not otherwise occur in winter months (Twiss et al., 2012). Additionally, clear and thin ice conditions may allow additional light penetration, leading to a more favorable environment for ice-covered phytoplankton growth (Leppäranta et al., 2012). FCR may be especially likely to display clear ice conditions, as ice cover is often very short in the reservoir relative to north temperate lakes (Weyhenmeyer et al., 2022), thus not providing enough time for ice layers to become opaque as snow falls and freezes into ice or snowpack to accumulate on-ice. Consequently, our study adds to the growing literature that suggests that ice cover can increase GPP and NEP, not just R (Figure S8 in Supporting Information S1).

Winter GPP and R estimates were significantly lower than in summer, but NEP was not significantly different between the seasons (Figure 4). Higher GPP and R estimates in the summer relative to winter have been observed in numerous studies (Hu et al., 2015; North et al., 2023; Rabaey et al., 2021), but similar rates of NEP among seasons are less common (Hu et al., 2015). Multiple studies have shown that NEP can shift from autotrophic in the summer to heterotrophic in the winter, with shoulder seasons (i.e., the spring and fall) showing intermediary rates between summer and winter (Brentrup et al., 2021; Rabaey et al., 2021). We note that these previous studies were conducted in higher-latitude glacially-formed lakes that experience multiple months of continuous ice cover (Brentrup et al., 2021; Rabaey et al., 2021). The intermittent ice observed at FCR provides a unique comparison to these systems, as we do not observe significant changes in NEP from summer to winter, possibly because the shorter ice cover duration allows for an extended period of high light conditions relative to opaque ice, in turn extending the phytoplankton growing period (Wetz et al., 2004).

4.2. Inter and Intra-Annual Variability in Lake Metabolism

To the best of our knowledge, only two other studies have quantified metabolism rates in lentic waterbodies for durations longer than one continuous year (Hu et al., 2015; Rabaey et al., 2021). In these studies (Hu et al., 2015; Rabaey et al., 2021), both conducted in naturally-formed lakes, the highest rates of GPP and R were observed in the summer and the lowest rates were observed in the winter, similar to our findings. Hu et al. (2015) also found that metabolism rates were more variable within a year across days than among years, while Rabaey et al. (2021) did not compare inter-annual variation in metabolism rates.

Contrary to expectation, we did not observe a shift in NEP across seasons. Unlike previous studies in which NEP shifted from positive to negative between summer and winter (Rabaey et al., 2021), leading to changes in annual

metabolism estimates (Brentrup et al., 2021), FCR exhibited similar NEP year-round (Figure 4c). This consistency across seasons may be potentially due to FCR's short ice cover duration or because it is a human-made reservoir and therefore may exhibit fundamentally different patterns of ecosystem functioning than the naturally-formed lakes examined by Brentrup et al. (2021) and Rabaey et al. (2021).

The prevalence of heterotrophy in reservoirs has been found to vary both over space and time, with previous studies largely focusing on summer or ice-free periods (Barbosa et al., 2023; Solomon et al., 2013; Williamson et al., 2021). Reservoirs have exhibited both net heterotrophy (Barbosa et al., 2023; Solomon et al., 2013) and autotrophy (Solomon et al., 2013), with some studies showing changes between years (Williamson et al., 2021). We observed small shifts from autotrophy to heterotrophy in the winter (Figure 5), in addition to other seasons (Figure 2b), which has also been observed in previous reservoir studies (Barbosa et al., 2023; Williamson et al., 2021). Throughout the year, we observed mostly heterotrophic conditions, which was consistent with three large oligotrophic reservoirs in Canada (Barbosa et al., 2023). It is possible that FCR consistently exhibited net heterotrophy because of its short residence time and continuous loading of allochthonous carbon (Park et al., 2009), motivating the collection of organic carbon quality data in future studies to test this hypothesis.

4.3. Water Chemistry Is an Important Driver of GPP

This study is one of the first to explore the role of water chemistry (C, N, and P concentrations) as drivers of variation in metabolism rates within a reservoir over time, as several previous studies focused on the role of chemistry across lakes (e.g., Hanson et al., 2003; Solomon et al., 2013) or only included meteorological and physical drivers (e.g., Brentrup et al., 2021; Richardson et al., 2017). Nutrients were important drivers of GPP, with TN appearing in all of the best-fitting AR models, and SRP appearing in half (Table 2). The consistent appearance of TN and SRP in the list of best-fitting models predicting GPP support co-limitation of phytoplankton growth in FCR, which has been previously observed in the reservoir (Hamre et al., 2017), as well as numerous other freshwater ecosystems (e.g., Elser et al., 2007; Lewis et al., 2020; Paerl et al., 2016; Volponi et al., 2023). The importance of TN (instead of nitrate or ammonium) also highlights the potential role of organic N in FCR, which has been found to stimulate phytoplankton growth more than inorganic N forms (Volponi et al., 2023). We observed that ammonium was negatively correlated with GPP, which contradicts previous work showing that ammonium is the preferred N form for phytoplankton uptake (Raven et al., 1992). Despite this unexpected relationship, other studies have found that high concentrations of ammonium can suppress algal growth rates (Glibert et al., 2016), and can lead to decreases in N-fixing cyanobacteria (Yang et al., 2023), which often dominate FCR's phytoplankton community in summer months (Lofton et al., 2022). Light was additionally found to be a driver of GPP (Table 2), which was consistent with previous studies (Hu et al., 2015; North et al., 2023), and highlights the important role ice may play altering GPP rates in FCR (Leppäranta et al., 2012).

There were no significant environmental drivers of R or NEP in our AR models (Table 2), which contradicted our expectation that inflow discharge or DOC would be a strong driver of R. Previous studies have shown that DOC is often positively correlated with R and is an important driver across lakes (Barbosa et al., 2023; Hanson et al., 2003; Solomon et al., 2013), but DOC did not appear in top models for R (Table 2). It is possible that our candidate environmental predictors did not include the most important drivers of R or NEP in FCR. For example, we did not include wind speed as a potential environmental driver because it was an input to the metabolism model to calculate k_t (Equation 3) or organic matter quality due to lack of data; both of these drivers have been found to be important in other freshwater ecosystems (Brentrup et al., 2021; Jane & Rose, 2018). We found the inclusion of water temperature (another input to the metabolism model) as an environmental predictor did not alter our results (Table S4 in Supporting Information S1), which was unexpected given previous work showing the importance of water temperature on R (Yvon-Durocher et al., 2012), suggesting that the environmental drivers of metabolism in FCR are complex and that monitoring of additional environmental variables is likely needed to improve our understanding of its metabolism.

In addition to expanding environmental drivers of metabolism in future work, our study's limitations motivate further follow-up analyses. First, our work underscores the importance of monitoring metabolism in additional reservoirs across years. Our study was limited by changes in DO and temperature sensors through the study, but differences in metabolism between years with different DO and temperature sensors were minimal (Figure 4). While we were only able to explore the effects of ice cover on metabolism in one reservoir, year-round monitoring and long-term ice cover records for additional lakes and reservoirs is needed to improve our understanding of how

winter conditions affect ecosystem function across a gradient of freshwater ecosystems. We additionally highlight limitations in our model approach for accounting for vertical transport of oxygen during mixed periods, which did not noticeably affect our results (Figure S5 in Supporting Information S1), but may be an important consideration in future studies (e.g., Rose et al., 2014; Solomon et al., 2013). Second, in our analysis of the effects of winter ice cover on metabolism, we were limited by the longest ice duration observed during our study period (35 days in 2016), which was two to four months shorter than previous winter metabolism studies (Brentrup et al., 2021; Obertegger et al., 2017). Given the shorter ice cover duration in FCR, our results are inherently different from prior ice-cover studies that experienced deep snowpack on the ice that altered light penetration and GPP rates (Leppäranta et al., 2012; North et al., 2023). Third, our monitoring data did not include records for ice thickness or transparency, which would have improved understanding of the underwater light environment in the winter and subsequent effects on GPP rates (Leppäranta et al., 2012), but were logistically impossible to collect due to the danger of sampling intermittent ice conditions. Future work studying ice-covered metabolism would benefit from including under-ice light measurements, when feasible. Finally, we were only able to present results on the effects of ice cover on pelagic metabolism estimates, given the data available. Littoral site metabolism estimates can differ significantly from pelagic estimates and be more sensitive to changes in environmental conditions (e.g., Lauster et al., 2006; Scordo et al., 2022; Van de Bogert et al., 2007; Ward et al., 2022); possibly leading to differential responses in littoral metabolism to ice cover than what we observed here.

4.4. What Is Winter and Its Role in Freshwater Ecosystem Function?

In this study, we classify seasons using operational definitions to understand how intermittent ice cover is affecting lake metabolism. Many previous winter limnology studies have either classified seasons based on presence/absence of thermal stratification or solar seasons classifications (equinox and solstices; Ladwig et al., 2021; Rabaey et al., 2021). Assessing thermal structure and density gradients from surface to sediments in a waterbody allows determination of classical limnological periods in dimictic waterbodies, which include summer stratification, spring and fall mixis, and ice-covered winter inverse stratification (Gray et al., 2020; Pierson et al., 2011; Woolway et al., 2022). However, this classification is not suited for waterbodies with intermittent ice and inverse stratification, as seasons cannot be easily delineated if "winter" starts and stops multiple times. The difficulty of using thermal stratification to delineate seasons because of intermittent ice led to our operational definition of winter, in which we defined winter as the duration of the earliest day of ice cover recorded in our study time period (20 December) to the latest day of ice cover recorded in our study period (22 February). This classification led us to adjust our classification of a lake-year to start on 20 December, similar to how hydrologic studies use the water year (start date of 1 October) to account for snowpack formation (Granato et al., 2017). With a consistent winter season across years, we were also able to compare the impacts of different ice cover durations on not only annual metabolism rates (Figure 2b), but within seasons as well (Figure 6). We note that multiple other delineations of seasons (thermal stratification, solar calendars) yielded qualitatively similar metabolism comparisons across seasons (Text S3, Figure S6 in Supporting Information S1), supporting the use of our operational definition of seasons.

Decreases in ice cover and the increased prevalence of intermittent ice cover on waterbodies accelerate the need to understand how changing winter is affecting freshwater ecosystem functioning. FCR at 37°N is a sentinel of future conditions for lakes located at higher latitudes, which will continue to experience shorter ice cover durations and increases in intermittency (Sharma et al., 2019). Decreasing ice cover is especially important given our contrasting findings to previous winter metabolism studies that found winter NEP to be more heterotrophic than summer NEP (Brentrup et al., 2021; Rabaey et al., 2021). If higher latitude lakes become more similar to FCR in the future, with more similar winter and summer NEP dynamics, the role of lakes and reservoirs as carbon sources or sinks may change.

5. Conclusions

Our results provide useful insight into the role of intermittent ice cover on reservoir ecosystem metabolism. We observed heterotrophic conditions across seasons, and no significant influence of winter rates on annual metabolism rates, differing from previous studies (e.g., Brentrup et al., 2021; Rabaey et al., 2021). We additionally found that water chemistry was a consistent driver of variability in GPP. Our results may foreshadow future metabolism dynamics in higher-latitude lakes and reservoirs as ice cover duration decreases and intermittency increases. Altogether, our work highlights the need for year-round metabolism studies spanning multiple years to

both provide better estimates of seasonal and annual metabolism, as well as establish baseline conditions as winter conditions continue to change.

Data Availability Statement

All data used in this analysis are published in the Environmental Data Initiative (EDI) repository and cited throughout the manuscript: Carey and Breef-Pilz (2022, 2023a, 2023b), Carey, Lewis, et al. (2022), Carey, Breef-Pilz, et al. (2023), Carey, Lewis, and Breef-Pilz (2023), Carey, Breef-Pilz, and Woelmer (2023), Carey, Howard, et al. (2023), and Carey, Wander, et al. (2023). Code used to conduct this analysis is published in a Zenodo repository (Howard et al., 2024).

References

Andersen, M. R., Sand-Jensen, K., Iestyn Woolway, R., & Jones, I. D. (2017). Profound daily vertical stratification and mixing in a small, shallow, wind-exposed lake with submerged macrophytes. *Aquatic Sciences*, *79*(2), 395–406. https://doi.org/10.1007/s00027-016-0505-0

Barbosa, P. M., Bodmer, P., Stadler, M., Rust, F., Tremblay, A., & Del Giorgio, P. A. (2023). Ecosystem metabolism is the dominant source of carbon dioxide in three young Boreal Cascade-reservoirs (La Romaine complex, Québec). *Journal of Geophysical Research: Biogeosciences*, *128*(4), e2022JG007253. https://doi.org/10.1029/2022JG007253

Bartoń, K. (2022). MuMIn: Multi-Model inference. R package version 1.47.1. Retrieved from https://CRAN.R-project.org/package=MuMIn

Block, B. D., Denfeld, B. A., Stockwell, J. D., Flaim, G., Grossart, H. F., Knoll, L. B., et al. (2019). The unique methodological challenges of winter limnology. *Limnology and Oceanography: Methods*, *17*(1), 42–57. https://doi.org/10.1002/lom3.10295

Box, G. E. P., & Pierce, D. A. (1970). Distribution of residual autocorrelations in autoregressive-integrated moving average time series. *Journal of the American Statistical Association*, *65*(332), 1509–1526. https://doi.org/10.2307/2284333

Brentrup, J. A., Richardson, D. C., Carey, C. C., Ward, N. K., Bruesewitz, D. A., & Weathers, K. C. (2021). Under-ice respiration rates shift the annual carbon cycle in the mixed layer of an oligotrophic lake from autotrophy to heterotrophy. *Inland Waters*, *11*(1), 114–123. https://doi.org/10.1080/20442041.2020.1805261

Carey, C. C., & Breef-Pilz, A. (2022). Ice cover data for falling Creek reservoir and Beaverdam reservoir, Vinton, Virginia, USA for 2013–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/917B3947D91470EECF979E9297ED4D2E

Carey, C. C., & Breef-Pilz, A. (2023a). Discharge time series for the primary inflow tributary entering Falling Creek Reservoir, Vinton, Virginia, USA 2013–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/791192BEF17F21E8C0641EA903440A16

Carey, C. C., & Breef-Pilz, A. (2023b). Time series of high-frequency meteorological data at Falling Creek Reservoir, Virginia, USA 2015–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/F3F97C7FDD287C29084BF52FC759A801

Carey, C. C., Breef-Pilz, A., Wander, H. L., Geisler, B., & Haynie, B. (2023). Secchi depth data and discrete depth profiles of water temperature, dissolved oxygen, conductivity, specific conductance, photosynthetic active radiation, redox potential, and pH for Beaverdam Reservoir, Carvins Cove Reservoir, Falling Creek Reservoir, Gatewood Reservoir, and Spring Hollow Reservoir in southwestern Virginia, USA 2013–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/EB17510D09E66EF79D7D54A18CA91D61

Carey, C. C., Breef-Pilz, A., & Woelmer, W. M. (2023). Time series of high-frequency sensor data measuring water temperature, dissolved oxygen, pressure, conductivity, specific conductance, total dissolved solids, chlorophyll a, phycocyanin, fluorescent dissolved organic matter, and turbidity at discrete depths in Falling Creek Reservoir, Virginia, USA in 2018–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/F6BB4F5F602060DEC6652FF8EB555082

Carey, C. C., Hanson, P. C., Thomas, R. Q., Gerling, A. B., Hounshell, A. G., Lewis, A. S. L., et al. (2022). Anoxia decreases the magnitude of the carbon, nitrogen, and phosphorus sink in freshwaters. *Global Change Biology*, *28*(16), 4861–4881. https://doi.org/10.1111/gcb.16228

Carey, C. C., Howard, D. W., Gantzer, P. A., McClure, R. P., Gerling, A. B., Lofton, M. E., et al. (2023). Time series of high-frequency sensors measuring water temperature and dissolved oxygen at discrete depths in Falling Creek Reservoir, Virginia, USA in 2012–2018 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/964A5BBBB4D5826B5ACB30098DBAE59A

Carey, C. C., Lewis, A. S. L., & Breef-Pilz, A. (2023). Time series of high-frequency profiles of depth, temperature, dissolved oxygen, conductivity, specific conductance, chlorophyll a, turbidity, pH, oxidation-reduction potential, photosynthetic active radiation, and descent rate for Beaverdam Reservoir, Carvins Cove Reservoir, Falling Creek Reservoir, Gatewood Reservoir, and Spring Hollow Reservoir in southwestern Virginia, USA 2013–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/5170B52F7514F54D834130DB0EFC5565

Carey, C. C., Lewis, A. S. L., Howard, D. W., Woelmer, W. M., Gantzer, P. A., Bierlein, K. A., et al. (2022). Bathymetry and watershed area for falling Creek reservoir, Beaverdam reservoir, and Carvins Cove reservoir [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/352735344150F7E77D2BC18B69A22412

Carey, C. C., Wander, H. L., Howard, D. W., Breef-Pilz, A., & Niederlehner, B. R. (2023). Water chemistry time series for Beaverdam reservoir, Carvins Cove reservoir, falling Creek reservoir, Gatewood reservoir, and spring Hollow reservoir in southwestern Virginia, USA 2013–2022 [Dataset]. *Environmental Data Initiative*. https://doi.org/10.6073/PASTA/457120A9DE886A1470C22A01D808AB2D

Catalán, N., Marcé, R., Kothawala, D. N., & Tranvik, L. J. (2016). Organic carbon decomposition rates controlled by water retention time across inland waters. *Nature Geoscience*, *9*(7), 501–504. https://doi.org/10.1038/ngeo2720

Cole, J. J., & Caraco, N. F. (1998). Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF 6. *Limnology & Oceanography*, *43*(4), 647–656. https://doi.org/10.4319/lo.1998.43.4.0647

Coloso, J. J., Cole, J. J., & Pace, M. L. (2011). Difficulty in discerning drivers of lake ecosystem metabolism with high-frequency data. *Ecosystems*, *14*(6), 935–948. https://doi.org/10.1007/s10021-011-9455-5

Doubek, J. P., & Carey, C. C. (2017). Catchment, morphometric, and water quality characteristics differ between reservoirs and naturally formed lakes on a latitudinal gradient in the conterminous United States. *Inland Waters*, *7*(2), 171–180. https://doi.org/10.1080/20442041.2017.1293317

Duka, M. A., Shintani, T., & Yokoyama, K. (2021). Thermal stratification responses of a monomictic reservoir under different seasons and operation schemes. *Science of the Total Environment*, *767*, 144423. https://doi.org/10.1016/j.scitotenv.2020.144423

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., et al. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, *10*(12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression* (3rd ed.). Sage. Retrieved from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Gerling, A. B., Browne, R. G., Gantzer, P. A., Mobley, M. H., Little, J. C., & Carey, C. C. (2014). First report of the successful operation of a side stream supersaturation hypolimnetic oxygenation system in a eutrophic, shallow reservoir. *Water Research*, *67*, 129–143. https://doi.org/10.1016/j.watres.2014.09.002

Gerling, A. B., Munger, Z. W., Doubek, J. P., Hamre, K. D., Gantzer, P. A., Little, J. C., & Carey, C. C. (2016). Whole-catchment manipulations of internal and external loading reveal the sensitivity of a century-old reservoir to hypoxia. *Ecosystems*, *19*(3), 555–571. https://doi.org/10.1007/s10021-015-9951-0

Glibert, P. M., Wilkerson, F. P., Dugdale, R. C., Raven, J. A., Dupont, C. L., Leavitt, P. R., et al. (2016). Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions: Pluses and minuses of NH_4^+ and NO_3. *Limnology & Oceanography*, *61*(1), 165–197. https://doi.org/10.1002/lno.10203

Granato, G. E., Ries III, K. G., & Steeves, P. A. (2017). Compilation of streamflow statistics calculated from daily mean streamflow data collected during water years 1901–2015 for selected U.S. Geological Survey streamgages. In *U.S. Geological Survey open-File Report 2017–1108*. https://doi.org/10.3133/ofr20171108

Gray, E., Mackay, E. B., Elliott, J. A., Folkard, A. M., & Jones, I. D. (2020). Wide-spread inconsistency in estimation of lake mixed depth impacts interpretation of limnological processes. *Water Research*, *168*, 115136. https://doi.org/10.1016/j.watres.2019.115136

Guildford, S. J., Bootsma, H. A., Fee, E. J., Hecky, R. E., & Patterson, G. (2000). Phytoplankton nutrient status and mean water column irradiance in Lakes Malawi and Superior. *Aquatic Ecosystem Health and Management*, *3*(1), 35–45. https://doi.org/10.1080/14634980008656989

Hampton, S. E., Galloway, A. W. E., Powers, S. M., Ozersky, T., Woo, K. H., Batt, R. D., et al. (2017). Ecology under lake ice. *Ecology Letters*, *20*(1), 98–111. https://doi.org/10.1111/ele.12699

Hamre, K. D., Gerling, A. B., Munger, Z. W., Doubek, J. P., McClure, R. P., Cottingham, K. L., & Carey, C. C. (2017). Spatial variation in dinoflagellate recruitment along a reservoir ecosystem continuum. *Journal of Plankton Research*, *39*(4), 715–728. https://doi.org/10.1093/plankt/fbx004

Hanson, P. C., Bade, D. L., Carpenter, S. R., & Kratz, T. K. (2003). Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnology & Oceanography*, *48*(3), 1112–1119. https://doi.org/10.4319/lo.2003.48.3.1112

Hanson, P. C., Carpenter, S. R., Kimura, N., Wu, C., Cornelius, S. P., & Kratz, T. K. (2008). Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. *Limnology and Oceanography: Methods*, *6*(9), 454–465. https://doi.org/10.4319/lom.2008.6.454

Hayes, N. M., Deemer, B. R., Corman, J. R., Razavi, N. R., & Strock, K. E. (2017). Key differences between lakes and reservoirs modify climate signals: A case for a new conceptual model. *Limnology and Oceanography Letters*, *2*(2), 47–62. https://doi.org/10.1002/lol2.10036

Hoellein, T. J., Bruesewitz, D. A., & Richardson, D. C. (2013). Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. *Limnology & Oceanography*, *58*(6), 2089–2100. https://doi.org/10.4319/lo.2013.58.6.2089

Hollander, M., & Wolfe, D. A. (1973). *Nonparametric statistical methods* (pp. 115–120). John Wiley & Sons.

Howard, D. W., Brentrup, J., Richardson, D., Lewis, A., Olsson, F., & Carey, C. (2024). dwh77/FCR_Metab: Metabolism estimates in falling Creek reservoir (v1.1). *Zenodo*. https://doi.org/10.5281/zenodo.11166352

Howard, D. W., Hounshell, A. G., Lofton, M. E., Woelmer, W. M., Hanson, P. C., & Carey, C. C. (2021). Variability in fluorescent dissolved organic matter concentrations across diel to seasonal time scales is driven by water temperature and meteorology in a eutrophic reservoir. *Aquatic Sciences*, *83*(30), 30. https://doi.org/10.1007/s00027-021-00784-w

Hu, Z., Xiao, Q., Yang, J., Xiao, W., Wang, W., Liu, S., & Lee, X. (2015). Temporal dynamics and drivers of ecosystem metabolism in a large subtropical shallow lake (lake Taihu). *International Journal of Environmental Research and Public Health*, *12*(4), 3691–3706. https://doi.org/10.3390/ijerph120403691

Huang, W., Zhang, Z., Li, Z., Leppäranta, M., Arvola, L., Song, S., et al. (2021). Under-ice dissolved oxygen and metabolism dynamics in a shallow lake: The critical role of ice and snow. *Water Resources Research*, *57*(5), e2020WR027990. https://doi.org/10.1029/2020wr027990

Idso, S. B. (1973). On the concept of lake stability. *Limnology & Oceanography*, *18*(4), 681–683. https://doi.org/10.4319/lo.1973.18.4.0681

IPCC. (2022). Climate change 2022: Impacts, adaptation, and vulnerability. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, et al. (Eds.), *Contribution of working Group II to the sixth assessment report of the intergovernmental panel on climate change* (p. 3056). Cambridge University Press. https://doi.org/10.1017/9781009325844

Jane, S. F., Mincer, J. L., Lau, M. P., Lewis, A. S. L., Stetler, J. T., & Rose, K. C. (2023). Longer duration of seasonal stratification contributes to widespread increases in lake hypoxia and anoxia. *Global Change Biology*, *29*(4), 1009–1023. https://doi.org/10.1111/gcb.16525

Jane, S. F., & Rose, K. C. (2018). Carbon quality regulates the temperature dependence of aquatic ecosystem respiration. *Freshwater Biology*, *63*(11), 1407–1419. https://doi.org/10.1111/fwb.13168

Jewson, D. H., Granin, N. G., Zhdanov, A. A., & Gnatovsky, R. Y. (2009). Effect of snow depth on under-ice irradiance and growth of Aulacoseira baicalensis in Lake Baikal. *Aquatic Ecology*, *43*(3), 673–679. https://doi.org/10.1007/s10452-009-9267-2

Klug, J. L., Richardson, D. C., Ewing, H. A., Hargreaves, B. R., Samal, N. R., Vachon, D., et al. (2012). Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. *Environmental Science and Technology*, *46*(21), 11693–11701. https://doi.org/10.1021/es302063v

Ladwig, R., Appling, A. P., Delany, A., Dugan, H. A., Gao, Q., Lottig, N., et al. (2022). Long-term change in metabolism phenology in north temperate lakes. *Limnology & Oceanography*, *67*(7), 1502–1521. https://doi.org/10.1002/lno.12098

Ladwig, R., Hanson, P. C., Dugan, H. A., Carey, C. C., Zhang, Y., Shu, L., et al. (2021). Lake thermal structure drives interannual variability in summer anoxia dynamics in a eutrophic lake over 37 years. *Hydrology and Earth System Sciences*, *25*(2), 1009–1032. https://doi.org/10.5194/hess-25-1009-2021

Lauster, G. H., Hanson, P. C., & Kratz, T. K. (2006). Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(5), 1130–1141. https://doi.org/10.1139/f06-018

Leppäranta, M., Heini, A., Jaatinen, E., & Arvola, L. (2012). The influence of ice season on the physical and ecological conditions in Lake Vanajanselkä, southern Finland. *Water Quality Research Journal*, *47*(3–4), 287–299. https://doi.org/10.2166/wqrjc.2012.003

Lewis, A. S. L., Kim, B. S., Edwards, H. L., Wander, H. L., Garfield, C. M., Murphy, H. E., et al. (2020). Prevalence of phytoplankton limitation by both nitrogen and phosphorus related to nutrient stoichiometry, land use, and primary producer biomass across the northeastern United States. *Inland Waters*, *10*(1), 42–50. https://doi.org/10.1080/20442041.2019.1664233

Lofton, M. E., Howard, D. W., McClure, R. P., Wander, H. L., Woelmer, W. M., Hounshell, A. G., et al. (2022). Experimental thermocline deepening alters vertical distribution and community structure of phytoplankton in a 4-year whole-reservoir manipulation. *Freshwater Biology*, *67*(11), 1903–1924. https://doi.org/10.1111/fwb.13983

Lovett, G. M., Cole, J. J., & Pace, M. L. (2006). Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems*, *9*(1), 152–155. https://doi.org/10.1007/s10021-005-0036-3

Magnuson, J. J., Robertson, D. M., Benson, B. J., Wynne, R. H., Livingstone, D. M., Arai, T., et al. (2000). Historical trends in lake and river ice cover in the Northern Hemisphere. *Science*, *289*(5485), 1743–1746. https://doi.org/10.1126/science.289.5485.1743

McClure, R. P., Lofton, M. E., Chen, S., Krueger, K. M., Little, J. C., & Carey, C. C. (2020). The magnitude and drivers of methane ebullition and diffusion vary on a longitudinal gradient in a small freshwater reservoir. *Journal of Geophysical Research: Biogeosciences*, *125*(3), e2019JG005205. https://doi.org/10.1029/2019jg005205

North, R., Venkiteswaran, J., Silsbe, G., Harrison, J., Hudson, J., Smith, R., et al. (2023). Winter matters: Year-round metabolism in temperate water bodies. *EarthArXiv*. https://doi.org/10.31223/X5RQ1V

Obertegger, U., Obrador, B., & Flaim, G. (2017). Dissolved oxygen dynamics under ice: Three winters of high-frequency data from Lake Tovel. *Italy. Water Resources Research*, *53*(8), 7234–7246. https://doi.org/10.1002/2017WR020599

Odum, H. T. (1956). Primary production in flowing waters. *Limnology & Oceanography*, *1*(2), 102–117. https://doi.org/10.4319/lo.1956.1.2.0102

Ogle, D. H., Doll, J. C., Wheeler, A. P., & Dinno, A. (2023). Fsa: Simple fisheries stock assessment methods. R package version 0.9.5. Retrieved from https://CRAN.R-project.org/package=FSA

Oleksy, I. A., Jones, S. E., & Solomon, C. T. (2022). Hydrologic setting dictates the sensitivity of ecosystem metabolism to climate variability in lakes. *Ecosystems*, *25*(6), 1328–1345. https://doi.org/10.1007/s10021-021-00718-5

Pace, M. L., Buelo, C. D., & Carpenter, S. R. (2021). Phytoplankton biomass, dissolved organic matter, and temperature drive respiration in whole lake nutrient additions. *Limnology & Oceanography*, *66*(6), 2174–2186. https://doi.org/10.1002/lno.11738

Paerl, H. W., Scott, J. T., McCarthy, M. J., Newell, S. E., Gardner, W. S., Havens, K. E., et al. (2016). It takes two to Tango: When and where dual nutrient (N & P) reductions are needed to protect lakes and downstream ecosystems. *Environmental Science & Technology*, *50*(20), 10805–10813. https://doi.org/10.1021/acs.est.6b02575

Palmer, M. A., & Richardson, D. C. (2009). VI.8 provisioning services: A focus on fresh water. In S. A. Levin, S. R. Carpenter, H. C. J. Godfray, A. P. Kinzig, M. Loreau, J. B. Losos, et al. (Eds.), *The princeton guide to ecology* (pp. 625–633). Princeton University Press. https://doi.org/10.1515/9781400833023.625

Park, H., Byeon, M., Shin, Y., & Jung, D. (2009). Sources and spatial and temporal characteristics of organic carbon in two large reservoirs with contrasting hydrologic characteristics. *Water Resources Research*, *45*(11), 2009WR008043. https://doi.org/10.1029/2009WR008043

Pernica, P., North, R. L., & Baulch, H. M. (2017). In the cold light of day: The potential importance of under-ice convective mixed layers to primary producers. *Inland Waters*, *7*(2), 138–150. https://doi.org/10.1080/20442041.2017.1296627

Pierson, D. C., Weyhenmeyer, G. A., Arvola, L., Benson, B., Blenckner, T., Kratz, T., et al. (2011). An automated method to monitor lake ice phenology. *Limnology and Oceanography: Methods*, *9*(2), 74–83. https://doi.org/10.4319/lom.2010.9.0074

Rabaey, J. S., Domine, L. M., Zimmer, K. D., & Cotner, J. B. (2021). Winter oxygen regimes in clear and turbid shallow lakes. *Journal of Geophysical Research: Biogeosciences*, *126*(3), e2020JG006065. https://doi.org/10.1029/2020JG006065

Raven, J. A., Wollenweber, B., & Handley, L. L. (1992). A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. *New Phytologist*, *121*(1), 19–32. https://doi.org/10.1111/j.1469-8137.1992.tb01088.x

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reinl, K. L., Harris, T. D., North, R. L., Almela, P., Berger, S. A., Bizic, M., et al. (2023). Blooms also like it cold. *Limnology and Oceanography Letters*, *8*(4), 546–564. https://doi.org/10.1002/lol2.10316

Richardson, D. C., Carey, C. C., Bruesewitz, D. A., & Weathers, K. C. (2017). Intra- and inter-annual variability in metabolism in an oligotrophic lake. *Aquatic Sciences*, *79*(2), 319–333. https://doi.org/10.1007/s00027-016-0499-7

Rose, K. C., Winslow, L. A., Read, J. S., Read, E. K., Solomon, C. T., Adrian, R., & Hanson, P. C. (2014). Improving the precision of lake ecosystem metabolism estimates by identifying predictors of model uncertainty. *Limnology and Oceanography: Methods*, *12*(5), 303–312. https://doi.org/10.4319/lom.2014.12.303

Sahoo, G. B., Forrest, A. L., Schladow, S. G., Reuter, J. E., Coats, R., & Dettinger, M. (2016). Climate change impacts on lake thermal dynamics and ecosystem vulnerabilities: Climate change impacts. *Limnology & Oceanography*, *61*(2), 496–507. https://doi.org/10.1002/lno.10228

Scordo, F., Lottig, N. R., Fiorenza, J. E., Culpepper, J., Simmons, J., Seitz, C., et al. (2022). Hydroclimate variability affects habitat-specific (open water and littoral) lake metabolism. *Water Resources Research*, *58*(1). https://doi.org/10.1029/2021WR031094

Sharma, S., Blagrave, K., Magnuson, J. J., O'Reilly, C. M., Oliver, S., Batt, R. D., et al. (2019). Widespread loss of lake ice around the Northern Hemisphere in a warming world. *Nature Climate Change*, *9*(3), 227–231. https://doi.org/10.1038/s41558-018-0393-5

Sharma, S., Richardson, D. C., Woolway, R. I., Imrit, M. A., Bouffard, D., Blagrave, K., et al. (2021). Loss of ice cover, shifting phenology, and more extreme events in northern Hemisphere lakes. *Journal of Geophysical Research: Biogeosciences*, *126*(10), 1–12. https://doi.org/10.1029/2021JG006348

Solomon, C. T., Bruesewitz, D. A., Richardson, D. C., Rose, K. C., Van de Bogert, M. C., Hanson, P. C., et al. (2013). Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe. *Limnology & Oceanography*, *58*(3), 849–866. https://doi.org/10.4319/lo.2013.58.3.0849

Song, S., Li, C., Shi, X., Zhao, S., Tian, W., Li, Z., et al. (2019). Under-ice metabolism in a shallow lake in a cold and arid climate. *Freshwater Biology*, *64*(10), 1710–1720. https://doi.org/10.1111/fwb.13363

Twiss, M. R., McKay, R. M. L., Bourbonniere, R. A., Bullerjahn, G. S., Carrick, H. J., Smith, R. E. H., et al. (2012). Diatoms abound in ice-covered Lake Erie: An investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010. *Journal of Great Lakes Research*, *38*(1), 18–30. https://doi.org/10.1016/j.jglr.2011.12.008

Van de Bogert, M. C., Carpenter, S. R., Cole, J. J., & Pace, M. L. (2007). Assessing pelagic and benthic metabolism using free water measurements: Benthic and pelagic metabolism. *Limnology and Oceanography: Methods*, *5*(5), 145–155. https://doi.org/10.4319/lom.2007.5.145

Volponi, S. N., Wander, H. L., Richardson, D. C., Williams, C. J., Bruesewitz, D. A., Arnott, S., et al. (2023). Nutrient function over form: Organic and inorganic nitrogen additions have similar effects on lake phytoplankton nutrient limitation. *Limnology & Oceanography*, *68*(2), 307–321. https://doi.org/10.1002/lno.12270

Ward, N. K., Brentrup, J. A., Richardson, D. C., Weathers, K. C., Hanson, P. C., Hewett, R. J., & Carey, C. C. (2022). Dynamics of the stream – Lake transitional zone affect littoral lake metabolism. *Aquatic Sciences*, *84*(31), 31. https://doi.org/10.1007/s00027-022-00854-7

Wetz, M., Wheeler, P., & Letelier, R. (2004). Light-induced growth of phytoplankton collected during the winter from the benthic boundary layer off Oregon, USA. *Marine Ecology Progress Series*, *280*, 95–104. https://doi.org/10.3354/meps280095

Weyhenmeyer, G. A., Obertegger, U., Rudebeck, H., Jakobsson, E., Jansen, J., Zdorovennova, G., et al. (2022). Towards critical white ice conditions in lakes under global warming. *Nature Communications*, *13*(1), 4974. https://doi.org/10.1038/s41467-022-32633-1

Williamson, T. J., Vanni, M. J., & Renwick, W. H. (2021). Spatial and temporal variability of nutrient dynamics and ecosystem metabolism in a hyper-eutrophic reservoir differ between a wet and dry year. *Ecosystems*, *24*(1), 68–88. https://doi.org/10.1007/s10021-020-00505-8

Winslow, L. A., Read, J., Woolway, R., Brentrup, J., Leach, T., Zwart, J., et al. (2019). rLakeAnalyzer: Lake Physics Tools. R package version 1.11.4.1. Retrieved from https://CRAN.R-project.org/package=rLakeAnalyzer

Winslow, L. A., Zwart, J. A., Batt, R. D., Dugan, H. A., Woolway, R. I., Corman, J. R., et al. (2016). LakeMetabolizer: An R package for estimating lake metabolism from free-water oxygen using diverse statistical models. *Inland Waters*, *6*(4), 622–636. https://doi.org/10.1080/IW-6.4.883

Woolway, R. I., Denfeld, B., Tan, Z., Jansen, J., Weyhenmeyer, G. A., & La Fuente, S. (2022). Winter inverse lake stratification under historic and future climate change. *Limnology and Oceanography Letters*, *7*(4), 302–311. https://doi.org/10.1002/lol2.10231

Woolway, R. I., Sharma, S., Weyhenmeyer, G. A., Debolskiy, A., Golub, M., Mercado-Bettín, D., et al. (2021). Phenological shifts in lake stratification under climate change. *Nature Communications*, *12*(1), 2318. https://doi.org/10.1038/s41467-021-22657-4

Xia, Y., Mitchell, K., Ek, M., Sheffield, J., Cosgrove, B., Wood, E., et al. (2012). Continental-scale water and energy flux analysis and validation for the North American land data assimilation system project phase 2 (NLDAS-2): 1. Intercomparison and application of model products. *Journal of Geophysical Research*, *117*(D3), 2011JD016048. https://doi.org/10.1029/2011JD016048

Yang, N., Li, Z., Wu, Z., Liu, X., Zhang, Y., Sun, T., et al. (2023). Differential effects of nitrate and ammonium on the growth of algae and microcystin production by nitrogen-fixing Nostoc sp. and non-nitrogen-fixing Microcystis aeruginosa. *Water Science and Technology*, *88*(1), 136–150. https://doi.org/10.2166/wst.2023.205

Yvon-Durocher, G., Caffrey, J. M., Cescatti, A., Dossena, M., Giorgio, P. D., Gasol, J. M., et al. (2012). Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature*, *487*(7408), 472–476. https://doi.org/10.1038/nature11205

References From the Supporting Information

Alizadeh, M. J., Kavianpour, M. R., Kamranzad, B., & Etemad-Shahidi, A. (2019). A weibull distribution based technique for downscaling of climatic wind field. *Asia-Pacific J Atmospheric Sciences*, *55*(4), 685–700. https://doi.org/10.1007/s13143-019-00106-z