Variability in ice cover does not affect annual metabolism estimates in a small eutrophic reservoir

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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

Abstract (250 words)

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 six 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 six 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, 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 (200 words):

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 six 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.

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 open-water period vary across lakes (Solomon et al., 2013), within years (Hu et al., 2015; Brentrup et al., 2021), 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 open-water 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 open-water, 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 under-ice metabolism as ice cover and thickness is decreasing on lakes worldwide (Magnuson et al., 2000; Sharma et al., 2021; Weyhenmeyer et al., 2022). However, estimating under-ice 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 six 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 six 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: 1) What is the inter- and intra-annual variability of metabolism in a dimictic reservoir that exhibits intermittent ice conditions in winter? 2) How do estimates of winter metabolism affect annual metabolism estimates? and 3) 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 towards 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 six-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, Section 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 (37.30°N, 79.84°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).

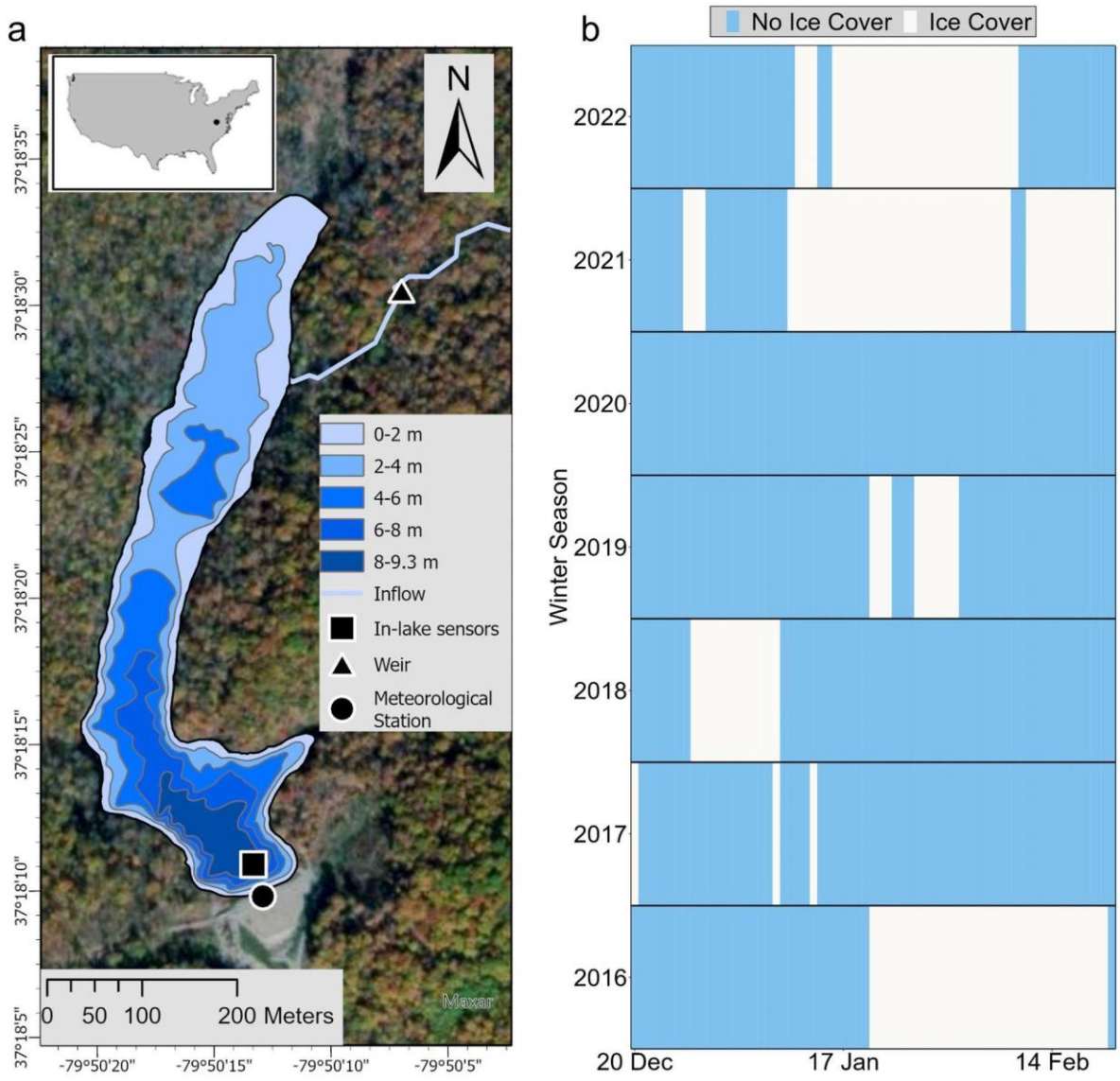

Figure 1. a) Map of Falling Creek Reservoir (FCR) and its primary inflow stream, located in Vinton, Virginia, USA. The inset map depicts the location of the reservoir within the coterminous USA. b) Time series of ice cover duration in FCR in each winter season (operationally defined as 20 December – 22 February, Section 2.5.2). White shading denotes ice cover and light blue shading denotes ice-free (open-water) periods.

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 minutes at 1 m below the surface (Carey, Howard, Gantzer, 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 ten 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 five-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 Supplementary Text S1 and Supplementary Figure 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 to 15 minutes using HOBO thermistors (HOBO Pendant Temperature Data Logger, Bourne, MA, USA; Carey, Howard, Gantzer, 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 minutes (Carey, Breef-Pilz, & Woelmer, 2023). We applied standardized gap-filling procedures to fill the continuous five 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 Supplementary Text S2).

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, 2023a 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-minute resolution to match dissolved oxygen 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 regressions developed between observed meteorology and data from the North American Land Data Assimilation System-2 (NLDAS-2; Xia et al., 2012; Supplementary Text S2, Supplementary Figures S2 and S3). Reservoir inflow discharge was calculated every fifteen 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, 2023b 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, Wander,

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, Howard, et al., 2023). DOC was analyzed using the persulfate catalytic method on a Total Organic Carbon Analyzer (TOCA) from OI Analytical from 2015-2016 (OI Analytical 1010 TOCA with 1051 autosampler, College Station, TX USA) and on a Vario TOC Cube from Elementar from 2016-2022 (vario TOC cube, Elementar Analysensysteme GmbH, Hanau, Germany; Carey, Wander, Howard, 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 (In-Situ 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 ten 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).

2.4 Metabolism model

Daily estimates of GPP and R were calculated using an open-water inverse modeling method that can account for under-ice and open-water 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 dissolved oxygen concentration (dDO/dt) are calculated as:

$$\frac{dDO}{dt} = GPP - R + D \text{ (eqn. 1)}$$

where *D* is atmospheric oxygen flux.

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

$$DO_{t+1} = DO_t + g \times I_t - r + D_t + \gamma_t \ (eqn. 2)$$

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.

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

$$D_t = d_t \times (-k_t) \times (DO_t - S_t) \ / \ z_t \ (eqn. 3)$$

Where k_t is the piston velocity of oxygen calculated using wind speed every ten minutes (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 1 indicates the DO sonde is above z_t and oxygen can exchange with the atmosphere, vs. 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 – 15 minute rates to daily rates of GPP and R reported in mg O_2 L^{-1} day^{-1} (Richardson et al., 2017).

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 open-water and under-ice 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 = 2302 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 one year of data that compared under-ice and open-water 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 groups of seasons, for individual seasons, and for individual years. 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 (Supplementary Text S3, Table S1, Figure S4). 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 hypolimnetic (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 two 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 breaking up 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

375 in R (R Core Team, 2023). Dunn post-hoc tests were used to determine statistical differences
376 between seasonal means when Kruskal-Wallis results were significant using the *FSA* package
377 in R (Ogle et al., 2023). To test the effect of including winter metabolism rates on annual
378 estimates, we used a paired t-test comparing annual estimates of NEP that included and
379 excluded winter rates.
380
381 *2.5.3 Q3: What are the most important drivers of variability in metabolism?*
382 To identify environmental drivers of metabolism, we developed autoregressive (AR)
383 models for GPP, R, and NEP at daily timesteps. We collated daily data for air temperature,
384 precipitation, fluorescent dissolved organic matter, chlorophyll-a, reservoir inflow discharge, TN,
385 nitrate, ammonium, TP, SRP, DOC, Schmidt stability, K_d, and $\bar{E}_{24}$. We then developed
386 correlation matrices to identify collinearity between potential environmental driver variables,
387 defined as when two variables had a Spearman rank correlation of $r > 0.5$. For variables that
388 had $r > 0.5$, we tested which of the correlated variables had a stronger correlation to the
389 metabolism variable of interest based on univariate scatterplots and retained only the variable
390 with a stronger correlation (following McClure et al., 2020).
391 After removing collinear variables, there were seven candidate variables for daily models
392 of NEP (precipitation, TP, DOC, SRP, nitrate, ammonium, $\bar{E}_{24}$), GPP (precipitation, TP, TN,
393 SRP, nitrate, ammonium, $\bar{E}_{24}$), and R (precipitation, TP, DOC, SRP, nitrate, ammonium, $\bar{E}_{24}$).
394 We z-transformed predictors to enable comparison of the magnitude of coefficients in AR
395 models. We then developed global models for each metabolism metric that included an AR1 lag
396 term to account for temporal autocorrelation (Box & Pierce, 1970) and all possible combinations
397 of the non-collinear predictor variables, and ranked models by AICc to determine which models
398 best predicted metabolism rates using the *dredge* function in the *MuMIn* package in R (Bartoń,
399 2022). All analyses were conducted in R version 4.2.3 (R Core Team, 2023), with all code
400 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 six-year study (Figure 2). 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} (Figure 2; 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 ($p = 0.08$).

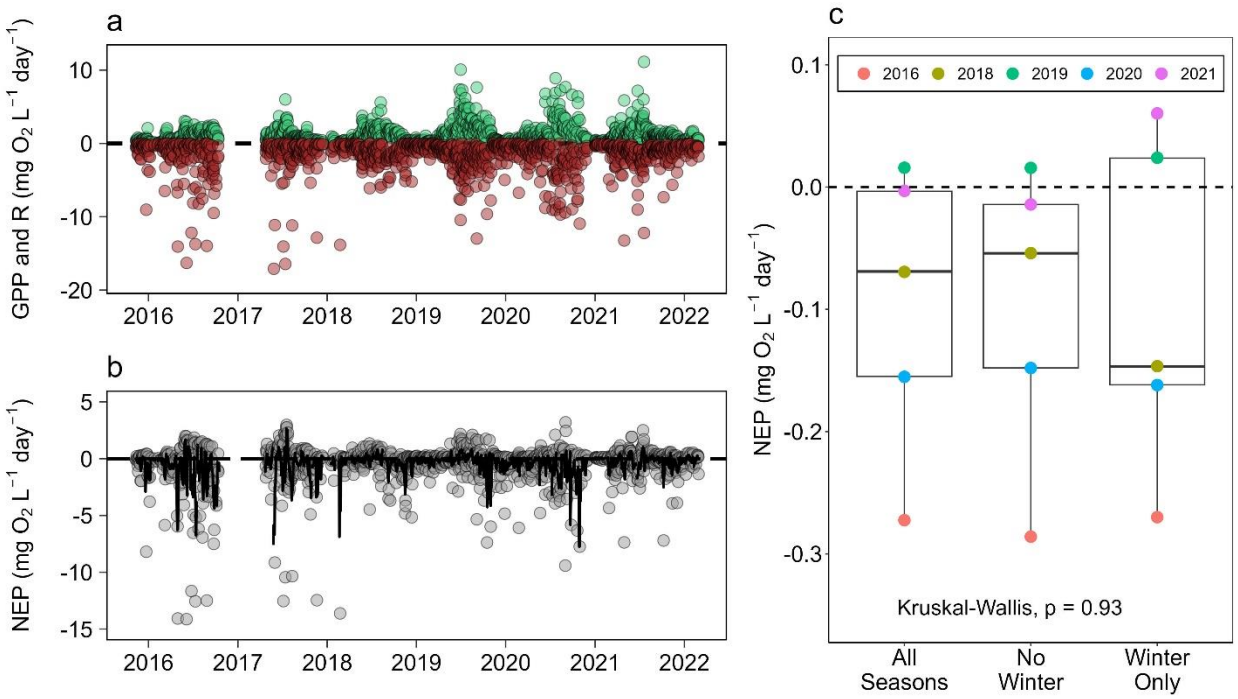

Figure 2. a) Daily estimates of GPP (green points), R (brown points) in FCR from November 2015 through February 2022. b) Daily estimates of NEP (gray points) and seven-day moving average of NEP (black line). c) Boxplots comparing annual median NEP calculated from daily estimates from all seasons; only 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 DO data.

Table 1. Summary table of daily GPP, R, and NEP (mg O_2 L^{-1} day^{-1}) aggregated throughout our study period. Values are medians ± 1 standard deviation for their respective study period. Columns denote different time periods. Ice-on and ice-off are a subset of the winter season. Seasons are operationally defined based on summer stratification and ice cover, as detailed in the Methods.

Metabolism Rate	Full Time Series	Spring	Summer	Fall	Winter		
					All	Ice-on	Ice-off
NEP (mg O_2 L^{-1} day^{-1})	-0.05±1.79	-0.08±2.45	-0.06±1.89	-0.03±1.49	-0.02±0.96	0.03±0.29	-0.09±1.07
GPP (mg O_2 L^{-1} day^{-1})	0.82±1.27	0.34±0.22	1.15±1.35	0.38±0.34	0.26±0.31	0.22±0.42	0.27±0.26
R (mg O_2 L^{-1} day^{-1})	-0.99±2.15	-0.46±2.45	-1.26±2.28	-0.51±1.49	-0.36±1.01	-0.21±0.48	-0.40±1.11

FCR exhibited greater inter-annual variation in NEP than GPP and R throughout our study period (Figure 2). Across the five 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 $H_4 = 16.7$, $p = 0.002$; Supplementary Figure S5, Supplementary Table S2). Median annual GPP and R were not as variable as NEP across years (Supplementary Figure S5), 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} (Supplementary Table S2). 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; Supplementary Table S2).

While NEP was highly variable between years (Supplementary Figure S5), GPP and R exhibited higher variation across seasons (Figure 3), 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; Figure 3a, 3b). GPP and R were greater in the summer than other seasons when aggregated across years (Table 1, Figure 3a, 3b). 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 3c).

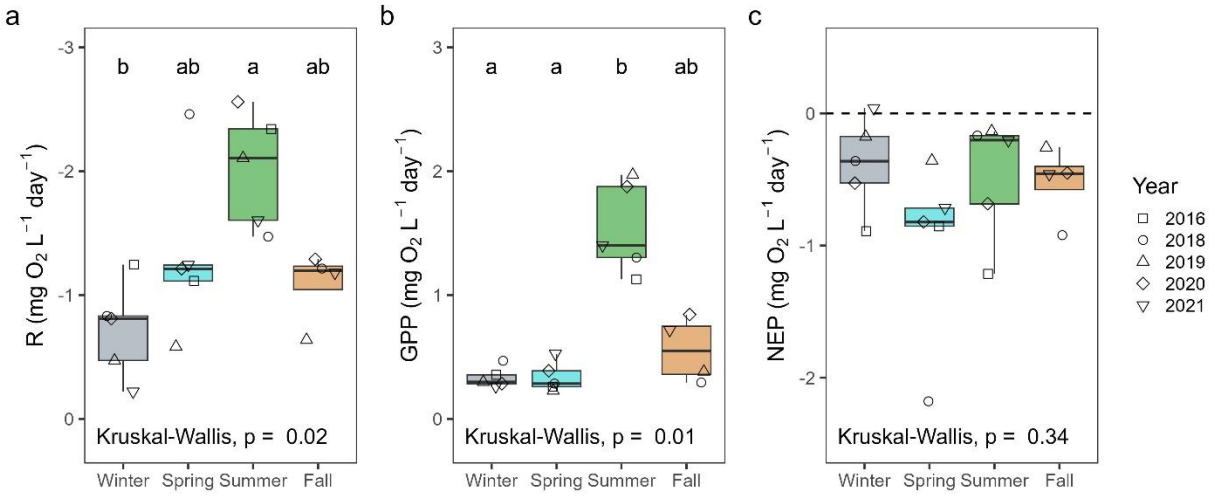

Figure 3. a, b, and c) Boxplots comparing median daily R, GPP, and NEP estimates across seasons per year. 2015, 2017, and 2022 were not included since they did not have estimates for multiple seasons.

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 Supplementary Table S2), 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 Supplementary Table S2). 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 Supplementary Table S2).

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 4). 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 5a). NEP was additionally not significantly different between ice-covered and ice-free days when aggregated across years, though rates were slightly higher under-ice (Wilcoxon test p = 0.07; Figure 5b). R was only significantly different between ice-covered and ice-free days in winter 2016 (lower under ice; Wilcoxon test p = 0.03). GPP was significantly different in 2016 and 2022, but the direction of effect differed between the two years (higher under ice in 2022, lower in 2016; Wilcoxon test p < 0.05, Supplementary Figure S6).

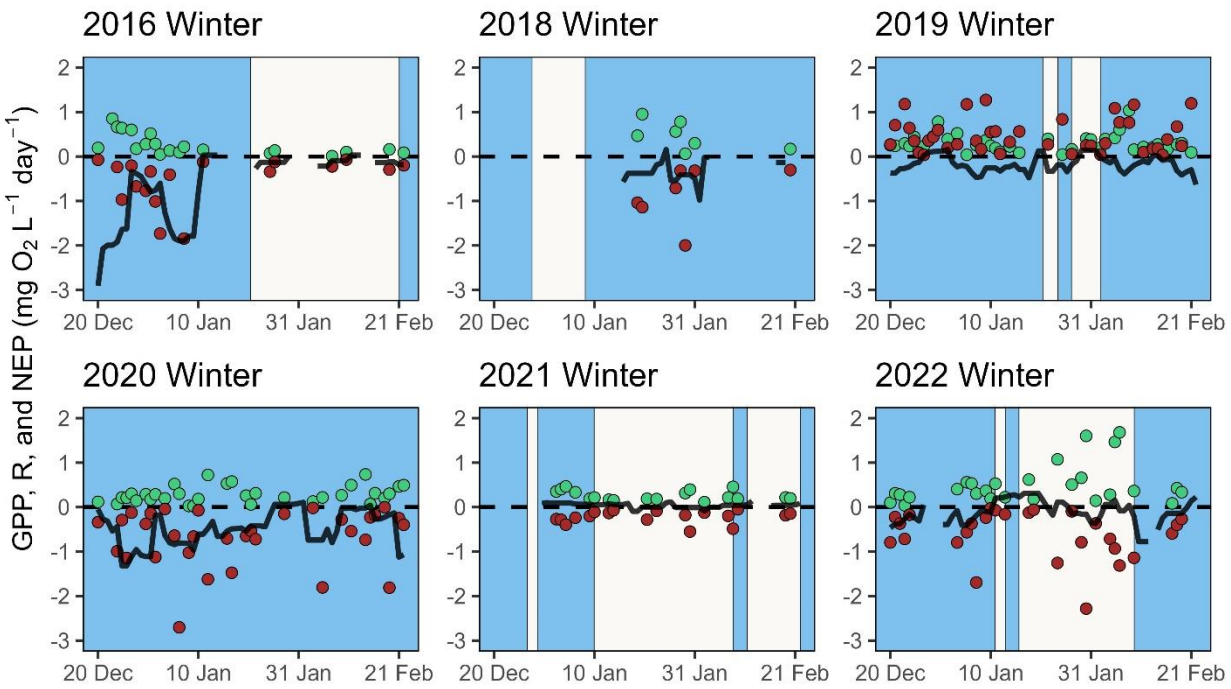

Figure 4. Daily estimates of GPP (green points), R (brown points), and seven-day rolling average of NEP (black line) in different winter seasons. Blue-shaded rectangles denote open-water periods and white rectangles denote periods of ice cover. Metabolism estimates are excluded for winter 2017 due to missing DO data.

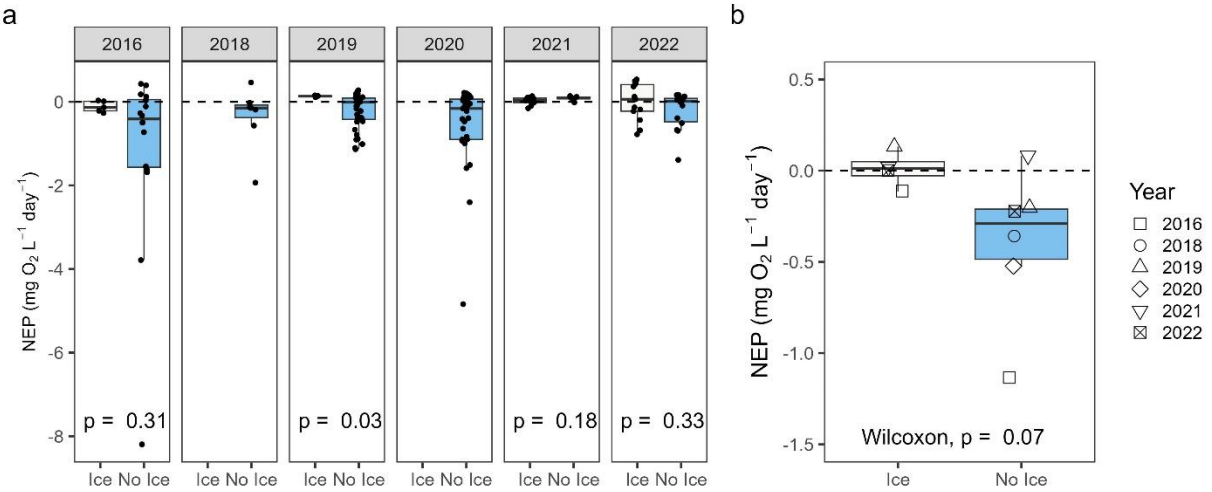

Figure 5. a) Boxplots of daily NEP rates for each winter season comparing days with ice cover (white) and days without ice cover (blue). b) Boxplots comparing ice-covered and ice-free median daily NEP estimates per year. There were no winter NEP estimates in 2018 on days with ice cover, and winter 2020 had no days of ice cover.

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 metabolism metrics, with substantially more variation explained by our candidate environmental predictors for GPP (R^2 = 0.55-0.57), vs. 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 (Supplementary Table S3).

Table 2. Best-fitting (within 2 AICc units of the top model), statistically significant autoregressive models for daily GPP, R, and NEP, listed in descending order. 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.

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

4 Discussion

We observed large variability in metabolism rates throughout six 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 3). NEP was generally higher on ice-covered days than ice-free days (Figure 5b), but this result was only statistically significant in winter 2019 (Figure 5a). GPP and R, but not NEP, differed significantly between seasons (Figure 3), whereas NEP was the only metabolism rate with significant inter-annual variation (Supplementary Figure S5). 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 Under-ice metabolism rates compared to open-water 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 one year (2019), which had intermediate ice coverage relative to the other years (Figure 4, Figure 5a), but it is possible that the duration of ice cover at FCR (0 to 35 days per year) was overall too short to have a substantial effect on annual estimates in our six-year study. Assuming that additional days of ice cover would exhibit the median NEP rates observed under-ice 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 (Supplementary Text S4, Table S4). 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 5). 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 phytoplankton growth under-ice (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 (Supplementary Figure S6).

Winter GPP and R estimates were significantly lower than in summer, but NEP was not significantly different between the seasons (Figure 3). 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 3c). 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 4), 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 (eqn. 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 (Supplementary Table S3), 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 dissolved oxygen and temperature sensors were minimal (Figure 3). 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. 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 under-ice metabolism would benefit from including under-ice light measurements, when feasible.

4.4 What is winter and its role in 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 winter inverse stratification under-ice (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 5). We note that multiple other delineations of seasons (thermal stratification, solar calendars) yielded qualitatively similar metabolism comparisons across seasons (Supplementary Text S3, Figure S4), 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 ^{o}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.

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Open Research

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

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