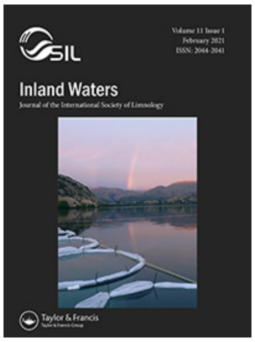

Inland Waters

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tinw20

Under-ice respiration rates shift the annual carbon cycle in the mixed layer of an oligotrophic lake from autotrophy to heterotrophy

Jennifer A. Brentrup, David C. Richardson, Cayelan C. Carey, Nicole K. Ward, Denise A. Bruesewitz & Kathleen C. Weathers

To cite this article: Jennifer A. Brentrup, David C. Richardson, Cayelan C. Carey, Nicole K. Ward, Denise A. Bruesewitz & Kathleen C. Weathers (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, DOI: 10.1080/20442041.2020.1805261

To link to this article: https://doi.org/10.1080/20442041.2020.1805261

INLAND WATERS
2021, VOL. 11, NO. 1, 114–123
https://doi.org/10.1080/20442041.2020.1805261

RESEARCH BRIEF

OPEN ACCESS

Under-ice respiration rates shift the annual carbon cycle in the mixed layer of an oligotrophic lake from autotrophy to heterotrophy

Jennifer A. Brentrup [a], David C. Richardson [b], Cayelan C. Carey [c], Nicole K. Ward [c], Denise A. Bruesewitz [d] and Kathleen C. Weathers [e]

[a]Department of Biological Sciences, Dartmouth College, Hanover, NH, USA; [b]Biology Department, SUNY New Paltz, New Paltz, NY, USA; [c]Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA; [d]Environmental Studies Program, Colby College, Waterville, ME, USA; [e]Cary Institute of Ecosystem Studies, Millbrook, NY, USA

ABSTRACT

Ecosystem metabolism is an integrative measure of the production and respiration of carbon in aquatic ecosystems. However, under-ice regions and mixing periods are infrequently sampled because of logistical challenges and assumptions of low biological activity, resulting in limited understanding of the contribution of winter epilimnetic metabolism to annual carbon cycling. Aquatic ecosystems can emit up to 76% of the carbon they receive from terrestrial landscapes as carbon dioxide to the atmosphere, making them significant contributors to Earth's carbon cycle. Consequently, studying metabolism under ice is especially important given that warmer winters have already shortened ice cover and lengthened ice transitional periods, potentially resulting in greater carbon dioxide emissions. Using a continuous year of epilimnetic high-frequency dissolved oxygen data, we found that gross primary production was low but not absent under ice and increased during the end of the under-ice period. Despite cold water temperatures, under-ice respiration was 1.2 times higher than summer respiration, and ice-on and ice-off periods were important contributors to annual metabolism estimates. On average, under-ice net ecosystem production (NEP) was negative, in contrast to positive NEP for the spring and summer periods. Including winter metabolism estimates flipped annual NEP from autotrophy to heterotrophy, demonstrating that year-round sampling is essential for accurately assessing carbon cycling in lakes.

ARTICLE HISTORY
Received 23 March 2020
Accepted 13 July 2020

KEYWORDS
autotrophy; carbon cycling; ecosystem metabolism; heterotrophy; primary production; winter limnology

Introduction

Over half of the world's lakes are seasonally ice covered (Hampton et al. 2017, Sharma et al. 2019), yet nearly all limnological data, including estimates of carbon (C) cycling, are collected during the ice-free period (Hanson et al. 2008, Staehr et al. 2010, Solomon et al. 2013). The production and decomposition of organic matter, which includes gross primary production (GPP) and respiration (R), still occurs under ice and therefore affects annual net ecosystem production (NEP). However, the magnitude, variability, and contribution of the under-ice period to year-round ecosystem metabolism have not been well studied because of the challenges associated with winter sampling (Block et al. 2018). As the duration of the under-ice period rapidly shrinks (Sharma et al. 2019), understanding the full annual cycle of metabolism, especially the variation in under-ice metabolism and its environmental drivers, is crucial for predicting the role of lakes in C cycling and providing early warning for changes in trophic status (e.g., Richardson et al. 2017).

Historically, temperate lakes were assumed to be dormant under ice because of cold temperatures and decreased light availability that limited biological activity (Scavia and Laird 1987, Simon 1987), with expectations of lower metabolic rates compared to the open-water period. Recent studies suggest more dynamic under-ice ecological interactions (e.g., Bertilsson et al. 2013, Hampton et al. 2017). High GPP rates due to algal blooms have been reported under ice (Twiss et al. 2012, Salmi and Salonen 2016), and winter R rates can exceed those in summer (Karlsson et al. 2013). In Swedish lakes, the carbon dioxide (CO_2) emissions during the week of ice thaw accounted for up to 56% of the annual flux and changed the annual CO_2 budget from a sink to a source (Karlsson et al. 2013).

CONTACT Jennifer A. Brentrup jennifer.a.brentrup@dartmouth.edu Department of Biological Sciences, Dartmouth College, Hanover, NH, USA
Supplemental data for this article can be accessed https://doi.org/10.1080/20442041.2020.1805261.

Continuous, year-round ecosystem metabolism estimates are rare because of the difficulties of sampling and maintaining under-ice sensors throughout the winter, especially the ice-on and ice-off transition periods (Block et al. 2018). These challenges have resulted in many studies based on discrete under-ice sampling events (Welch and Bergmann 1985, Karlsson et al. 2008), which may miss short-term changes in metabolism dynamics. However, automated sensors that collect high-frequency oxygen data year-round can be used to detect changes under ice. Simultaneously collecting high-frequency meteorological and physical data can also help determine any seasonal differences in the drivers of GPP and R that may alter annual metabolism estimates.

The limited number of winter metabolism studies to date suggest lakes tend to be heterotrophic during the winter (Obertegger et al. 2017, Song et al. 2019). However, under-ice metabolism rates are often aggregated into one period, which can obscure R and GPP that may vary among the multiple, distinct under-ice phases characterized by different stratification patterns that affect nutrient upwelling and the distribution of organisms (Kirillin et al. 2012, Bruesewitz et al. 2015). Here, we examined metabolism dynamics during 3 under-ice phases: Phase 1 beginning at ice-on with mixing before inverse stratification has established, Phase 2 representing the inverse stratification period, and Phase 3 corresponding to deeper mixing and loss of inverse stratification prior to ice-off (Bruesewitz et al. 2015).

Using a continuous year-round dataset of daily epilimnetic lake metabolism estimates, we explored the following questions: (1) What are the patterns of under-ice metabolism and how does under-ice NEP compare with summer and annual rates? (2) What is the contribution of the different under-ice phases and mixing transition periods to annual epilimnetic metabolism and the C budget? and (3) How do the environmental correlates with under-ice metabolism compare between the summer stratified and annual periods?

Study site

Located in New Hampshire, USA, Lake Sunapee (43°24′N; 72°2′W) is a dimictic, oligotrophic lake with a surface area of 16.6 km^2, maximum depth of 33.7 m, and residence time of 3.1 yr (Bruesewitz et al. 2015). The catchment is 80% forested with near-shore development. Sunapee has low epilimnetic summer nutrients (TP = 4 – 8 μg L^{-1}, TN = 150 – 200 μg L^{-1}), dissolved organic carbon concentrations (DOC < 2.5 mg L^{-1}), and is seasonally thermally stratified with a maximum thermocline depth of ~7–9 m (Carey et al. 2014, Bruesewitz et al. 2015). Since 1869, ice off on Sunapee was occurring ~1 day earlier each decade (Bruesewitz et al. 2015).

In 2007, the Lake Sunapee Protective Association (LSPA) deployed a monitoring buoy anchored in the lake near Loon Island (43°23′29″N; 72°3′27″W) at 15 m for 466 days (27 Aug 2007 to 5 Dec 2008). An optical dissolved oxygen (DO) sensor (Zebra-Tech D-Opto, Nelson, New Zealand; Supplemental Material) deployed at 1 m, a string of thermistors (Apprise Technology TempLine, MN, USA) at 0.5 m increments from 1 to 4 m and 1 m increments from 4 to 14 m, and meteorological sensors recorded data at 10 min intervals (LSPA et al. 2020). The data for this analysis were curated after Richardson et al. (2017; Supplemental Material).

Methods

Lake-year phenology

We identified seasonal time periods of stratification, mixing, and under-ice phases based on calculated mean daily Schmidt stability using the *rLakeAnalyzer* package (Winslow et al. 2018) and following Bruesewitz et al. (2015; Supplemental Material). Starting in fall 2007, we identified 6 phenological time periods: fall mixing, under-ice Phase 1 (which began on the day of ice-on), Phase 2 (inverse stratification), Phase 3 (which lasted until the day of ice-off), spring mixing, summer stratification, and back to fall mixing for a complete lake year (11 Oct 2007 to 18 Sep 2008; Supplemental Table S1). During winter 2007–2008, Sunapee was ice covered for ~5 months, and the maximum ice depth was <1 m (Bruesewitz et al. 2015).

Metabolism model

We estimated epilimnetic GPP and R rates using inverse modeling to fit daily GPP and R parameters with a maximum likelihood method based on DO concentration, water temperature profiles, photosynthetically active radiation (PAR), and wind speed data (Richardson et al. 2017; Supplemental Material). We followed Richardson et al. (2017) to model metabolism on days with open water, assuming no atmospheric exchange on ice-covered days (6 Dec 2007 to 25 Apr 2008). Daily NEP was calculated as GPP−R for each day with reasonable estimates and adequate model fits. We were able to fit acceptable daily GPP and R parameters for 57% of the entire time series (Supplemental Table S2). To test for differences in NEP among the under-ice, summer stratification, and lake-year time periods, we performed a *t*-test with a Holm correction for 3 comparisons and degrees of freedom corrected for autocorrelation (Burnham and

Anderson 2002). We calculated the percent contribution of each phenology period to epilimnetic GPP and R over the lake year by summing daily interpolated GPP and R for each period and multiplying by the proportion of days in that period.

Estimating carbon production

We converted oxygen (O_2)-based R (mg L^{-1} d^{-1}) to C-based R (mg L^{-1} d^{-1}) using a respiratory oxidation ratio (*OR*), defined as the molar ratio of O_2 oxidized to C during aerobic respiration (Richardson et al. 2013). We used a range of values to represent the respiration of different C sources with different nutrient stoichiometry (1 for terrestrially derived DOC to 1.4 for plankton; Richardson et al. 2013). Similarly, we scaled oxygen-based rates of GPP to C fixed via photosynthesis using the photosynthetic quotient for net primary production (OR_{ab}), defined as the moles of O_2 released per mole of fixed C. OR_{ab} was calculated from a range of values for primary producers that use different nitrogen sources for photosynthesis (1–1.3; Raine 1983). C-based NEP was calculated as the difference between GPP and R as C. We averaged all pairwise combinations of *OR* and OR_{ab} and calculated a loess-smoothed fit for the mean, minimum, and maximum C rate estimates.

Environmental correlates

We examined the effects of 9 meteorological and physical variables on metabolism estimates for the under-ice, summer stratification, and lake-year periods (Supplemental Material). Daily summaries of water temperature, above-lake PAR, wind speed, and Schmidt stability were calculated over a 26 h solar day from 1 h before sunrise to 1 h after sunset (Richardson et al. 2017). Snow depth and precipitation were available as daily sums; snow depth was used for the under-ice period, whereas precipitation was used for the summer stratification period, and both were used for the lake-year period. Other likely environmental drivers of metabolism include under-ice PAR, but we lacked data to include them in this study. Thus, our analysis focused on exploring if any relationships existed between the available environmental correlates and metabolism estimates.

For each environmental variable, we calculated the relationship between each metabolism metric (GPP, R, NEP) as absolute values with time series of *z*-scores for under-ice, summer stratification, and lake-year periods by fitting a regression coefficient (β) as an explanatory variable and modeled the residuals using the *auto.arima* function in the R forecast package, which fits the best ARIMA model based on minimizing Akaike information criteria (AICc) values (Hyndman and Khandakar 2008; Supplemental Material). We calculated whether each β was significantly different from 0 using a one-sample *t*-test and Holm-corrected *p*-values for the 9 variables tested in each time period. We present the variables that had significant relationships with the metabolism metrics (see Supplemental Table S3 for all results). All statistical analyses were performed in R v3.6.3.

Results

Patterns of under-ice and annual metabolism

Epilimnetic GPP and R showed high daily variability year-round, and under-ice metabolic rates were similar and sometimes greater than open-water rates (Fig. 1a). Cyclical changes in GPP and R aligned with the lake mixing and stratification transitions (Fig. 1a–b). Under-ice Phase 1 had the highest mean R, which was 2 times greater than mean summer stratification R (Fig. 1a, Supplemental Table S2). During the under-ice period, DO drawdown occurred from a high of 108% to a low of 93% before DO increased rapidly again as the ice melted (Supplemental Fig. S1). GPP was highest during Phase 1 and fall mixing but low during Phase 2 and Phase 3. During Phase 1 and 3, the water column was mixed and only inversely stratified during Phase 2, with the DO sensor situated below the inverse stratification depth (Fig. 1b). Following spring mixing, the thermocline depth decreased to 4.3 m, after which it steadily increased again to 9.7 m.

Throughout the lake year, Sunapee's epilimnion varied between an atmospheric C sink and source depending on assumptions regarding the C composition (Fig. 1c). If *OR* was assumed to be high (1.4), Sunapee's epilimnion was an atmospheric C sink and autotrophic for the entire lake year, although highly variable in Phase 2. If *OR* was assumed to be low (1), Sunapee was heterotrophic for the majority of the time series, but close to 0 for the spring mixing and early summer stratification period (Fig. 1c). We estimated a positive annual epilimnetic production (as C) of 111 mg L^{-1} by extrapolating the summer stratification period only. However, when we integrated across the entire lake year, the epilimnetic production estimate was reduced to 0.77 mg L^{-1} (Fig. 1c).

Time period contributions

Under-ice Phase 1 GPP and R proportionally contributed the most to total lake year GPP and R

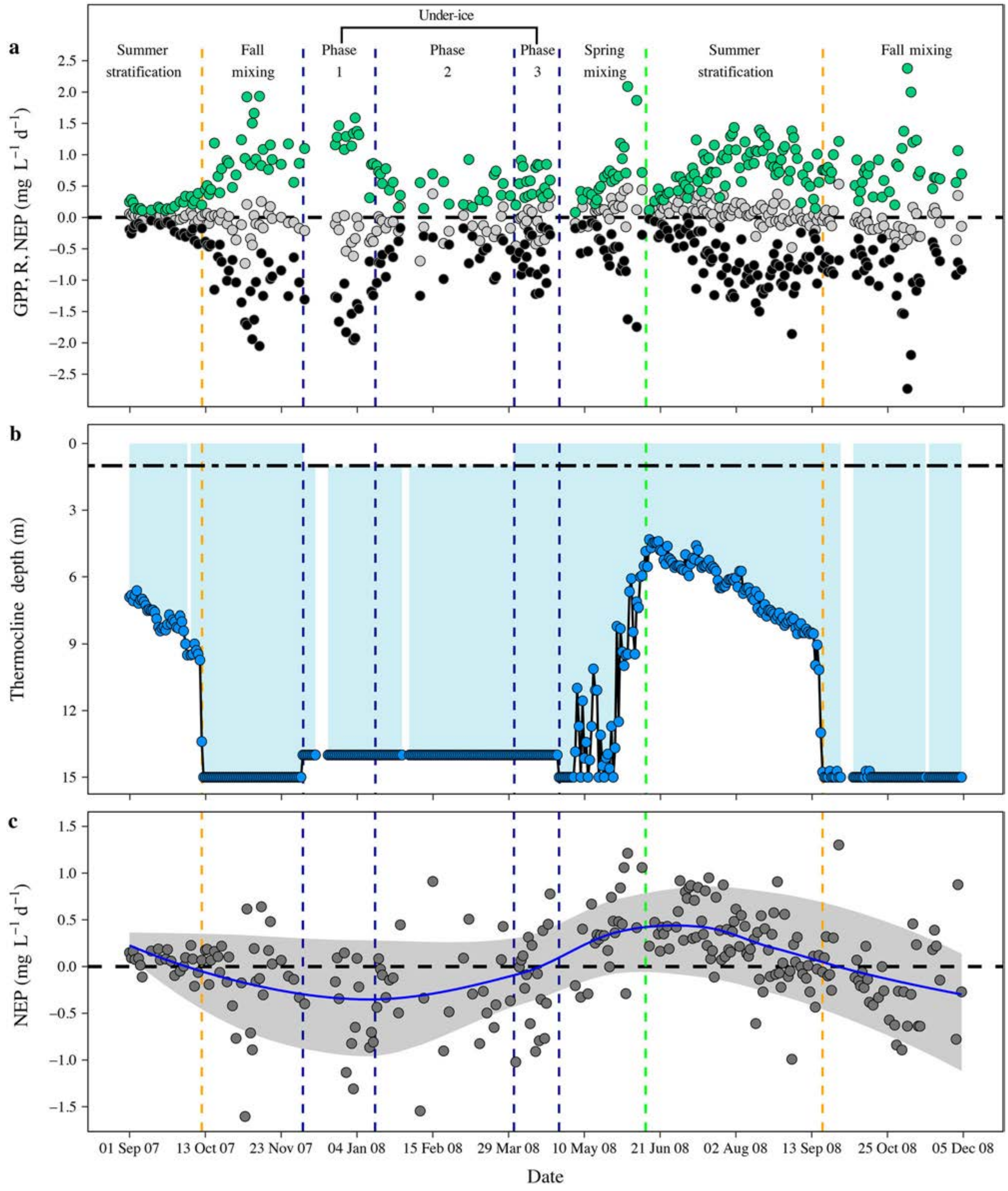

Figure 1. (a) Daily metabolism volumetric estimates (O_2) of gross primary production (GPP = green circles), respiration (R = black circles), and net ecosystem production (NEP = gray circles) for Lake Sunapee, New Hampshire, from 1 September 2007 to 5 December 2008. Dark blue dashed lines correspond to the 3 under-ice phases, orange dashed lines represent the start of the fall mixing periods after summer stratification ends, and green dashed line corresponds to the end of spring mixing and the start of summer stratification. (b) Mean daily thermocline depth estimates over the same time period. Black dashed line corresponds to the depth of the sensor during the study period (1 m), and the light blue shaded region corresponds to the mixed layer depth the epilimnetic sensor is sampling over, which is below the 1 m ice depth in the winter. White breaks are periods of missing data, and the colored dashed lines are the same as (a). (c) Estimates of epilimnetic net ecosystem production (NEP) converted from dissolved oxygen to carbon rates (C). Negative numbers indicate higher rates of carbon breakdown and respiration (heterotrophy) and positive numbers correspond to higher rates of carbon fixation (autotrophy). The blue solid line represents the loess smoothed fit of the mean carbon estimate. The gray shaded region corresponds to the range of the carbon estimates from the loess smoothed fit. Colored dashed lines are the same as (a).

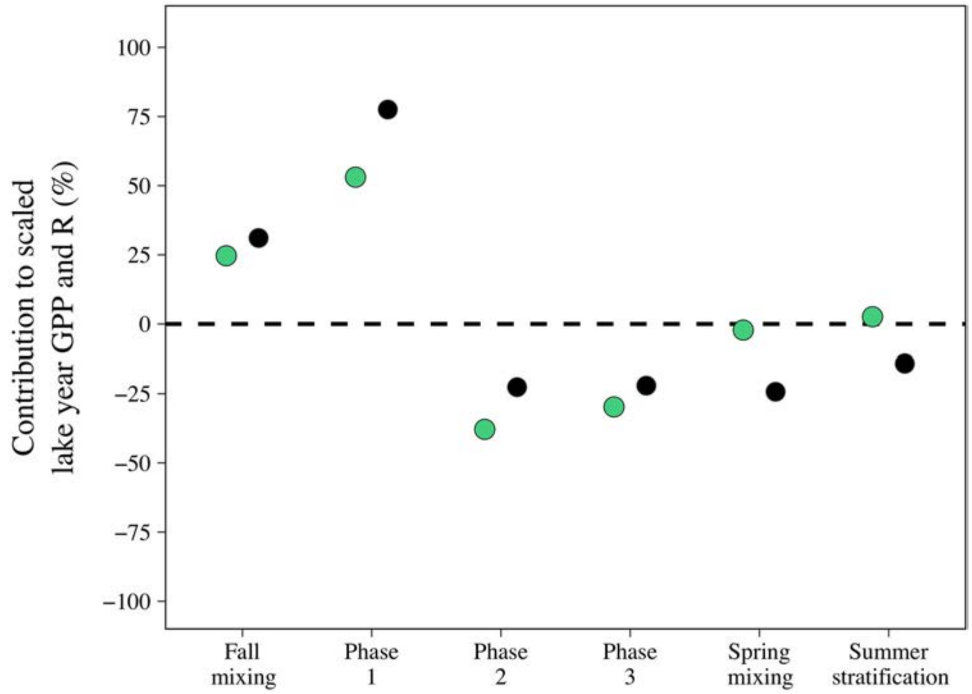

Figure 2. The percent contribution of daily interpolated gross primary production (GPP = green circles) and respiration (R = black circles) for Lake Sunapee, New Hampshire, scaled in each phenology period to the lake year (11 Oct 2007 to 18 Sep 2008). Positive values indicate periods that contributed more to the lake year than expected given the number of days in that period. Negative values indicate periods that contributed less than expected. For colour, see online version.

because of the high daily rates, while GPP in under-ice Phases 2 and 3 proportionally contributed 30–38% less than expected given the number of days in those periods (Fig. 2). The summer period proportionally contributed the least to total lake year R, which coincided with when the lake was autotrophic and strongly stratified. The fall mixing period was the second largest contributor to total lake year GPP and R (Fig. 2).

On average, annual NEP (as O_2) was negative (−0.011 [standard deviation 0.01] mg L^{-1} d^{-1}; Fig. 1c and 3; Supplemental Table S2) but close to zero for the lake year. In the summer stratification period, Sunapee was autotrophic with a positive mean NEP (0.09 [0.02] mg L^{-1} d^{-1}; Fig. 3). During the under-ice period, NEP flipped, and Sunapee was heterotrophic with a negative mean NEP (−0.14 [0.03] mg L^{-1} d^{-1}; Fig. 3). Phase 1 had the lowest mean NEP (−0.26 [0.05] mg L^{-1} d^{-1}), but NEP was higher for the rest of the under-ice phases (Fig. 1c, Supplemental Table S2). NEP was significantly different among the under ice, summer stratification, and entire lake year (*t*-test, $p < 0.05$), and under-ice NEP had a larger range than summer stratification NEP (Fig. 3).

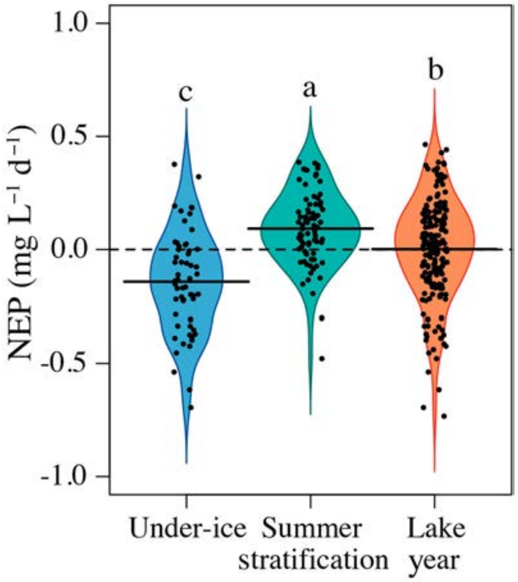

Figure 3. Net ecosystem production (NEP as O_2) for the under-ice (6 Dec 2007 to 25 Apr 2008; $n = 57$ d), summer stratification (13 Jun to 18 Sep 2008; $n = 77$ d), and aggregated lake-year periods (11 Oct 2007 to 18 Sep 2008; $n = 187$ d) for Lake Sunapee, New Hampshire. The black line is the mean value for each time period. Letters indicate significant differences between each of the time periods.

Environmental correlates with lake metabolism

Environmental correlates with the metabolism metrics varied for each time period, except for maximum wind speed and total precipitation, which were negatively correlated with GPP and R for both the summer stratification and lake-year periods (Fig. 4). During the lake year, R was significantly negatively correlated with maximum Schmidt stability (Fig. 4), and we found no significant relationships between GPP and PAR (Supplemental Table S3). The only significant under-ice relationship was the negative correlation between GPP and the coefficient of variation of water temperature (Fig. 4), even though snow depth was hypothesized to be an important correlate by decreasing under-ice light availability and thus GPP (Supplemental Table S3). Water temperature was highly variable during the under-ice and lake-year periods, and R was not significantly correlated with either water temperature metric in any time period (Fig. 4). Warmer water temperatures and a more stable water column during the summer stratification period led to higher NEP and a significant positive correlation, but no significant correlations were found between any of the metrics and NEP for the lake-year or under-ice periods (Fig. 4).

Discussion

Under ice was a dynamic period with high, but variable, daily GPP and R cycles. In Sunapee, epilimnetic metabolism shifted from autotrophic based on only summer estimates to heterotrophic for the lake year (Fig. 1 and 3). All 3 under-ice phases were important contributors to the annual epilimnetic metabolic balance (Fig. 2). Phase 1 accounted for 53% and 78% proportionally higher GPP and R estimates, respectively, than expected, given the high daily rates and short duration relative to the rest of the lake year periods. Over the lake year, GPP and R fluctuated seasonally, closely following the phenology of water column mixing and stratification periods (Fig. 1). Accounting for an entire lake year, the mean C production estimate was close to 0, whereas if C fixation was calculated over just the typical open-water period, Sunapee's epilimnion would seem to be a strong C sink (Fig. 1c). Therefore, studies that focus

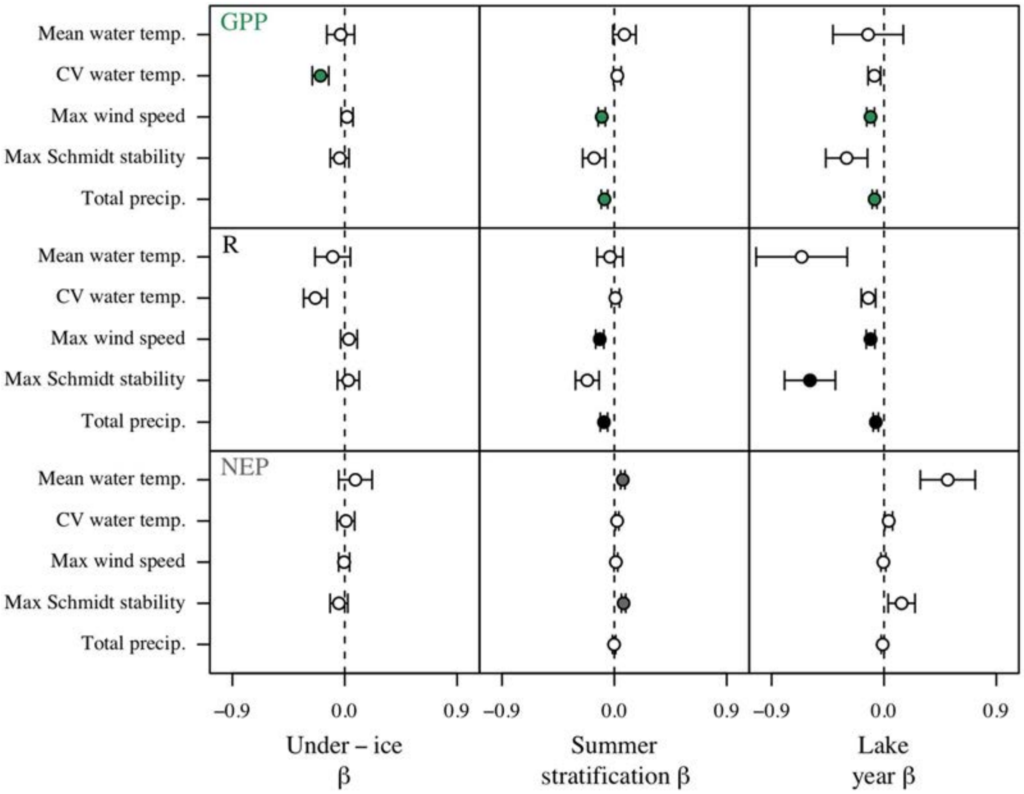

Figure 4. Significant slope coefficients (β) for the relationship between gross primary production (GPP), respiration (R), net ecosystem production (NEP), and environmental variables for the under-ice, summer stratification, and lake-year periods in Lake Sunapee, New Hampshire. The environmental variables shown include solar day mean and coefficient of variation (CV) of epilimnetic water temperature, maximum wind speed, maximum Schmidt stability, and total precipitation (summer stratification and lake year only). Total daily snow depth (under ice and lake year only) and summed daily PAR were tested but were not significant (Supplemental Material). Filled circles represent slope coefficients significantly different from 0 (green = GPP, black = R, gray = NEP). For colour, see online version.

on open-water metabolism (e.g., Solomon et al. 2013) may miss intra annual dynamics and overestimate the magnitude of epilimnetic autotrophy in oligotrophic lakes.

During the under-ice phases, the high GPP may have been due to the unique habitat conditions ice cover on lakes creates by acting as a barrier that prevents wind-driven mixing, allowing some light penetration and providing a substrate on which phytoplankton can grow (Hampton et al. 2017). Sunapee is a large lake with a long fetch that can mix phytoplankton out of the photic zone during open-water periods; however, for the under-ice period, water temperature variability was negatively correlated with GPP, suggesting that ice cover may have created a stable surface layer that facilitated phytoplankton growth (Fig. 4). In addition, low snowfall at the beginning of the winter may have led to higher light availability under the ice than later in the winter (Bruesewitz et al. 2015), potentially explaining the high GPP in Phase 1. Further, zooplankton grazing rates are typically low under-ice and may contribute to phytoplankton blooms, and thus high GPP (Twiss et al. 2012, Salmi and Salonen 2016, Hampton et al. 2017). However, we were unable to quantitatively explore under-ice light availability and zooplankton grazing here but recommend their inclusion in future work.

Our data contribute to the recent evidence that winter R is often higher than previously assumed (Denfeld et al. 2018). Although R should slow with colder water temperatures (Yvon-Durocher et al. 2012), Phase 1 had some of the highest daily R observed during the year. Internal nutrient loading during fall mixing likely led to increased microbial growth and R, even as ice formed (Bertilsson et al. 2013). Under-ice R was double summer R, indicating that despite cold water temperatures, microbes may still be highly active during winter (MacIntyre et al. 2018). We chose not to apply the common 20 °C correction to standardize GPP and R (Solomon et al. 2013, Richardson et al. 2017) because the scaling relationship may not hold at water temperatures close to freezing. The relatively high under-ice R is consistent with studies documenting large CO_2 fluxes following ice-off due to CO_2 accumulation trapped under ice from winter R (Striegl and Michmerhuizen 1998, Baehr and DeGrandpre 2004, Karlsson et al. 2013, Denfeld et al. 2015). The continuous under-ice data indicated that after Phase 1, R did not continue to increase as the winter progressed, possibly because of lower availability of high-quality DOM and a lack of external, lateral CO_2 inputs (Denfeld et al. 2015, 2018). An alternative mechanism that could have led to lower DO and high R under-ice may have been nitrification, which can be an important process driving under-ice oxygen consumption (Knowles and Lean 1987, Powers et al. 2017). However, ammmonium (NH_4^+-N) and nitrate (NO_3^--N) concentrations are markedly low in Sunapee (<10 µg L^{-1}; Ward et al. 2020), so under-ice nitrification rates are most likely low. Linking metabolism estimates with nitrification and methane oxidation rates, CO_2, and DOM quality measurements could better disentangle the potential mechanisms for under-ice O_2 drawdown and CO_2 accumulation.

Despite a lack of under-ice metabolism research, other studies have examined just DO or CO_2 concentration and observed significant declines in DO and increases in CO_2 under ice, indicating that lakes are generally heterotrophic during the winter, and CO_2 supersaturation in boreal lakes can be larger in winter than in other seasons (Welch and Bergmann 1985, Striegl and Michmerhuizen 1998, Striegl et al. 2001, Kortelainen et al. 2006, Karlsson et al. 2008). The epilimnetic DO consumption rates under ice were low and variable in Sunapee but similar to epilimnetic DO changes in another large, oligotrophic lake (Obertegger et al. 2017). The largest decrease of 0.054 mg L^{-1} d^{-1} occurred in Phase 3 (Supplemental Fig. S1), which was lower than the typical range of DO consumption rates 0.1–10 mg L^{-1} d^{-1} (Kirillin et al. 2012). Compared to winter R estimates from DIC measurements, Sunapee winter R was higher than winter R in a shallow Swedish lake and a range of Canadian lakes (Welch and Bergmann 1985, Karlsson et al. 2008).

Sunapee cycled from autotrophy to heterotrophy and back again during the lake year, and the metabolism shifts happened with the breakdown and formation of water column stratification. For the summer stratification period, GPP and R were negatively correlated with maximum wind speed and precipitation, highlighting that storms can decrease water column stability and light availability, and thus production (Fig. 4; Klug et al. 2012). The coupling of metabolism and stability indicates that stratification could be affecting metabolism drivers such as nutrient availability, DOC quality, and phytoplankton biomass, but we lacked fine-scale data on these variables to determine their importance. The differences in the environmental correlates between the time periods indicate that different processes influence metabolism under-ice compared to summer stratification, so further research on seasonal drivers will improve predictions for changes in annual metabolism dynamics.

Throughout the lake year, R and GPP were generally closely linked, indicating reliance of R on autochthonous C sources (Richardson et al. 2017), but we acknowledge the correlation between GPP and R could be an artifact of our model choice (Honti and Istvanovics 2019), and additional data are needed to test this hypothesis. We also observed periods when GPP exceeded R during summer stratification and spring mixing, suggesting excess autotrophic production was transported out of the epilimnion, settling into the sediments before it could be respired. By contrast, when R exceeded GPP, allochthonous DOC or old algal C could have supplemented autotrophic production (Klug et al. 2012, Richardson et al. 2017). Daily GPP:R was <1 for all of the under-ice phases and fall mixing periods, corresponding to times with low light availability and high terrestrial C loading from leaf fall or benthic habitats. Storm-driven or seasonal loading of high quality allochthonous DOC could also facilitate R exceeding GPP (Hanson et al. 2015).

We estimated annual variability in ecosystem metabolism at one epilimnetic site; however, vertical (Obrador et al. 2014, Giling et al. 2017) and additional spatial metabolism estimates (Van de Bogert et al. 2012) can provide a more complete understanding of overall lake C cycling. Metabolism estimates from a single epilimnetic sensor in one location may underestimate whole-lake metabolism in clear lakes when the water column is stratified, but during the under-ice and summer stratified periods an epilimnetic sensor captures the mixed layer of the lake where the majority of the photic zone is located and photosynthesis can occur. Obrador et al. (2014) found that the majority of production (79–100%) and respiration (54–96%) in lakes occurs in the epilimnion, and GPP decreases with depth. Thus, mixed-layer metabolism estimates can be a reasonable proxy for whether a lake is autotrophic or heterotrophic (e.g., Hanson et al. 2008, Staehr et al. 2010, Solomon et al. 2013). In summer, the hypolimnion of Lake Sunapee is likely heterotrophic, so NEP would potentially be lower if hypolimnetic metabolism estimates were included.

Our findings support recent examples illustrating that under ice is an important period in lake ecosystems (Hampton et al. 2017, Obertegger et al. 2017, Song et al. 2019). A shortage of winter metabolism estimates biases our understanding of seasonal dynamics toward the ice-free and, more specifically, summer stratification period (Stanley et al. 2019). Based on summer stratification metabolic estimates, Richardson et al. (2017) found mean epilimnetic NEP in Sunapee from 2008 to 2013 was shifting toward heterotrophy, but using a continuous year-round dataset, we found on an annual basis that the mixed layer may have already been heterotrophic. Year-round, continuous, high-frequency estimates of annual ecosystem metabolism are essential to make robust conclusions about carbon cycling in lakes.

Acknowledgements

We thank the Lake Sunapee Protective Association (LSPA), especially June and Peter Fichter, John Merriman, and Robert Wood, for building and maintaining the buoy, sensors, and data, and Bethel Steele for data assistance. We would also like to thank Dr. Pauliina Salmi and Dr. Michael Pace for their helpful reviews that improved this manuscript. This work was supported by the Dartmouth College Biological Sciences Department and Ecology, Evolution, Environment and Society program, Global Lake Ecological Observatory Network, LSPA, the Frey Foundation; and the National Science Foundation under Grant ICER-1517823, DEB-175639, CNS-1737424, EF-1137327, and NSF-1851436. KCW facilitated the collection of the buoy data. CCC and DCR conceived the study questions. DCR, CCC, DAB, and JAB curated the level 0 data. JAB, DCR, and NKW led the data analysis; JAB wrote the manuscript with help from DCR, CCC, and NKW, and all authors edited the manuscript. The authors declare no conflicts of interest.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Department of Biological Sciences Dartmouth College and Ecology, Evolution, Environment and Society program, Global Lake Ecological Observatory Network, LSPA, the Frey Foundation; and the National Science Foundation under Grant ICER-1517823, DEB-175639, CNS-1737424, EF-1137327, and NSF-1851436. KCW facilitated the collection of the buoy data. CCC and DCR conceived the study questions. DCR, CCC, DAB, and JAB curated the level 0 data. JAB, DCR, and NKW led the data analysis; JAB wrote the manuscript with help from DCR, CCC, and NKW, and all authors edited the manuscript.

ORCID

Jennifer A. Brentrup http://orcid.org/0000-0002-4818-7762
David C. Richardson http://orcid.org/0000-0001-9374-9624
Cayelan C. Carey http://orcid.org/0000-0001-8835-4476
Nicole K. Ward http://orcid.org/0000-0001-7549-0153
Denise A. Bruesewitz http://orcid.org/0000-0001-6108-5181
Kathleen C. Weathers http://orcid.org/0000-0002-3575-6508

References

Baehr MM, DeGrandpre MD. 2004. In situ pCO_2 and O_2 measurements in a lake during turnover and stratification: observations and modeling. Limnol Oceanogr. 49(2):330–340.

Bertilsson S, Burgin A, Carey CC, Fey SB, Grossart H-P, Grubisic LM, Jones ID, Kirillin G, Lennon JT, Shade A, et al. 2013. The under-ice microbiome of seasonally frozen lakes. Limnol Oceanogr. 58(6):1998–2012.

Block BD, Denfeld BA, Stockwell JD, Flaim G, Grossart HPF, Knoll LB, Maier DB, North RL, Rautio M, Rusak JA, et al. 2018. The unique methodological challenges of winter limnology. Limnol Oceanogr-Meth. 243(1):95–116.

Bruesewitz DA, Carey CC, Richardson DC, Weathers KC. 2015. Under-ice thermal stratification dynamics of a large, deep lake revealed by high-frequency data. Limnol Oceanogr. 60(2):347–359.

Burnham KP, Anderson DR. 2002. Model selection and multimodal inference: a practical information-theoretic approach, 2nd ed. New York (NY): Springer.

Carey CC, Weathers KC, Ewing HA, Greer ML, Cottingham KL. 2014. Spatial and temporal variability in recruitment of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic lake. Freshwater Sci. 33(2):577–592.

Denfeld BA, Klaus M, Laudon H, Sponseller RA, Karlsson J. 2018. Carbon dioxide and methane dynamics in a small Boreal lake during winter and spring melt events. J Geophys Res-Biogeosci. 123(8):2527–2540.

Denfeld BA, Wallin MB, Sahlée E, Sobek S, Kokic J, Chmiel HE, Weyhenmeyer GA. 2015. Temporal and spatial carbon dioxide concentration patterns in a small boreal lake in relation to ice-cover dynamics. Boreal Env Res. 20:679–692.

Giling DP, Staehr PA, Grossart HP, Andersen MR, Boehrer B, Escot C, Evrendilek F, Gómez-Gener L, Honti M, Jones ID, et al. 2017. Delving deeper: metabolic processes in the metalimnion of stratified lakes. Limnol Oceanogr. 62(3):1288–1306.

Hampton SE, Galloway AWE, Powers SM, Ozersky T, Woo KH, Batt RD, Labou SG, O'Reilly CM, Sharma S, Lottig NR, et al. 2017. Ecology under lake ice. Ecol Lett. 20:98–111.

Hanson PC, Carpenter SR, Kimura N, Wu C, Cornelius SP, Kratz TK. 2008. Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. Limnol Oceanogr Meth. 6(9):454–465.

Hanson PC, Pace ML, Carpenter SR, Cole JJ, Stanley EH. 2015. Integrating landscape carbon cycling: research needs for resolving organic carbon budgets of lakes. Ecosystems. 18:363–375.

Honti M, Istvanovics V. 2019. Error propagation during inverse modeling leads to spurious correlations and misinterpretation of lake metabolism. Limnol Oceanogr Meth. 17:17–24.

Hyndman RJ, Khandakar Y. 2008. Automatic time series forecasting: the forecast package for R. J Stat Softw. 27(3):1–22.

Karlsson J, Ask J, Jansson M. 2008. Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake. Limnol Oceanogr. 53(3):948–954.

Karlsson J, Giesler R, Persson J, Lundin E. 2013. High emission of carbon dioxide and methane during ice thaw in high latitude lakes. Geophys Res Lett. 40(6):1123–1127.

Kirillin G, Leppäranta M, Terzhevik A, Granin N, Bernhardt J, Engelhardt C, Efremova T, Golosov S, Palshin N, Sherstyankin P, et al. 2012. Physics of seasonally ice-covered lakes: a review. Aquat Sci. 74(4):659–682.

Klug JL, Richardson DC, Ewing HA, Hargreaves BR, Samal NR, Vachon D, Pierson DC, Lindsey AM, O'Donnell DM, Effler SW, et al. 2012. Ecosystem effects of a tropical cyclone on a network of lakes in Northeastern North America. Environ Sci Technol. 46(21):11693–11701.

Knowles R, Lean DRS. 1987. Nitrification: a significant cause of oxygen depletion under winter Ice. Can J Fish Aquat Sci. 44:743–749.

Kortelainen P, Rantakari M, Huttunen JT, Mattsson T, Alm J, Juutinen S, Larmola T, Silvola J, Martikainen PJ. 2006. Sediment respiration and lake trophic state are important predictors of large CO_2 evasion from small boreal lakes. Global Change Biol. 12:1554–1567.

LSPA, Weathers KC, Brentrup JA, Richardson DC, Carey CC, Ward NK, Bruesewitz, DA. 2020. Data from: Ecosystem metabolism estimates from Lake Sunapee, NH, USA and meteorological driver data at the Newport, NH, USA NOAA NCDC weather station from August 2007–December 2008 [dataset]. Environmental Data Initiative. [accessed 2020 Oct 29]. https://doi.org/10.6073/pasta/d1c9e809bec3620c4f89080dc6b8bac8

MacIntyre S, Cortés A, Sadro S. 2018. Sediment respiration drives circulation and production of CO_2 in ice-covered Alaskan Arctic lakes. Limnol Oceanogr. 3:302–310.

Obertegger U, Obrador B, Flaim G. 2017. Dissolved oxygen dynamics under ice: three winters of high-frequency data from Lake Tovel, Italy. Water Resour Res. 53(8):7234–7246.

Obrador B, Staehr PA, Christensen JPC. 2014. Vertical patterns of metabolism in three contrasting stratified lakes. Limnol Oceanogr. 59(4):1228–1240.

Powers SM, Baulch HM, Hampton SE, Labou SG, Lottig NR, Stanley EH. 2017. Nitrification contributes to winter oxygen depletion in seasonally frozen forested lakes. Biogeochemistry. 136:119–129.

Raine RCT. 1983. The effect of nitrogen supply on photosynthetic quotient of natural phytoplankton assemblages. Bot Mar. 26:417–423.

Richardson DC, Carey CC, Bruesewitz DA, Weathers KC. 2017. Intra- and inter-annual variability in metabolism in an oligotrophic lake. Aquat Sci. 79(2):319–333.

Richardson DC, Newbold JD, Aufdenkampe AK, Taylor PG, Kaplan LA. 2013. Measuring heterotrophic respiration rates of suspended particulate organic carbon from stream ecosystems. Limnol Oceanogr. 11(5):247–261.

Salmi P, Salonen K. 2016. Regular build-up of the spring phytoplankton maximum before ice-break in a boreal lake. Limnol Oceanogr. 61(1):240–253.

Scavia D, Laird GA. 1987. Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol Oceanogr. 32(5):1017–1033.

Sharma S, Blagrave K, Magnuson JJ, O'Reilly CM, Oliver S, Batt RD, Magee MR, Straile D, Weyhenmeyer GA, Winslow L, et al. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nat Clim Change. 9:227–231.

Simon M. 1987. Biomass and production of small and large free-living and attached bacteria in Lake Constance. Limnol Oceanogr. 32(3):591–607.

Solomon CT, Bruesewitz DA, Richardson DC, Rose KC, Van de Bogert MC, Hanson PC, Kratz TK, Larget B, Adrian R, Babin BL, et al. 2013. Ecosystem respiration: drivers of daily variability and background respiration in lakes around the globe. Limnol Oceanogr. 58(3):849–866.

Song S, Li C, Shi X, Zhao S, Tian W, Li Z, Bai Y, Cao X, Wang Q, Huotari J, et al. 2019. Under-ice metabolism in a shallow lake in a cold and arid climate. Freshwater Biol. 64 (10):1710–1720.

Staehr PA, Sand-Jensen K, Raun AL, Nilsson B, Kidmose J. 2010. Drivers of metabolism and net heterotrophy in contrasting lakes. Limnol Oceanogr. 55(2):817–830.

Stanley EH, Collins SM, Lottig NR, Oliver SK, Webster KE, Cheruvelil KS, Soranno PA. 2019. Biases in lake water quality sampling and implications for macroscale research. Limnol Oceanogr. 64(4):1572–1585.

Striegl RG, Kortelainen P, Chanton JP, Wickland KP, Bugna GC, Rantakari M. 2001. Carbon dioxide partial pressure and ^{13}C content of north temperate and boreal lakes at spring ice melt. Limnol Oceanogr. 46:941–945.

Striegl RG, Michmerhuizen CM. 1998. Hydrologic influence on methane and carbon dioxide dynamics at two north-central Minnesota lakes. Limnol Oceanogr. 43(7):1519–1529.

Twiss MR, McKay RML, Bourbonniere RA, Bullerjahn GS, Carrick HJ, Smith REH, Winter JG, D'souza NA, Furey PC, Lashaway AR, 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. J Great Lakes Res. 38(1):18–30.

Van de Bogert MC, Bade DL, Carpenter SR, Cole JJ, Pace ML, Hanson PC, Langman OC. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol Oceanogr. 57(6):1689–1700.

Ward NK, Steele BG, Weathers KC, Cottingham KL, Ewing HA, Hanson PC, Carey CC. 2020. Differential responses of maximum versus median chlorophyll-a to air temperature and nutrient loads in an oligotrophic lake over 31 years. Water Resour Res. 56(7):e2020WR027296.

Welch HE, Bergmann MA. 1985. Winter respiration of lakes at Saqvaqjuac, N.W.T. Can J Fish Aquat Sci. 42 (3):521–528.

Winslow LA, Read JS, Woolway R, Brentrup JA, Leach TH, Zwart JA, Albers S, Collinge D. 2018. rLakeAnalyzer: Lake Physics Tools. R Package version 1.11.4.

Yvon-Durocher G, Caffrey JM, Cescatti A, Dossena M, del Giorgio P, Gasol JM, Montoya JM, Pumpanen J, Staehr PA, Trimmer M, et al. 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature. 487:472–476.