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Difficulty in Discerning Drivers of Lake Ecosystem Metabolism with High-Frequency Data

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Abstract

High-frequency measurements are increasingly available and used to model ecosystem processes. This growing capability provides the opportunity to resolve key drivers of ecosystem processes at a variety of scales. We use a unique series of high-frequency measures of potential predictors to analyze daily variation in rates of gross primary production (GPP), respiration (R), and net ecosystem production (NEP = GPP − R) for two north temperate lakes. Wind speed, temperature, light, precipitation, mixed layer depth, water column stability, chlorophyll *a*, chromophoric dissolved organic matter (CDOM), and zooplankton biomass were measured at daily or higher-frequency intervals over two summer seasons. We hypothesized that light, chlorophyll *a*, and zooplankton biomass would be strongly related to variability in GPP. We also hypothesized that chlorophyll *a*, CDOM, and temperature would be most strongly related to variability in R, whereas NEP would be related to variation in chlorophyll *a* and CDOM. Consistent with our hypotheses, chlorophyll *a* was among the most important drivers of GPP, R, and NEP in these systems. However, multiple regression models did not necessarily include the other variables we hypothesized as most important. Despite the large number of potential predictor variables, substantial variance remained unexplained and models were inconsistent between years and between lakes. Drivers of GPP, R, and NEP were difficult to resolve at daily time scales where strong seasonal dynamics were absent. More complex models with greater integration of physical processes are needed to better identify the underlying drivers of short-term variability of ecosystem processes in lakes and other systems.

Key words: lake metabolism; gross primary production; ecosystem respiration; net ecosystem production; chromophoric dissolved organic matter; high-frequency data; ecosystem drivers; multiple regression.

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Introduction

Ecosystem properties are increasingly subject to high-frequency measurement. For example, the application of eddy correlation methods allows calculation of net ecosystem gas exchange for terrestrial ecosystems (Lasslop and others 2010) and more recently benthic habitats in aquatic ecosystems (Berg and others 2003). The power to monitor

ecosystem processes using high-frequency methods is likely to grow as new sensors of increasing sophistication and portability become available (Porter and others 2009). A variety of international, national, and regional programs are being implemented to provide high-frequency measures over large scales of various environmental and ecological processes (for example, Hanson 2008; Keller and others 2008).

Even though ecosystem processes like primary production and respiration can be estimated at high frequency, and key drivers of these processes are understood in most systems, it is unclear how or whether these drivers explain the substantial within system variation observed at a variety of temporal scales. Here, we investigate how well we can model ecosystem metabolism with independent drivers at daily time scales within a season where changes in temperature and biomass are small. We examine a pair of lake ecosystems where we have routinely measured high-frequency diel dissolved oxygen (DO) dynamics to derive daily estimates of gross primary production (GPP), ecosystem respiration (R), and the balance between these processes known as net ecosystem production (NEP; NEP = GPP − R) (Cole and others 2000; Carpenter and others 2005; Coloso and others 2008).

Prior studies of daily, free-water estimates of GPP, R, and NEP (collectively ''lake metabolism'') in a wide variety of lakes (Gelda and Effler 2002; Tsai and others 2008; Staehr and others 2010b) and other aquatic systems (Goodwin and others 2008; Hagerthey and others 2010) document multiple scales of variation. Among lakes, mean annual or seasonal metabolism can be predicted. For example, the variability in metabolism across lakes is driven primarily by total phosphorus and dissolved organic carbon (Hanson and others 2003; Sand-Jensen and Staehr 2007). Total phosphorus controls the autotrophic component by stimulating GPP, whereas dissolved organic carbon, primarily from allochthonous sources, is associated with increases in R and net heterotrophy of lakes (Cole and others 2000; Hanson and others 2003; Dodds and Cole 2007; Sand-Jensen and Staehr 2007).

Spatial and temporal variability in metabolic rates within lakes arises because lakes are not homogeneous, but rather are complex systems made up of numerous habitats that have different physical, chemical, and biological properties. Vertically, lakes are often stratified by temperature and have dramatically different levels of light, oxygen, and nutrients throughout the water column. These vertical divisions can result in large differences in metabolic rates. Coloso and others (2008) found that whereas GPP declines with depth, R is unrelated to depth. Horizontally within the upper mixed layer, the lake is divided into the open water pelagic zone and the more benthically dominated littoral zone. The littoral and pelagic may both make significant contributions to whole-lake metabolism (Vadeboncoeur and others 2002, 2008). In some unproductive lakes, littoral sites can have higher rates of metabolism than pelagic sites (Lauster and others 2006; Van de Bogert and others 2007); however, another study found that rates of metabolism were generally similar across surface waters (Coloso and others 2008). Thus, spatial heterogeneity of metabolic rates may depend on the morphology and spatial complexity of the lake, and may also be influenced by wind driven mixing (Van de Bogert and others 2007).

Given this complexity, the drivers of intra-lake metabolism are not well resolved. Staehr and Sand-Jensen (2007) studied the drivers of daily metabolism in a shallow, eutrophic lake in Denmark. During the summer months, they found that GPP and R were primarily related to chlorophyll *a*. However, despite the dominance of chlorophyll *a* in the system, statistical model fits were relatively weak suggesting that other physical, chemical, or biological drivers may be more important. Another study was able to explain about 80% of variation in daily metabolic rates in both a dystrophic lake and a eutrophic lake, and found that temperature and chlorophyll *a*, respectively, were the primary drivers (Staehr and others 2010b). However, the relationships were primarily driven by the large seasonal changes in temperature, irradiance, and chlorophyll *a* that occurred over the study period (from April to December) in Denmark. Those relationships disappear if they are only examined during the summer growing season.

In this study, we use multiple linear regression models to investigate the large day-to-day variability in metabolic rates measured during the course of two summers in two small, oligo-to-mesotrophic temperate lakes. We test a variety of possible drivers using a unique set of high-frequency measures that include wind speed, temperature, light (photosynthetically active radiation, PAR), precipitation, mixed layer depth, water column stability, chlorophyll *a*, chromophoric dissolved organic matter (CDOM, similar to dissolved organic carbon), and zooplankton biomass. All these drivers vary at the daily time scale and could affect metabolism with the possibility of different effects emerging than might be observed at longer time scales (for example, weeks, seasonal, annual). We specifically hypothe-

sized that chlorophyll *a* and PAR would be positively related to GPP, whereas zooplankton would be negatively related to GPP due to grazing. Further, we hypothesized that chlorophyll *a* and CDOM would be positively related to R as these variables are related to autotrophic and heterotrophic R, respectively, and temperature would be positively related as R generally increases with increased temperature (Carignan and others 2000). NEP represents the balance of autotrophic and heterotrophic processes and we hypothesized it would be most closely related to chlorophyll *a* and CDOM, again reflecting the autotrophic and heterotrophic aspects, respectively, of these two variables. We also evaluate more complex models that incorporate physical drivers such as vertical mixing and wind speed. We examine the models derived from this analysis for their consistency between years and between lakes. We find more complex models than hypothesized with moderate explanatory power indicating the difficulty of resolving drivers of ecosystem processes even with high-frequency measurements.

Materials and Methods

Study Site and Data Collection

During the summers of 2008 and 2009, lake metabolism and other variables were measured in Peter and Paul Lakes at the University of Notre Dame Environmental Research Center in the upper peninsula of Michigan (89°30.2′ W, 46°15.1′ N). Peter and Paul are small, pristine lakes with relatively low productivity and they both stratify during the summer season (Table 1). The lakes are adjacent to each other and are separated by a dike. These lakes have been extensively studied and are described in more detail elsewhere (Carpenter and Kitchell 1993).

A sampling buoy was moored near the center of each lake and several instruments were attached to the mooring line. YSI multiparameter sondes (model 6600 V2) fitted with optical DO probes (model 6150) and temperature, and conductivity probes (model 6560) were used to collect continuous oxygen and temperature data. The sondes were hung from the buoy at a depth of 0.7 m and were programmed to sample every 5 min. The DO probes were calibrated in air-saturated water prior to each deployment and calibrated again in air-saturated water following each retrieval. These calibrations were used to correct the data for electrode drift, with the assumption that any drift was linear (Coloso and others 2008). A continuous record was maintained by replacing each sonde with a freshly calibrated and charged sonde each week.

We also deployed WET Labs ECO fluorometers to measure chromophoric dissolved organic matter (CDOM; Belzile and others 2006) at the same sites, logging interval, and exchange schedule as for the DO sondes. The raw fluorescence recorded by the instruments is sensitive to temperature. To account for this effect, CDOM data were corrected using the temperature readings from the sondes, and a lab calibration in which the CDOM of a water sample was measured at multiple temperatures (Figure 1).

A meteorological station (HOBO Micro Station Data Logger and sensors, Onset) mounted on the Peter Lake buoy measured PAR, air temperature, wind speed, and wind direction at 5-min intervals for the duration of the summer. Rainfall was measured daily using a manual rain gauge. In 2009, NexSens thermistor chains (SDL500 datalogger and

Table 1. Characteristics of the Two Study Lakes

Lake characteristic	Peter Lake	Paul Lake
Area (ha)	2.6	1.7
Max depth (m)	19.6	15.0
Mean depth (m)	6.0	3.9
Mean weekly Z_{mix} (m)	2.7	2.6
Chlorophyll *a* (μg l^{-1})	5.4	4.3
Total phosphorus (μg l^{-1})	15.1	10.1
Total nitrogen (μg l^{-1})	433.5	310.5
Dissolved organic carbon (mg l^{-1})	5.4	4.4

Values of chlorophyll a, nutrients, and dissolved organic carbon are the averages from 2005 to 2008 in the upper mixed layer of the lakes.

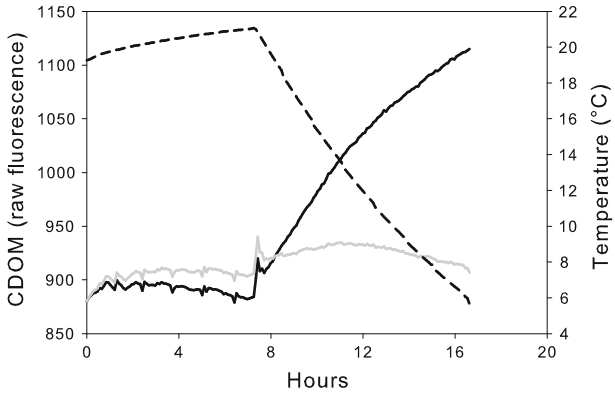

Figure 1. Lab calibration of CDOM data used to correct the negative relationship between CDOM fluorescence and water temperature. The *solid black line* is raw CDOM, the *solid gray line* is corrected CDOM, and the *dashed line* is temperature.

T-Node temperature string) were deployed in both lakes to measure high-frequency temperature profiles. Thermistors were placed at half meter intervals from 0.5 to 4.0 m with an additional thermistor at 5.0 m, which was always below the upper mixed layer in both lakes. Temperature profiles were recorded at 5-min intervals. Manual temperature profiles at 0.5 m intervals were also taken weekly with a YSI model 58 (2008) and YSI Professional Plus (2009) meter.

The depth of the mixed layer (Z_{mix}) was calculated for each temperature profile (both manual and high frequency) as the depth at which the temperature changes 1°C or more over a half meter change in depth. Weekly estimates of Z_{mix} from manual profiles were linearly interpolated to a daily time series. In 2009, the high-frequency temperature profiles were used to calculate Z_{mix} for every 5-min interval, which were then averaged to get daily values of Z_{mix}. Peter and Paul lakes frequently experienced short-term stratification (occurring on a diel cycle) that occurred within the stably stratified upper mixed layer. In these instances, the shallowest stratified depth was considered to be Z_{mix}. The sondes are assumed to measure metabolism from the lake surface to Z_{mix}. The thermal structure of the lake was also measured by calculating stability(E), which is a measure of the resistance of a particle of water to vertical movement within the water column (Knauss 1997). Low stability indicates vertical mixing, whereas high stability indicates stratified conditions. Stability was calculated at each depth as

$$E = \frac{1}{\rho_0}\frac{\partial \rho}{\partial z} - \frac{g}{c^2}, \quad (1)$$

where ρ_0 is a reference density (1 kg l^{-1}), ρ is the density at depth z, g is gravitational acceleration, and c is the speed of sound in water. The density was calculated for each depth from the temperature (T) using the following equation (Kalff 2002).

$$\rho = 1 - 6.63 \times 10^{-6}(T-4)^2. \quad (2)$$

In addition to the high-frequency measurements made with automated sensors, daily samples of chlorophyll *a* and zooplankton biomass were also collected and analyzed in the laboratory. Surface water chlorophyll *a* samples were filtered, frozen, extracted with methanol, and analyzed with a fluorometer (Holm-Hansen and Rieman 1978; Marker and others 1980). Daily zooplankton biomass was measured gravimetrically by concentrating calibrated vertical net (153 μm mesh) tows onto filters to measure dry weights. Daily values were the mean of four replicate zooplankton samples. Zooplankton samples were checked weekly for chlorophyll *a* and inorganic content to ensure that the sample mass was dominated by zooplankton and not significantly (>10%) contaminated by algae or inorganic particles.

Metabolism Model

Daily values of metabolism were estimated following the calculations outlined in Cole and others (2000), which used the general model originally described by Odum (1956):

$$\frac{d\mathrm{DO}}{d\mathrm{t}} = \mathrm{GPP} - \mathrm{R} + \frac{D}{Z_{mix}}, \quad (3)$$

where dDO/dt (mmol O_2 m^{-3} day^{-1}) is the change in DO over time, and D is the diffusive exchange with the atmosphere. Other changes in DO due to physical or chemical processes (for example, advection) are assumed to be negligible (Staehr and others 2010a). Although simple, this model has been widely used over the last 50 years (McIntire and others 1964; Bott and others 1985; Petersen and others 1997; Hagerthey and others 2010) and has recently been shown to perform as well as other more complicated nonlinear and mechanistic models (Hanson and others 2008). In 2009, we measured Z_{mix} at weekly and 5-min intervals, but only at weekly intervals in 2008. Thus, metabolism calculations for both years were made with daily time series that were linearly interpolated from weekly Z_{mix} measurements (Cole and others 2000; Lauster and others 2006; Coloso and others 2008). The frequency at which Z_{mix} is measured can affect the estimates of metabolism (Coloso and others 2011). Briefly, metabolic rates were calculated as follows using a program written in MATLAB (The MathWorks Inc., version 7.6). As described in equation (3), the change in DO between any 5-min measurement interval is due to net ecosystem production (NEP = GPP − R) and diffusive exchange with the atmosphere. D can be calculated at any given time using the following equation:

$$D = k(\mathrm{DO_{sat}} - \mathrm{DO_w}). \quad (4)$$

DO_{sat} is the DO concentration in equilibrium with the atmosphere, whereas DO_w is the measured DO concentration of the water. D can be either positive (flux of oxygen into the lake) or negative (flux out of the lake) depending on whether DO in the lake is above or below saturation. k is the piston velocity, which drives the rate of exchange between the lake and the atmosphere. For every measurement interval, the value of k for oxygen at each temper-

ature is calculated from k_{600} (Jahne and others 1987), which is a piston velocity that has been normalized to a Schmidt number of 600 (600 is the Schmidt number for CO_2 at 20°C). Schmidt numbers, which are proportional to k and are gas and temperature specific, allow for the conversion of k from one gas to another. k_{600} was calculated from wind speeds measured on Peter Lake (Cole and Caraco 1998). Our method may underestimate k_{600} and thus gas flux because factors other than wind affect exchange (MacIntyre and others 2010); however, gas flux in these two lakes is very small relative to metabolism such that even if we doubled our estimates of gas flux it would have little effect on our metabolic estimates.

As gas flux can be calculated, NEP can be estimated for any given time. Given that GPP is zero in the absence of light, it is assumed that night-time NEP is equal to night-time R (R_{night}). However, during the day NEP results from both GPP and R. Daytime R (R_{day}) cannot be directly measured and so we assumed that R_{day} is equal to R_{night}, as has been done previously (Cole and others 2000; Lauster and others 2006; Coloso and others 2008). R_{day} is likely larger than R_{night} (Pace and Prairie 2005), which would cause both GPP and R to be higher than our estimates, but would not have an effect on NEP (Cole and others 2000; Staehr and others 2010a). The 5-min estimates of R were averaged over the entire day, whereas daily values of GPP were calculated as the sum of R_{day} and daytime NEP. Daily NEP was calculated by subtracting R from GPP.

The sondes were deployed in the surface waters of the lake and were assumed to measure metabolism occurring between the lake surface and Z_{mix}. Because of this, estimates of metabolism made here only include GPP and R that occurred within the upper mixed layer of the lake. However, both GPP and R occurred below the mixed layer (Coloso and others 2008). Furthermore, the centrally located sondes in this study may have missed some portion of littoral metabolism (Van de Bogert and others 2007). Thus, the metabolism estimates are only for a portion of the lake.

Regression Models

Multiple linear regression models were created for GPP, R, and NEP for both Peter and Paul lakes in 2008 and 2009 using R software (R Project for Statistical Computing, version 2.7.2). Volumetric rates of metabolism were used in the models because they are independent of the mixing depth and thus Z_{mix} could be used as a predictor variable. In 2008, the pool of possible predictor variables used in the models included daily mean values of water temperature, PAR, chlorophyll *a*, CDOM, zooplankton biomass, wind speed, rainfall, and weekly values of Z_{mix} which were interpolated to a daily time series. PAR was averaged over 24 h to account for the difference in day length throughout the summer. For comparison with 2008, the 2009 models used the same pool of predictor variables. Additionally, a second set of models was created for 2009 that used values of GPP, R, and NEP calculated with high-frequency Z_{mix} and also included mean daily values of both Z_{mix} and stability in the pool of potential predictors. Stability was calculated for every depth interval, but only stability between 0.5 and 1 m was used as a predictor variable because that interval included the sonde and best reflected the dynamic nature of the thermal structure of the lake. The two sets of 2009 models serve as a comparison to examine the importance of the high-frequency temperature data.

Due to autocorrelation that is present for most of the metabolism daily time series, models incorporated autoregressive term(s) following the general formula below:

$$Y_t = b_1 x_{1t} + b_2 x_{2t} + b_n x_{nt} + \varphi Y_{t-1} + b_0 + \varepsilon, \quad (5)$$

where Y is the response variable at time t, x_n are the predictor variables, b_n are the parameters of the model, φ is the autoregressive coefficient, and ε is the error. The autoregressive component of the model (that is, AR(1), AR(2), and so on) was chosen separately for each metabolism time series based upon the autocorrelation function and partial autocorrelation function plots of model residuals, as well as the Durbin Watson test for positive autocorrelation. The model residuals were also checked for normality, and the metabolism time series were log or square-root transformed if necessary to meet the regression assumptions.

The predictor variables used in the final models were selected using the all possible subsets approach described by Sheather (2009). This approach uses the ''leaps'' package (version 2.7) in R to find the best subset of predictor variables for models ranging in size from one variable to all of the predictor variables. For a model of a given size, the best subset is determined to be those variables that maximize the adjusted R^2. Models with the best subsets of each size were run, and the final model was chosen as the one which minimized the corrected Akaike information criterion (AIC_c). Predictor variables in the final models were tested for collinearity by ensuring that all variance inflation factors were less than 10 (Janke and Tinsley 2005; Kutner and others 2005).

Results

Rates of metabolism in Peter and Paul lakes were generally similar between the two years of study, although rates were higher in 2008 (Figure 2). Metabolic rates in Paul Lake were higher than Peter Lake in both years. Paul Lake was net heterotrophic in both years, whereas Peter Lake was net autotrophic, although NEP was nearly in balance in 2009. Metabolic rates in these lakes in 2008 and 2009 were generally similar to estimates from previous years (Carpenter and others 2005; Van de Bogert and others 2007).

In both lakes, there were no strong seasonal trends in metabolism, except for Paul Lake in 2008 where GPP and R clearly increased until mid-summer and then declined (Figure 2). Despite the lack of strong trends, the daily rates of metabolism in both lakes were variable. For example, in 2008 GPP in Peter Lake ranged from 3.5 to 35.0 mmol O_2 m^{-3} day^{-1}, whereas GPP ranged from 2.8 to 36.6 mmol O_2 m^{-3} day^{-1} in Paul Lake. On average over the 2 years, R was more variable than GPP in Peter Lake with a CV of 52% for R compared to a CV of 44% for GPP. However, in Paul lake, GPP was more variable with a CV of 40% compared to 34% for R. Rates of NEP were also variable in both lakes, and at the daily time scale, the lakes varied between slight net autotrophy and net heterotrophy (Figure 2). The short-term variability in the daily rates was different between Peter and Paul as metabolic rates between the two lakes were not well correlated (that is, Paul Lake GPP was not correlated with Peter Lake GPP). The correlation coefficients for 2009 were 0.09 for GPP, 0.11 for R, and 0.27 for NEP. This suggests that the internal drivers are different in these two lakes and are important to metabolic rates.

The independent predictor variables used to model daily metabolism had varying dynamics as illustrated in Figure 3 for Peter Lake in 2009, but in general seasonal trends were absent or modest. Correlations between the predictor variables were generally low, although many were significant ($P < 0.05$; Tables A1–A4). The relationships between the variables were inconsistent between years and across lakes in both magnitude and direction. For example, chlorophyll *a* and zooplankton biomass had a strong negative relationship in Peter Lake in 2008, with a Pearson's

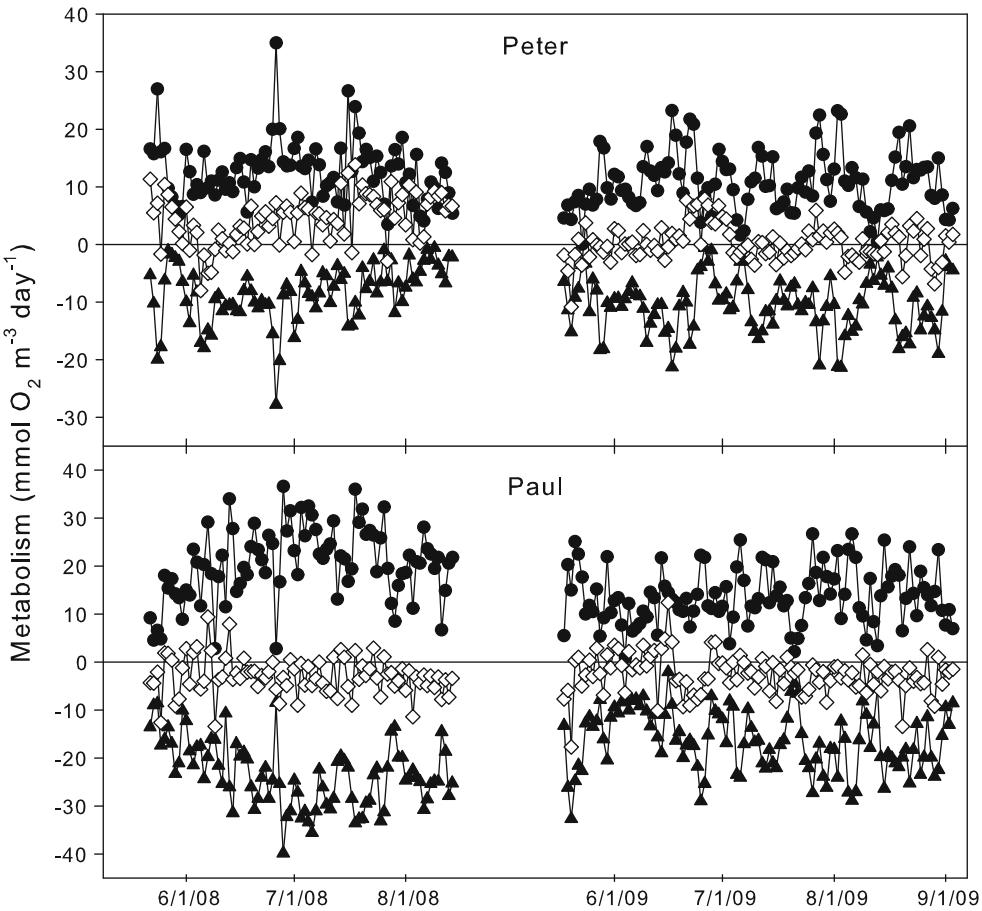

Figure 2. Daily metabolism estimates for Peter and Paul Lakes during the summers of 2008 and 2009. Gross primary production (*filled circles*), ecosystem respiration (*filled triangles*), and net ecosystem production (*open diamonds*). Ecosystem respiration is displayed as negative for ease of graphing.

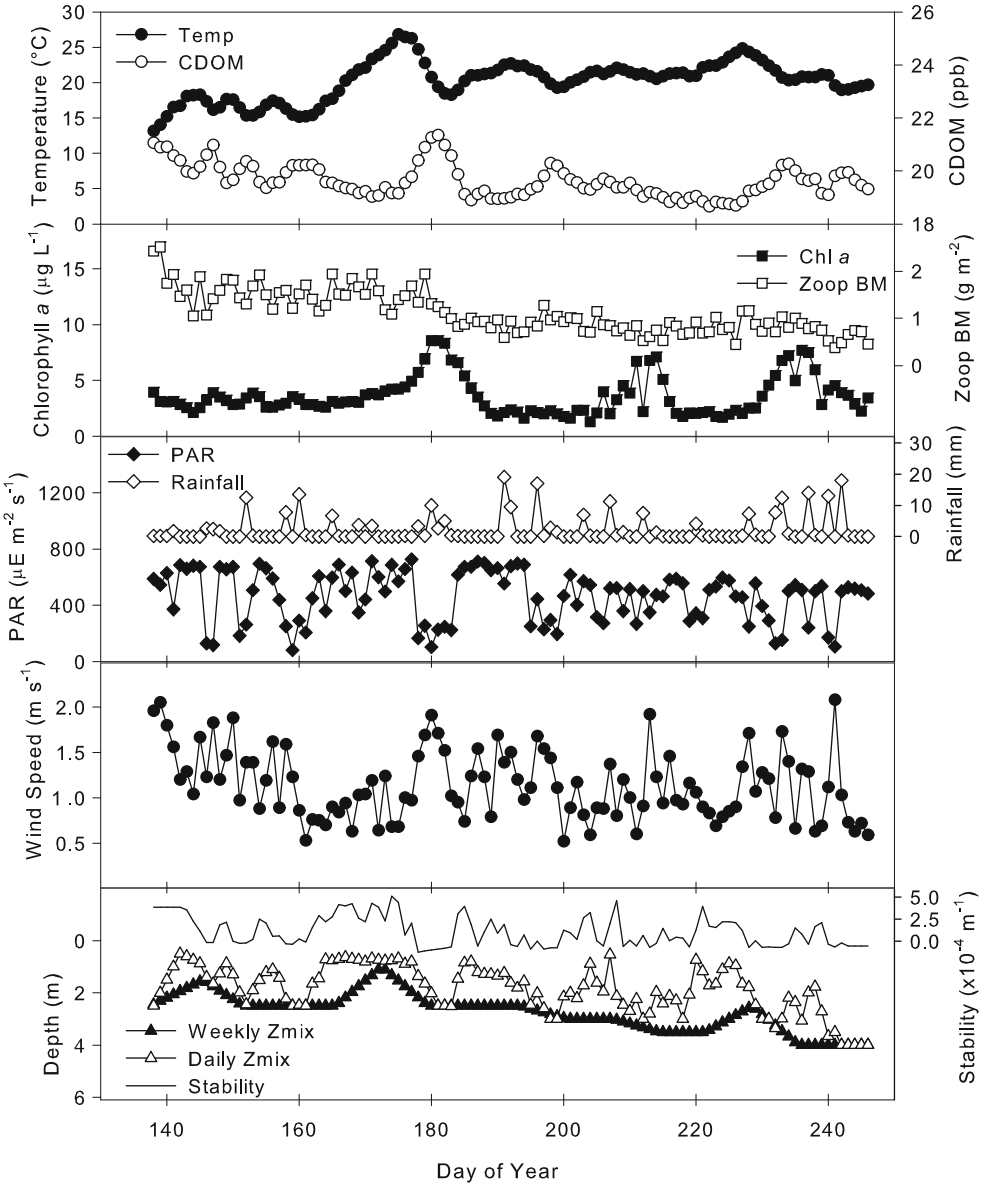

Figure 3. Seasonal variability of the predictor variables in Peter Lake in 2009. Temperature, colored dissolved organic matter (CDOM), photosynthetically active radiation (PAR), wind speed, stability, and daily depth of the mixed layer (Z_{mix}) are daily means of high-frequency 5-min measurements. Chlorophyll *a*, zooplankton biomass, and rainfall were manually measured daily. Weekly Z_{mix} was measured from manual weekly temperature profiles and then interpolated to a daily time series.

correlation coefficient of −0.63. However, in 2009, the same correlation (chlorophyll *a* and zooplankton biomass) was only 0.01. In Paul Lake, the correlation was strongly positive in 2008 with a coefficient of 0.42, but was only 0.05 in 2009. Thus, the relationship between chlorophyll *a* and zooplankton biomass, as with many of the other variables, was not simple and sampling for only 1 year or in only one lake could have led to inaccurate conclusions about interdependencies

Eight potential predictors were used to build the models for GPP, R, and NEP with some of these variables emerging as more important than others. All of the variables were in at least one model, but some were in many models. As hypothesized, chlorophyll *a* was the most frequent significant variable as it was incorporated in 9 of the 12 models, whereas temperature and wind speed were both in 7 of the models (Tables 2 and 3). These three variables were each in more than half of the models. Furthermore, every model contained at least one of those variables and 75% of the models contained two, indicating that chlorophyll *a*, temperature, and wind speed were the three most important drivers of variation in metabolism in Peter and Paul Lakes. Although chlorophyll *a* was important in both lakes, temperature and PAR were more important in Paul Lake, whereas wind speed was more important in Peter Lake. Chlorophyll *a* had a positive relationship with GPP and R in both lakes and years; however, the direction of the relationships with temperature, wind speed, and PAR differed among lakes.

Table 2. Model Results for Peter Lake of Gross Primary Production (GPP), Ecosystem Respiration (R), and Net Ecosystem Production (NEP)

Year	Dependent variable	R^2	$\frac{\varepsilon SD}{\bar{Y}_{obs}}$	Predictor variable	Coefficient	*t* value	*P*	Partial R^2
2008	GPP	0.30	0.143	GPP_{t-1}	0.25	2.48	0.0153	0.09
				Wind	−0.49	−4.00	0.0001	0.09
				Z_{mix}	−0.49	−3.07	0.0029	0.07
				Chl *a*	0.13	3.08	0.0029	0.04
				ZoopBM	2.71	1.92	0.0580	0.02
	R	0.43	0.243	R_{t-1}	0.46	4.60	<0.0001	0.23
				Z_{mix}	−0.49	−1.78	0.0795	0.10
				ZoopBM	3.90	1.61	0.1116	0.08
				Wind	−0.42	−1.89	0.0629	0.02
	NEP	0.34		Chl *a*	1.19	4.59	<0.0001	0.20
				Wind	−3.16	−3.12	0.0025	0.09
				PAR	0.01	2.25	0.0270	0.05
2009	GPP	0.43	0.353	GPP_{t-1}	0.64	6.90	<0.0001	0.29
				GPP_{t-2}	−0.26	−2.76	0.0069	0.03
				Chl *a*	0.78	3.23	0.0017	0.09
				Wind	−1.77	−1.59	0.1140	0.01
				Rainfall	0.14	1.62	0.1081	0.01
	R	0.55	0.315	R_{t-1}	0.75	−3.41	0.0010	0.37
				R_{t-2}	−0.31	3.09	0.0026	0.04
				Temperature	−0.43	−2.62	0.0103	0.03
				Chl *a*	0.66	2.81	0.0060	0.03
				CDOM	−2.36	−2.78	0.0065	0.02
				Rainfall	0.14	1.80	0.0758	0.02
	NEP	0.51		Chl *a*	0.69	4.70	<0.0001	0.17
				Temperature	0.45	4.56	<0.0001	0.13
				Z_{mix}	−1.27	−4.21	0.0001	0.08
				Wind	−2.70	−4.38	<0.0001	0.07
				CDOM	1.38	2.60	0.0108	0.05

GPP was log transformed and R was square-root transformed in 2008. The dependent variable in all other models was not transformed. Models for GPP and R in 2008 had AR(1) components. 2009 GPP and R models had AR(1) and AR(2) components, whereas NEP had no autoregressive component in both years. n = 85 in 2008 and n = 109 in 2009. Variables are as follows: Chl a, chlorophyll a (μg l^{-1}); CDOM, colored dissolved organic matter (ppb); PAR, photosynthetic active radiation (μE m^{-2} s^{-1}); rainfall (mm); temperature (°C); wind speed (m s^{-1}); Z_{mix}, depth of the mixed layer (m); ZoopBM, zooplankton biomass (g m^{-2}). $\frac{\varepsilon SD}{\bar{Y}_{obs}}$ is the standard deviation of the model residuals divided by the mean observed dependent variable.

In relation to our original hypotheses, we accessed how often variables were included in the final models for four cases: Paul 2008, Paul 2009, Peter 2008, and Peter 2009 (Tables 2 and 3). Chlorophyll *a* was significant in models for GPP in three of four cases, and PAR was significant for GPP in two of four cases. Zooplankton biomass was not related to GPP. For R, chlorophyll *a* was significant in the models in two of four cases and temperature in three of four cases. CDOM was only a significant model variable for R in Peter Lake 2009. Chlorophyll *a* was a key factor in the variation of NEP (four of four cases), whereas CDOM was included only in Paul 2008. Overall, the originally hypothesized relations were generally evident for chlorophyll *a* (for GPP, R, and NEP), mostly evident for temperature (in relation to R) and for PAR (in relation to GPP) in Paul Lake.

The multiple linear regression models explained 12–55% of the daily variance in metabolic rates. An example of the model fits is illustrated in Figure 4 for Peter Lake in 2009. In both lakes and years, the models for R performed the best as three of the four models had R^2 values greater than 0.5. Another measure of a model's performance is to divide the standard deviation of the model residuals by the mean observed dependent variable ($\frac{\varepsilon SD}{\bar{Y}_{obs}}$, Tables 2 and 3). Low values of this statistic indicate better model performance because the model error is low relative to the mean of what the model is trying to predict. Based on this statistic, the 2008 model of Peter Lake GPP performed the best, but overall the models for R had better fits than the models of GPP.

Although chlorophyll *a*, temperature, and wind speed accounted for much of the overall explained variance, the models differed between years and

Table 3. Model Results for Paul Lake of Gross Primary Production (GPP), Ecosystem Respiration (R), and Net Ecosystem Production (NEP)

Year	Dependent variable	R^2	$\frac{\varepsilon SD}{\overline{Y}_{obs}}$	Predictor variable	Coefficient	*t* value	*P*	Partial R^2
2008	GPP	0.32	0.305	GPP_{t-1}	0.14	1.19	0.2365	0.09
				CDOM	2.90	2.92	0.0045	0.09
				Chl *a*	1.05	2.05	0.0436	0.07
				PAR	0.01	2.43	0.0173	0.05
				Z_{mix}	−4.82	−1.84	0.0699	0.02
	R	0.55	0.180	R_{t-1}	0.48	5.06	<0.0001	0.32
				Temperature	0.87	3.52	0.0007	0.21
				Z_{mix}	−2.96	−1.98	0.0516	0.02
	NEP	0.32		NEP_{t-1}	−0.24	−2.42	0.0178	0.04
				PAR	0.01	4.67	<0.0001	0.13
				Temperature	−1.05	−3.43	0.0010	0.11
				Chl *a*	1.16	4.41	<0.0001	0.07
				CDOM	1.31	1.69	0.0957	0.03
2009	GPP	0.22	0.373	GPP_{t-1}	0.32	3.64	0.0004	0.10
				Wind	4.84	3.54	0.0006	0.08
				Temperature	0.30	1.62	0.1091	0.03
				PAR	0.01	1.72	0.0885	0.02
	R	0.54	0.268	R_{t-1}	0.71	8.34	<0.0001	0.34
				R_{t-2}	−0.36	−4.13	0.0001	0.05
				Temperature	0.65	3.84	0.0002	0.10
				Wind	3.79	3.12	0.0024	0.04
				Chl *a*	2.20	2.58	0.0114	0.02
				PAR	0.00	1.59	0.1155	0.01
	NEP	0.12		Temperature	−0.41	−3.36	0.0043	0.09
				Chl *a*	−1.22	−2.08	0.0400	0.03

All 2008 models and GPP in 2009 had AR(1) components. In 2009, R had AR(1) and AR(2), while NEP had no autoregressive component. n = 85 in 2008 and n = 109 in 2009. Variables are as described in Table 2. $\frac{\varepsilon SD}{\overline{Y}_{obs}}$ *is the standard deviation of the model residuals divided by the mean observed dependent variable.*

between lakes (Tables 2 and 3). The models varied both in their performance and in their structure. Comparing the Peter Lake models to those from Paul Lake revealed few similarities suggesting that despite the close proximity of these lakes, the metabolism in each lake is driven by different variables. Furthermore, within each lake, the set of predictor variables used in the 2008 models were different than the set of predictor variables in the 2009 models. In all the cases, only one or two predictor variables overlapped between the 2008 and 2009 models, except for R in Peter Lake where none of the predictor variables were the same. Thus, the models were no more similar within a lake than they were between lakes.

Additional models of 2009 metabolism were built using the high-frequency temperature data. For these models, the dependent variables (GPP, R, and NEP) were calculated using high-frequency Z_{mix}, the pool of predictor variables included stability, and mean daily values of Z_{mix} replaced weekly values. The addition of high-frequency temperature data tended to improve model fits, especially for those models that included stability (Table 4). However, improvements in model fits were modest, indicating that high-frequency measures of thermal stratification only accounted for a portion of the remaining unexplained variance in the models.

Discussion

Estimates of metabolism in Peter and Paul Lakes are quite variable at the daily time scale. Values of CV over the 2 years were as much as 47% for GPP and 60% for R. These values are similar to those reported by Staehr and Sand-Jensen (2007) for a eutrophic Danish lake, in which the CV for GPP and R during the summer was 76 and 55%, respectively. This result further supports the conclusion of Staehr and Sand-Jensen (2007) that estimates of metabolism made over only a few days are unreliable estimates of the mean rate for the entire season.

The multiple regression models were able to explain more than half the variance in some cases and were successful at identifying important drivers of

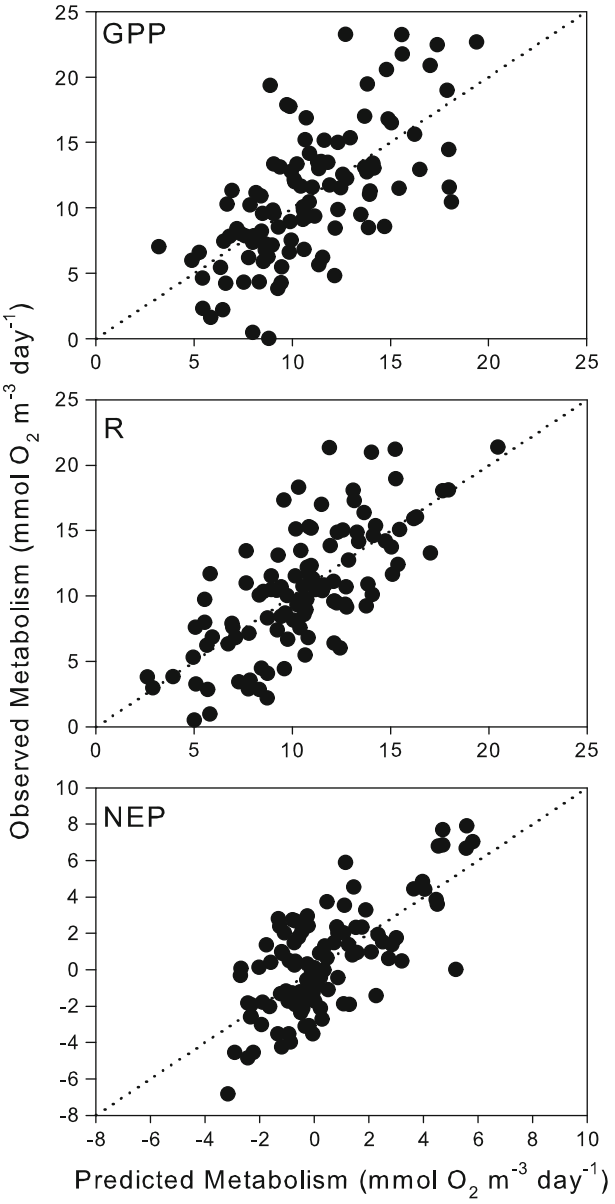

Figure 4. Observed rates of gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP) versus the model predictions for Peter Lake in 2009. The *dotted lines* are the 1:1 lines.

metabolism in these two lakes. Chlorophyll *a*, temperature, and wind speed were important drivers in most models and accounted for much of the explained variance. These three variables, chlorophyll *a* in particular, were important in both Peter and Paul Lakes. However, overall the models were inconsistent in both structure and performance.

The inconsistencies in model structure were not the result of the errors in model selection. Frequently in the process of model selection, several competing models had similar values of AIC_c (within 1 AIC_c unit; Table A5). Typically those models only differed from the chosen model by the addition or subtraction of a single variable. Occasionally, competing models differed by several variables. Chlorophyll *a*, wind speed, and temperature were the three most frequently significant variables in the competing models as they were in the chosen models. The method of selecting the model with the lowest AIC_c was used here for simplicity and to ensure an unbiased decision. Using an alternative method of selection may have caused some models to be different, but would not have changed the results significantly or made the models more consistent.

Although the models were able to explain more than half the variance in some cases, in most cases at least half of the variance was unexplained. These model fits were similar to those in Staehr and Sand-Jensen (2007). Their models explained 29% of GPP and 35% of R during the summer season, and they found chlorophyll *a* to be the most important driver of metabolism during that time in the eutrophic lake. Their results are surprising because their system was dominated by high biomass and substantial variation in chlorophyll *a*, yet 70% of the variance in the metabolic rates was driven by something else. Our models used several more potential predictor variables, including CDOM, zooplankton biomass, and water column stability, and were able to explain up to 55% of daily variance, but like the Staehr and Sand-Jensen (2007) results, much of the variance remained unexplained. Daily rates of metabolism have proven difficult to model even in widely differing systems such as these (that is, the Danish lake versus Peter and Paul Lakes), which differ greatly in their level of productivity.

The lack of strong model fits in this study and the Staehr and Sand-Jensen (2007) study raises the question, what can account for the unexplained variance in daily estimates of metabolism? There are a number of possible explanations that involve limitations of the models and error in the metabolism estimates. The first and most simple explanation is that the models were missing one or more important predictor variable. Nutrients, such as nitrogen, phosphorus, and silica were not used in the models, but they could be important drivers as phytoplankton in these lakes are nutrient limited. Furthermore, the photosynthetic efficiency of phytoplankton can decrease with nutrient stress (Parkhill and others 2001), thus affecting GPP even if phytoplankton biomass does not change. Daily or higher frequency measurements of nutrients are

Table 4. Results for the Models in Peter and Paul Lakes that Used Water Column Stability (m^{-1})

Lake	Year	Dependent variable	R^2	$\frac{\varepsilon SD}{\bar{Y}_{obs}}$	Predictor variable	Coefficient	*t* value	*P*	Partial R^2
Peter	2009	GPP	0.44	0.351	GPP_{t-1}	0.65	7.02	<0.0001	0.30
					GPP_{t-2}	−0.24	−2.67	0.0088	0.03
					Chl *a*	0.79	3.33	0.0012	0.09
					Stability	−4855.84	−2.03	0.0453	0.02
					Rainfall	0.15	1.67	0.0987	0.01
Paul	2009	GPP	0.34	0.344	GPP_{t-1}	0.21	2.40	0.0182	0.08
					Stability	19420.00	3.86	0.0002	0.08
					Temperature	1.09	3.94	0.0002	0.06
					Wind	2.92	2.00	0.0485	0.05
					PAR	0.01	3.38	0.0010	0.04
					CDOM	−1.89	−2.25	0.0270	0.02
					Chl *a*	2.31	2.35	0.0210	0.01
Paul	2009	R	0.61	0.247	R_{t-1}	0.61	7.25	<0.0001	0.29
					R_{t-2}	−0.36	−4.43	<0.0001	0.04
					Temperature	1.34	5.56	<0.0001	0.13
					Stability	17866.27	4.18	0.0001	0.06
					CDOM	−1.36	−1.88	0.0626	0.03
					Chl *a*	3.03	3.58	0.0005	0.02
					PAR	0.01	3.10	0.0025	0.02
					Wind	1.93	1.54	0.1259	0.02

Autoregressive components are the same as those in the 2009 models of Tables 2 and 3. n = 85 in 2008 and n = 109 in 2009. Variables are as described in Table 2. $\frac{\varepsilon SD}{\bar{Y}_{obs}}$ *is the standard deviation of the model residuals divided by the mean observed dependent variable.*

uncommon and thus their short-term dynamics are neither easily measured nor well understood. Incorporating short-term nutrient dynamics into the models could improve their performance.

Physical processes that were not measured could also help to explain some of the remaining variance. This study used high-frequency measurements of thermal stratification in the second year and the derived estimates of water column stability improved model fits in some cases (Table 4). Finer scale measurements over the entire water column could further increase model fits by revealing increased stratification within the mixed layer. Surface microlayers could impact metabolic rates because they affect gas exchange with the atmosphere, are enriched in both dissolved and particulate organic and inorganic compounds, and have decreased rates of GPP and elevated rates R compared to subsurface water (Baastrup-Spohr and Staehr 2009). Other physical processes such as internal waves, boundary layer dynamics, advection, and entrainment of water masses have been demonstrated to have short-term effects on metabolic rates, primarily by transporting nutrient-rich water into the mixed layer (Ostrovsky and others 1996; Eckert and others 2002; MacIntyre and others 2006; Bruce and others 2008). Incorporating a hydrodynamic model that includes these physical processes into our metabolism model could greatly improve our estimates of metabolism and reduce the large amount of the unexplained variance.

The remaining variance in the models could also be due to other sources of metabolism that are not explained in the model. Benthic metabolic rates are often larger, per unit area, than pelagic rates and can contribute significantly to whole-lake GPP and R (Vadeboncoeur and others 2002, 2008; Lauster and others 2006; Van de Bogert and others 2007). Sondes are integrative across surface waters such that a centrally located pelagic sonde (such as we used) detects some mixture of benthic and pelagic metabolism. In Peter Lake, it has been demonstrated that the amount of benthic metabolism that is measured by the pelagic sonde depends in part on wind speed (Van de Bogert and others 2007). On calm days, benthic and pelagic metabolism are different, indicating that the pelagic sonde is not measuring much benthic metabolism. However, on days with moderate wind, the metabolism is more homogeneous across the surface waters and thus a portion of the total metabolism measured by the pelagic sonde is from benthic sources (Van de Bogert and others 2007). Therefore, some of the variance in the daily estimates of metabolism from pelagic sondes could be due to the occasional but variable inclusion of some portion of benthic metabolism, which is likely to also have high, short-term variance.

In addition to other variables that were not accounted for, the large amount of unexplained variance could be a result of relationships between the metabolic rates and their drivers that operate at multiple time scales. Variability in DO is controlled by numerous drivers that act at multiple time scales from minutes to days (Langman and others 2010), and the same is likely true for metabolic rates. These complex relationships could have confounding effects on metabolism as drivers of metabolism may have both immediate impacts and longer-term effects. For example, strong wind can have immediate impacts on metabolism by increasing lake circulation and Z_{mix}, and could also create internal seiches that can last for days and cause entrainment of hypolimnetic waters in the epilimnion, which has been reported to enhance lake productivity (Ostrovsky and others 1996). Metabolic rates could therefore be affected both during windy conditions and also days after the wind had diminished, which would confound the relationship between wind speed and metabolism. These complex relationships likely exist between metabolism and many of its drivers, as well as between the drivers themselves, and could be the reason for the inconsistencies in model structure and in the relationships between the predictor variables.

Finally, the poor model fits could be due to noise in the metabolism time series caused by sampling error. Van de Bogert and others (2007) compared rates of metabolism measured from six sondes deployed concurrently in the same location in Peter Lake and found a CV of 9%. To determine how much impact that amount of error would have on the model fits, we created predictions of GPP and R using chlorophyll *a*, temperature, and wind speed, and used their fitted values to create a new time series. We then added error to each time series by randomly drawing from a normal distribution with a mean equal to the mean of the new time series and a standard deviation that was 9% of that mean. When the models were rerun, the added error reduced the model fits of both GPP and R and caused about 20% of the daily variance in metabolism to be unexplained. Thus, the ability to model daily estimates of metabolism may be limited by resolution of the metabolic signal, for even with a perfect model we can only explain 80% of the variance.

As metabolic rates may be too stochastic to be resolved at the daily time scale, we aggregated the data at longer time scales and reran the models. First, we reran the models using weekly averages of the dependent and predictor variables. These weekly models were overall able to explain more of the variation in the metabolic rates than the daily models; however, the results were not consistent. Although some models were able to explain substantially more variability (for example, R^2 for Paul Lake GPP in 2008 increased from 0.32 to 0.79), others remained about the same and a few decreased (for example, R^2 for Peter Lake R in 2009 decreased from 0.55 to 0.12). The weekly models explained 13–83% and increased the average R^2 of all the models from 0.39 to 0.57. Next, we ran models using the mean rates of metabolism for the entire summer in Peter and Paul Lakes using additional data from Cole and others (2000), Carpenter and others (2005), and Van de Bogert and others (2007). We used 8 years of data from Paul Lake and 6 years from Peter Lake. Seasonal mean values of total phosphorus (TP), dissolved organic carbon (DOC), and chlorophyll *a* were used as the potential predictor variables. Nutrients were added to Peter Lake in several years (Cole and others 2000; Carpenter and others 2005), therefore data from those years were not used. Aggregating data to the seasonal scale substantially increased our ability to model metabolism in both lakes. Using only TP as a predictor variable, models of GPP, R, and NEP for Peter Lake explained 92, 86, and 61% of the variance, respectively. The models of GPP and R in Paul Lake used both TP and DOC, whereas the model for NEP only used TP. GPP and R both had a R^2 of 0.69, and NEP had a R^2 of 0.34. Therefore, although modeling metabolism at the daily time scale can be difficult and inconsistent, aggregating to longer time scales improves prediction of metabolic rates. More studies are needed to generalize about whether aggregating data across daily or longer time scales will lead to better predictive models of metabolism. Current efforts like the Global Lake Ecological Observatory Network (GLEON) could provide the data to address this question (Hanson 2008).

This study highlights the difficulty of modeling daily rates of lake metabolism. We suggest similar issues prevail in other types of ecosystems where processes like GPP and respiration vary substantially at daily time scales. In our case, problems with model design and sampling error led to generally weak model performance and inconsistent model structure. We anticipate the need for model development to include additional high-frequency predictor variables and the potential for processes that occur at multiple time scales.

High-frequency observations of ecosystem processes have the potential to both enlighten and confuse. The temporal and spatial resolution of these measurements requires assessment especially

in the context of physical processes such as hydrological mixing or air mass movements. Environmental variation in both driver and response variables may obscure well-known relationships. Ecosystem science is clearly entering an era where sensors will greatly enhance the capacity to observe systems. High-frequency data are not a panacea but instead raise new problems while providing the means to test novel models that may better identify the underlying drivers and dynamics of ecosystem processes.

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