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Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe

Christopher T. Solomon,[a*] Denise A. Bruesewitz,[b] David C. Richardson,[c] Kevin C. Rose,[d] Matthew C. Van de Bogert,[e] Paul C. Hanson,[e] Timothy K. Kratz,[f] Bret Larget,[g] Rita Adrian,[h] Brenda Leroux Babin,[i] Chih-Yu Chiu,[j] David P. Hamilton,[k] Evelyn E. Gaiser,[l] Susan Hendricks,[m] Vera Istvánovics,[n] Alo Laas,[o] David M. O'Donnell,[p] Michael L. Pace,[q] Elizabeth Ryder,[r] Peter A. Staehr,[s] Thomas Torgersen,[t] Michael J. Vanni,[u] Kathleen C. Weathers,[v] Guangwei Zhu[w]

[a] Department of Natural Resource Sciences, McGill University, Ste. Anne de Bellevue, Québec, Canada

[b] Marine Science Institute, University of Texas, Port Aransas, Texas

[c] Department of Biology, State University of New York, New Paltz, New York

[d] Smithsonian Environmental Research Center, Edgewater, Maryland

[e] Center for Limnology, University of Wisconsin, Madison, Wisconsin

[f] Trout Lake Station, Center for Limnology, University of Wisconsin, Boulder Junction, Wisconsin

[g] Departments of Botany and Statistics, University of Wisconsin, Madison, Wisconsin

[h] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[i] Department Of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana

[j] Biodiversity Research Center, Academia Sinica, Taipei, Taiwan

[k] Environmental Research Institute, University of Waikato, Hamilton, New Zealand

[l] Department of Biological Sciences and the Southeast Environmental Research Center, Florida International University, Miami, Florida

[m] Hancock Biological Station, Murray State University, Murray, Kentucky

[n] Water Quality Management Group, Hungarian Academy of Sciences, Budapest, Hungary

[o] Center for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartumaa, Estonia

[p] Upstate Freshwater Institute, Syracuse, New York

[q] Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia

[r] Marine Institute, Newport, County Mayo, Ireland

[s] Department of Bioscience, Aarhus University, Roskilde, Denmark

[t] Department of Marine Sciences, University of Connecticut, Groton, Connecticut

[u] Department of Zoology and Graduate Program in Ecology, Evolution, and Environmental Biology, Miami University, Oxford, Ohio

[v] Cary Institute of Ecosystem Studies, Millbrook, New York

[w] Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China

[*] Corresponding author: chris.solomon@mcgill.ca

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Abstract

We assembled data from a global network of automated lake observatories to test hypotheses regarding the drivers of ecosystem metabolism. We estimated daily rates of respiration and gross primary production (GPP) for up to a full year in each lake, via maximum likelihood fits of a free-water metabolism model to continuous high-frequency measurements of dissolved oxygen concentrations. Uncertainties were determined by a bootstrap analysis, allowing lake-days with poorly constrained rate estimates to be down-weighted in subsequent analyses. GPP and respiration varied considerably among lakes and at seasonal and daily time scales. Mean annual GPP and respiration ranged from 0.1 to 5.0 mg O_2 L^{-1} d^{-1} and were positively related to total phosphorus (TP) but not dissolved organic carbon (DOC) concentration. Within lakes, significant day-to-day differences in respiration were common despite large uncertainties in estimated rates on some lake-days. Daily variation in GPP explained 5% to 85% of the daily variation in respiration after temperature correction. Respiration was tightly coupled to GPP at a daily scale in oligotrophic and dystrophic lakes, and more weakly coupled in mesotrophic and eutrophic lakes. Background respiration ranged from 0.017 to 2.1 mg O_2 L^{-1} d^{-1} and was positively related to indicators of recalcitrant allochthonous and autochthonous organic matter loads, but was not clearly related to an indicator of the quality of allochthonous organic matter inputs.

Introduction

Gross primary production (GPP) and respiration are perhaps the two most fundamental processes in ecosystems. At the cellular or organismal level, they describe biochemical pathways that make organic carbon molecules and energy available to cells. When these cellular processes are integrated across an entire ecosystem, the result – ecosystem-level gross primary production, ecosystem respiration, or collectively ecosystem metabolism – describes biogeochemical and trophic processes occurring at the system level.

There is substantial interest in understanding the controls on ecosystem metabolism in aquatic (Mulholland et al. 2001; Hanson et al. 2003; Roberts et al. 2007) and terrestrial (Lloyd and Taylor 1994; Baldocchi et al. 2001) systems. This interest dates back many years but has increased markedly in recent decades as research on global carbon cycles has expanded, because ecosystem metabolism is the primary control on carbon cycling in the biosphere. Lakes are hotspots for carbon cycling on the landscape, and play an appreciable role in regional and global carbon cycles (Cole et al. 2007; Tranvik et al. 2009). Consequently, understanding the controls on ecosystem metabolism in lakes is essential for describing the broader carbon cycle or predicting its response to ongoing environmental change.

In this paper we use a unique dataset to test existing models of the controls on ecosystem metabolism in lakes. Previous studies of ecosystem metabolism have generally faced a tradeoff between the temporal and spatial intensity of their sampling – they have either compared a few temporally discrete measurements among many lakes, or have made continuous and temporally extensive measurements in up to a few lakes. We have combined the strengths of those two approaches, estimating daily rates of ecosystem metabolism for up to a full year in each of 25 lakes from around the globe. We briefly describe patterns in gross primary production and net ecosystem production, but focus our analysis on describing rates of respiration within and among these lakes, as detailed in the hypotheses below.

Our first objective was to quantify day-to-day variation in respiration within each lake, and ask to what extent this variation was attributable to uncertainty in the estimates or to ecological processes. While gradual seasonal changes in ecosystem metabolism have been well-known for many years, recent studies using the free-water method have demonstrated substantial day-to-day variation around the seasonal mean (Cole et al. 2000; Staehr and Sand-Jensen 2007; Coloso et al. 2011a). In general it has been assumed that this variation is mostly due to methodological noise that should be averaged out to obtain more reliable estimates at coarser (weekly or monthly) temporal grains. This assumption has not been tested, because the direct calculation or 'bookkeeping' method of estimating metabolism from continuous dissolved oxygen (DO) data (Cole et al. 2000), which has been used in most studies to date, does not permit any quantification of the uncertainty surrounding the point estimate of respiration or GPP on a given day. In contrast, we estimated metabolic rates by maximum likelihood fits of a simple process model, and quantified the uncertainty in estimated rates with a bootstrap analysis. We used these results to test Hypothesis 1, that statistically significant day-to-day differences in respiration within a given lake would be rare.

Our second objective was to describe the relationship between respiration and the autochthonous (GPP) and allochthonous (terrestrial organic matter) inputs to the lake. Conceptually, total respiration can be apportioned into components attributable to the respiration of autotrophs, or to the respiration of heterotrophs metabolizing various substrates (Fig. 1; (del Giorgio and Williams 2005). This conceptual model leads to Hypotheses 2 and 3.

Hypothesis 2 concerns the dependence of respiration on GPP. Respiration is coupled to GPP because, except at short time scales, autotrophs and heterotrophs cannot collectively respire more autochthonous primary production than the autotrophs produce; in other words, R_{Auto} plus $R_{Hetero,Autoch}$ cannot exceed GPP (Fig. 1). Data and models suggest that the proportion of GPP that is respired is high (≥80%) except in very eutrophic lakes, where substantial production escapes immediate respiration and is instead buried or exported (Caraco and Cole 2004). Hypothesis 2 states that the respiration-GPP coupling should be high (slope of respiration on GPP between 0.8 and 1.0) in oligotrophic and dystrophic lakes, but decrease substantially with productivity in eutrophic lakes.

Hypothesis 3 concerns 'background' or 'baseline' respiration that is supported by allochthonous organic matter inputs and recalcitrant autochthonous organic matter, instead of by contemporary autochthonous production. Background respiration is equal to $R_{Hetero,Alloch}$ plus $R_{Hetero,Autoch-Slow}$ (Fig. 1). This rate is difficult to measure; several studies have estimated average background respiration across sets of lakes (del Giorgio and Peters 1994; del Giorgio et al. 1999; Cole et al. 2000) but to our knowledge only one has made lake-specific estimates to test potential drivers of variation (Mccallister and del Giorgio 2008). In principle, background respiration in a given lake should be related to the input, persistence, and degradability of refractory organic matter (del Giorgio and Williams 2005). This was the basis for our Hypothesis 3, that background respiration should increase with indicators of the quantity and quality of allochthonous organic matter loads and with indicators of the size of the available pool of recalcitrant autochthonous organic matter.

Methods

Lakes included in this analysis were selected from among those affiliated with the Global Lake Ecological Observatory Network (GLEON), based on the availability of data required for the free-water method of estimating metabolism (Odum 1956; Cole et al. 2000; Van De Bogert et al. 2007). High-frequency time series of dissolved oxygen (DO), photosynthetically active radiation (PAR), water temperature profiles, and wind speed were measured at regular intervals on automated buoys at each lake. Data sets were screened to remove out-of-range values, ‘flatline’ sequences of identical values over many readings, and isolated anomalous readings that were not formally out of range but which were extreme outliers relative to the readings over the surrounding minutes, hours, and days. Gaps of <60 min in PAR and water temperature data were filled by linear interpolation, and gaps in wind speed data were filled with the mean daily wind speed as long as data were available for at least 80% of the time points for that lake-day. When gaps in the PAR, water temperature, or wind speed data exceeded these thresholds we discarded the lake-day from further analysis. We also discarded lake-days for which >20% of the DO values were missing. Additional details about the data set and the lakes are provided (Table 1). The complete data set is available from the first author upon request.

We described diel dissolved oxygen dynamics for each lake-day with a simple model similar to those used by Van de Bogert et al. (2007) and Hanson et al. (2008):

$$Y_{t+1} = Y_t + \iota \bullet I_t - \rho + F_t + \gamma_t \qquad (1)$$

where Y_{t+1} and Y_t are the dissolved oxygen concentrations at times t+1 and t; I_t is the photosynthetically active radiation; ι is a parameter describing the average rate of photosynthesis per unit of PAR; ρ is a parameter describing the average rate of respiration; F_t is the flux of O_2 between the lake and the atmosphere; and γ_t is the process error. The atmospheric flux was calculated as:

$$F_t = d_t \bullet -k_t \bullet (Y_t - S_t) / z_{mix,t} \tag{2}$$

where k_t is the piston velocity of O_2 (Cole and Caraco 1998); S_t is the saturation concentration of O_2 given the water temperature and local average atmospheric pressure (Weiss 1970); $z_{mix,t}$ is the mixed layer depth, calculated as the shallowest depth at which the rate of density change exceeded 0.075 kg m^{-3} m^{-1} (Coloso et al. 2011*b*); and d_t is a dummy variable derived from $z_{mix,t}$, which indicates whether thermal stratification above the dissolved oxygen sensor prevents oxygen exchange with the atmosphere ($d_t = 0$) or whether the water column sampled by the sensor is free to exchange with the atmosphere ($d_t = 1$). We used a Nelder-Mead optimization algorithm to find the values of ι and ρ (both constrained positive) that minimized the negative log-likelihood of the errors, γ_t, for a given lake-day. These process errors are autocorrelated:

$$\gamma_{t+1} = \phi \bullet \gamma_t + \varepsilon_t \tag{3}$$

so for each lake-day we estimated the autocorrelation coefficient ϕ and the variance (σ^2) of the uncorrelated, normal errors ε. We report the results as gross primary production ($GPP=\iota \bullet \Sigma I_t$) and respiration ($\rho$), with units of mg O_2 L^{-1} d^{-1}. Examples of the input data and model fits are provided for several typical lake-days (Fig. 2). We used the R statistical package for model fitting and all subsequent analyses (R Development Core Team 2009). Model code is available from the first author upon request.

We used a bootstrapping procedure to estimate the uncertainty in estimated GPP and respiration. For each lake-day we used the estimated ϕ and σ^2 to generate a bootstrap time series of process errors γ_{boot} with the same autocorrelation structure as the real γ time series. These errors were added to the fitted Y values, creating a time series of dissolved oxygen pseudodata that we then used to fit Eq. 1. We repeated this process 10,000 times for each lake-day to obtain estimates of the variance and bootstrapped 95% confidence intervals for the parameters ι

and ρ. The bootstrap analysis revealed one lake-day (Rotoiti, 09 June 2009) for which estimates of ι and ρ were extremely uncertain; the standard deviation of the bootstrap estimates for these parameters on this lake-day were respectively 9000 and 94,000, whereas the maximum standard deviations across all of the other lake-days were 24 and 88. We therefore excluded this lake-day from further analysis. We tested Hypothesis 1 (significant day-to-day differences in respiration are rare) by looking, within each lake, for overlap between the 95% confidence interval (CI) for day n and the 95% CI for day $n+1$.

We fit regression models to describe the relationship between respiration and GPP in each lake and to estimate respiration-GPP coupling and background respiration. Autocorrelation and partial autocorrelation plots indicated that time series of respiration and GPP were autoregressive processes (Chatfield 2004). Based on these plots we considered models as complex as fifth-order autoregressive, or AR(5). Including this many autoregressive terms improved fits in some lakes (as judged by Akaike information criterion, AIC), but AR(1) models were sufficient for most lakes and yielded estimates of the non-autoregressive model parameters that were quite similar to those obtained from the higher-order models. For simplicity of interpretation, we therefore chose to fit AR(1) models for all of the lakes. Specifically, we used `R`'s arima() function to find the maximum likelihood estimates of the parameters in the following equation:

$$R_{20,t} = \alpha \bullet R_{20,t-1} + \beta_0 + \beta_1 \bullet P_{20,t} + \varepsilon_t \qquad (4)$$

$$\varepsilon_t \sim N(0,\sigma^2)$$

where $R_{20,t}$ and $P_{20,t}$ are the respiration and primary production on day t standardized to 20°C in order to remove the effect of mean daily water temperature on these rates (Holtgrieve et al. 2010). The parameters of primary interest in this equation are β_0 and β_1, which describe respectively the ‘background respiration’ not directly tied to autotrophic production and the slope of the relationship between R_{20} and P_{20} (Fig. 3). We fit Eq. 4 first to the nominal set of maximum likelihood estimates of respiration and GPP (we refer to this later as the 'nominal fit'), and then to each of the 10,000 bootstrapped sets of estimates of respiration and GPP, in order to incorporate the uncertainty in the original estimates of respiration and GPP into the uncertainty in the estimated parameters of Eq. 4.

The results of this analysis were used to test Hypothesis 2 (differences in respiration-GPP coupling with lake trophy) and Hypothesis 3 (background respiration related to allochthonous loads and recalcitrant autochthonous pool). For Hypothesis 2, we plotted the bootstrapped distribution of β_1 for each lake against total phosphorus (TP) concentration, and asked whether the resulting plot conformed qualitatively to the predicted pattern. For Hypothesis 3, we used similar plots as well as simple linear regressions to test relationships between β_0 and indicators of the quantity of allochthonous organic matter inputs, the quality of allochthonous organic matter inputs, and the quantity of autochthonous organic matter inputs to the recalcitrant, 'slow' pool. These indicators were, respectively, the ratio of watershed area to lake volume ($A_{watershed}$:V_{lake}); water color measured as absorbance at 440 nm (a_{440}); and the β_1 estimates, low values of which indicate that substantial phytoplankton production escapes water column respiration and may be deposited on the sediments.

Results

Lake characteristics

The lakes in our data set ranged considerably in surface area ($5 \cdot 10^{-3}$ to $2.3 \cdot 10^{5}$ km^2), mean depth (0.7 to 31 m), residence time (0.03 to 10.4 years), TP concentration (4 to 186 μg L^{-1}), dissolved organic carbon (DOC) concentration (1.3 to 17.3 mg L^{-1}), and other characteristics

(Table 1). They were predominantly in the north temperate zone, although four were subtropical and two were in the south temperate zone. Lakes with high $A_{watershed}$:V_{lake} tended to have short residence times and high TP and DOC concentrations, although TP and DOC were not significantly correlated (Table 2). DOC concentrations and water color (a_{440}) also tended to be higher in small and shallow lakes (Table 2).

Daily, seasonal, and annual rates of GPP, respiration, and net ecosystem production (NEP)

Gross primary production and respiration varied considerably among lakes and at seasonal and daily time scales (Fig. 4). Peak rates of GPP varied among lakes from 0.4 to 25 mg O_2 L^{-1} d^{-1}, and peak rates of respiration from 0.4 to 20 mg O_2 L^{-1} d^{-1}. Seasonal patterns in GPP and respiration were apparent in most of the lakes for which data sets spanned multiple seasons, although the timing of this seasonal variation, and its amplitude relative to shorter-term variation, was variable. For instance, Kentucky Lake had a much stronger mid-summer peak than Lake Pontchartrain even though the two lakes are at similar latitudes; tropical Yuan Yang Lake had a late, wet-season peak; and Lough Feeagh, which experiences a mild oceanic climate relative to its latitude, showed a clear but weak mid-summer peak (Fig. 4).

Mean annual GPP and respiration were strongly related to TP concentration ($p<0.0001$ for log-transformed linear regressions), but not to DOC concentration ($p>0.28$; Fig. 5). This pattern held regardless of whether we used all of the available estimates of GPP and respiration for each lake or just the summer estimates, whether we used temperature-corrected or uncorrected rates, or whether we restricted the data set to include only days with reasonably narrow confidence intervals on respiration and GPP (coefficient of variation CV<50%). Mean daily NEP (GPP-respiration) was between -1.0 and 1.0 mg O_2 L^{-1} d^{-1} for most lakes, although several lakes with high TP and moderate DOC concentrations had large positive NEP (Fig. 5, Table 3).

Uncertainty and variability in respiration

A surprising proportion of the day-to-day variability in respiration was apparently attributable to ecological variability, not just model uncertainty, in contrast to Hypothesis 1. Confidence intervals for estimates of respiration and GPP were wide for some lake-days and narrow for others (Fig. 6). Despite the fact that confidence intervals were sometimes wide, significant day-to-day differences in rates (as indicated by non-overlapping confidence intervals between day i and day i+1) were quite common, occurring on 2-50% of days (median 15%). The proportion of days on which these significant day-to-day differences occurred was negatively related to lake area and perhaps also to the time interval of the DO measurements (linear regression: $y = 0.27 - 0.025 \cdot \log_{10}(\text{lakeArea}) - 0.0024 \cdot \text{timeInterval}$; $p<0.0001$, $p=0.06$, $p=0.09$ for partial *t*-tests of the intercept, lakeArea, and timeInterval coefficients). The negative relationship with lake area implies that large lakes exhibit either smaller day-to-day variability in respiration point estimates (i.e., less ecological variability), or larger within-day uncertainty around those point estimates (i.e., more model uncertainty). We considered the first explanation by calculating the standard deviation of the daily respiration rates for each lake, after taking first differences to remove the mean and seasonal trend from the respiration rate time series. This analysis did not reveal any effect of lake size on day-to-day variability in respiration. We considered the second explanation by calculating the coefficient of variation of the bootstrapped estimates of respiration for each lake-day, and comparing this set of CVs to lake area. This analysis showed that most lakes had some days on which the CV of the bootstrapped respiration rates was large (i.e., CV>100%; between 0% and 77% of days, median 14% of days, no relationship between proportion of days and lake area), and that there was a significant negative relationship between the CV of respiration and lake area only when these extreme days were included in the data set. Thus days on which dissolved oxygen dynamics yield high uncertainties in respiration estimates occur in small and large lakes at similar frequency, but in small lakes the magnitude of that uncertainty rarely reaches the extremely high levels sometimes seen in large lakes. This agrees well with our intuition, based on visual inspection of daily DO-time plots from each lake, that small lakes generally exhibited diel oxygen dynamics that were less noisy and more similar to the sinusoidal pattern described by the model than were those in large lakes. Thus while ecological variability is similar across the lake size gradient, model uncertainty may be higher in large lakes due to large-scale water movements that cause significant deviations from expected diel DO curves.

Nominal fits of the autoregressive models (Eq. 4) to the maximum likelihood estimates of respiration and primary production for each lake explained between 5% and 85% of the observed variation in R_{20} (Table 4, Fig. 7). The amount of explained variation was not related to the number of days for which metabolism estimates were available, nor to the average uncertainty of those metabolism estimates. Model predictions were generally higher than observations on days when observations were near-zero (Fig. 7, *see* e.g., Acton, Mendota, Sparkling), and in some lakes were lower than observations on days when observations were very high (Fig. 7, *see* e.g., Mendota, Müggelsee, Rotoiti). Standard errors for the parameter estimates from these nominal fits were generally fairly small (Table 4), and for β_0 (but not β_1) the bootstrapped standard errors were even smaller than the nominal ones. The reduction in the β_0 standard errors in the bootstrapped relative to the nominal analysis indicates that incorporating the within-day uncertainty into the analysis of the among-day relationship between R_{20} and P_{20} improved our ability to estimate β_0 precisely.

Coupling of respiration to GPP

Coupling between respiration and primary production at the daily scale (β_1) was generally strong in oligotrophic and dystrophic lakes and weaker in eutrophic lakes, as predicted by Hypothesis 2 (Fig. 8). Estimates of β_1 were close to 1 for most lakes at TP up to 20-40 μg L^{-1}, but decreased considerably as TP increased beyond that level. There were two major exceptions to this pattern: Lake Sunapee (TP=5.3 μg L^{-1}) and Sparkling Lake (TP=10.0 μg L^{-1}) had much lower β_1 estimates than other lakes of similar productivity. Both of these lakes had many days with near-zero estimates of respiration, which caused the autoregressive model to over-predict respiration rates when they were low and under-predict them when they were high, and therefore drove low estimates of β_1 (Fig. 7). Excluding these potentially invalid estimates, in general both oligotrophic and dystrophic lakes showed strong coupling of respiration and primary production with $\beta_1 \approx 1$; it was only in high-TP, moderate-DOC lakes that β_1 was substantially less than 1.

One lake (Taihu, TP=186 μg L^{-1}, rightmost bar in Fig. 8) had a very uncertain estimate of β_1, with 25th and 75th percentiles of 0.32 and 1.06. This uncertainty was largely due to the very high bootstrapped variances for the metabolism parameters ι and ρ on two days, 12 and 29 December; these two days had the highest variances for these parameters of any lake-day excluding the one clearly anomalous day from Rotoiti that we discarded (*see* Methods). If these two days are excluded from the Taihu analysis, the median estimate of β_1 is unchanged but the 25th and 75th percentiles change to 0.49 and 0.70.

Background respiration

Background respiration varied across lakes in a manner consistent with the allochthonous load and autochthonous load effects described in Hypothesis 3 (Fig. 9). Median estimates of background respiration ranged from 0.017 to 2.1 mg O_2 L^{-1} d^{-1}. Background respiration increased with $A_{watershed}$:V_{lake}, an indicator of allochthonous organic matter load (Fig. 9A; p=0.005,

R^2=0.31 for log-log regression). Similarly, background respiration was higher in lakes where the input of autochthonous organic matter to the relatively slow-turnover pool was high, as indicated by weak respiration-GPP coupling (Fig. 9B; p=0.005, R^2=0.32 after dropping Sunapee and Sparkling, for which β_1 estimates were suspect as described above; p=0.09 with all lakes included; β_0 log-transformed). There was no correlation between $A_{watershed}$:V_{lake} and respiration-GPP coupling (r=0.03), so their effects were orthogonal; partial t-tests indicated significant effects of each predictor on background respiration even with the other predictor included in the model (p<0.03). In contrast, there was not clear support for the prediction that background respiration would be negatively related to organic matter recalcitrance, as indicated by water color (a_{440}; Fig. 9C). The data were suggestive of a quadratic relationship, whereby background respiration increased with water color up to a_{440}=2.2 m^{-1} but decreased with further increases in water color beyond that point. However, neither quadratic nor linear terms for a_{440} were significantly related to background respiration (p>0.3, log-log regression).

Discussion

In this paper we harnessed GLEON, a grassroots network of researchers and automated ecological observatories, to assemble a metabolism data set unique in its combination of temporally intensive, temporally extensive, and spatially extensive observation of lakes. Networked observatories are increasingly common in lakes, streams, oceans, and terrestrial ecosystems, so opportunities for research at this scale will continue to grow. While there are significant logistical challenges associated with this kind of work, the payoff is the ability to ask questions in ways that would have been impossible even a decade ago. In our analysis we focused on three questions about patterns in daily rates of ecosystem respiration, as well as a more general description of average annual rates. We discuss our results regarding each of these topics below.

Does average annual respiration increase with DOC?

Limnologists increasingly view DOC concentration as a master variable, akin to TP concentration, which describes many aspects of the structure and function of lake ecosystems (Prairie 2008). With respect to ecosystem metabolism, a simple, common conceptual model is that DOC increases respiration, just as TP increases GPP; thus lakes with higher DOC concentrations should tend towards heterotrophy. We did not observe a relationship between DOC concentration and average annual respiration in this data set (Fig. 5). A slightly more elaborate conceptual model emphasizes several complexities: first, limnologists usually measure TP and DOC concentrations, whereas for some processes it is the loads rather than the concentrations that matter; second, loads or concentrations of TP and DOC may be correlated, although that correlation could differ regionally or as the result of anthropogenic activities; third, DOC quality varies; and fourth, the shading effect of DOC can reduce GPP and, thereby, the autotrophic component of respiration. These complexities may help to explain our results and the lack of consensus apparent in the literature about the effects of DOC on community or ecosystem respiration, with some surveys reporting a clear effect of DOC on respiration while others report no effect (Table 5). Resolving this puzzle will require that limnologists begin to couple measurements of respiration with characterization of organic matter loads in terms of quantity and quality (Prairie et al. 2002; del Giorgio and Williams 2005; Hanson et al. 2011).

Uncertainty and variability in metabolism estimates

Our explicit consideration of uncertainty in metabolism estimates was an important and valuable part of our analysis. It is also relatively unusual; most estimates of aquatic ecosystem metabolism to date have used a mathematical bookkeeping approach (Odum 1956; Cole et al. 2000), which does not permit quantification of uncertainty. Recent developments of statistical metabolism models using maximum likelihood and Bayesian approaches, like the one that we used here, offer a useful alternative to the bookkeeping approach (Van De Bogert et al. 2007; Holtgrieve et al. 2010). While the simplicity of the bookkeeping approach will continue to dictate its use in some settings, we believe that broader use of statistical metabolism models will benefit the field. The uncertainty estimates that can be extracted from these models allow individual metabolism estimates, or apparent differences in metabolism between two time points, to be interpreted appropriately (Fig. 6). They also allow the methodological uncertainty in the estimates to be carried through to models seeking to explain the drivers of variation in metabolic rates, as in our bootstrap analysis of Eq. 4. This kind of analysis is analogous to a weighted regression, in which observations with high variance receive less weight in fitting the model. The high variance in metabolism estimates that we observed on some days underscores the value of such an analysis.

As an example of the value of carrying through these uncertainties, and of the potential consequences of ignoring them, we compared two estimates of β_1, the slope of respiration on GPP. The nominal point estimates (Table 4) are derived from fitting Eq. 4 to a single data set, the maximum likelihood point estimates of respiration and GPP for each day in a given lake. The bootstrap point estimates (medians in Fig. 8) are derived from fitting Eq. 4 to many bootstrapped data sets in order to account for the uncertainty in the respiration and GPP estimates for each day in a given lake. We saw that the nominal estimates were generally lower than the bootstrapped estimates (slope of bootstrapped on nominal = 0.81 ± 0.03 SE in simple linear regression). This occurred because in most lakes there were days with positive respiration and near-zero but highly uncertain GPP, and/or days with positive GPP and near-zero but highly uncertain respiration. In other words, in most lakes plots of respiration vs. GPP show points lined up along x ~ 0 and/or along y ~ 0. When the uncertainty in these points is ignored, resulting estimates of β_1 are biased lower; down-weighting these points in proportion to their uncertainty reduces or eliminates that bias. Lake Sunapee provides an extreme example of this effect, with a nominal $\beta_1 = -0.21$ but a median bootstrap $\beta_1 = 0.16$. Similar effects could occur in any analysis seeking to relate metabolism estimates to drivers like temperature, mixing depth, algal biomass, and so forth.

Where does this uncertainty come from? Generally speaking, process errors and low signal-to-noise ratios are the two important sources of uncertainty in metabolism models like the one described by Eqs. 1-3. Process errors occur when the dissolved oxygen concentration changes as a result of some process that is not explicitly included in the model, or due to the misspecification of a process that is in the model. For instance, horizontal or vertical mixing of water bodies with different DO concentrations (perhaps as a result of spatial heterogeneity in metabolic rates) can cause significant DO excursions (Gelda and Effler 2002; Lauster et al. 2006; Van De Bogert et al. 2012). Our model, like most others, does not attempt to explicitly model these mixing events, and therefore treats them as process errors. Low signal-to-noise ratios occur when changes in DO due to metabolic processes are small relative to sensor chatter, environmental patchiness, and other sources of stochastic variation in DO observations. A detailed analysis of parameter uncertainties from some of the lakes in our data set has been undertaken by K. Rose (unpubl.), who found that daily PAR (which affects the signal-to-noise ratio of the DO data) and lake number (an indicator of water column physical stability relative to destabilizing forces and therefore of process errors related to stratification and mixing) were both significant predictors of parameter uncertainty, especially in larger lakes.

Several methodological improvements could potentially reduce the uncertainty in metabolism estimates. Perhaps the simplest improvement to implement (and one with almost no marginal cost) is to measure DO concentrations fairly frequently, at intervals of 1 to perhaps 10 minutes at the most, depending on the response time of the sensor. Our analysis indicated that frequent measurements probably reduced parameter uncertainty; this makes sense because more frequent measurements give a clearer picture of oxygen dynamics and therefore help to constrain model fits. Some other improvements are costlier or more difficult to implement, and therefore their utility should be assessed relative to the needs of the study. For instance, multi-compartment or spatially averaging models could allow spatial heterogeneity and mixing dynamics to be incorporated explicitly instead of treated as process errors (Van De Bogert et al. 2007; Staehr et al. 2012b; Van De Bogert et al. 2012), although such models are unlikely to improve on the simpler version that we used here without additional data to constrain the processes in question (Hanson et al. 2008). As another example, statistical filtering techniques and state-space models can help to improve the signal-to-noise ratio in DO data or allow the simultaneous quantification of observation and process errors, especially when DO measurements are made frequently (Coloso et al. 2008; Batt and Carpenter 2012).

A substantial amount of variability in respiration was not explained by temperature or GPP in our autoregressive models (Fig. 7). Previous studies that have sought to relate daily variability in respiration to a variety of predictor variables have similarly found substantial unexplained variability (Staehr and Sand-Jensen 2007; Tsai et al. 2008; Coloso et al. 2011a). As our study emphasizes, some of this unexplained variability is due to the uncertainty of the respiration and primary production estimates themselves. Some variability may also be attributable to spatial heterogeneity in rates, in combination with changes in the size or orientation of the sensor footprint (Lauster et al. 2006; Van De Bogert et al. 2007; Van De Bogert et al. 2012). Finally, some variability should be due to the biomass, activity, and perhaps the composition of the heterotrophic assemblage, and to the quantity and quality of substrates available for respiration. Some of these factors have received attention in the literature already; for instance, Tsai et al. (2008), Staehr et al. (2010), and Coloso et al. (2011*a*) identified DOC or colored dissolved organic matter as significant predictors of daily respiration in at least some lake-years. There is a clear need, however, for further empirical studies and models to better describe why respiration varies at short time scales in lakes.

Coupling of respiration to GPP

Our results were broadly consistent with Hypothesis 2, which predicted that coupling between respiration and primary production should be strong in oligotrophic and dystrophic lakes, and weaker in eutrophic lakes where substantial production may escape immediate respiration. While the relationship between average respiration and average GPP across lakes has been well characterized (del Giorgio and Peters 1994; Duarte and Agusti 1998), with the exception of this study there are to date relatively few estimates of the relationship between daily (or similar) respiration and GPP within lakes (Staehr et al. 2010; Coloso et al. 2011a; Laas et al. 2012). Those that are available generally indicate strong coupling of respiration to GPP. In a set of four fertilized lakes with TP between 10 and 100 μg L^{-1}, weekly respiration and GPP estimates, when fit to the model of Caraco and Cole (2004), were consistent with a 90% d^{-1} rate of respiration (Cole et al. 2000).

A recent study by Sadro et al. (2011) highlights the substrate limitation of heterotrophs that presumably drives tight coupling between respiration and GPP in oligotrophic systems. In oligotrophic, alpine Emerald Lake, these authors observed overnight respiration of up to 46% of daytime GPP by heterotrophic bacterioplankton alone. Considering additional sources of respiration including autotrophs and metazoans, it is clear that most of each day's GPP must be respired before the next day dawns in oligotrophic lakes like this.

Estimates of β_1 (respiration-GPP coupling) were significantly greater than 1 in Kentucky Lake (lower bound of 95% CI = 1.06) and Lake Rotorua (lower bound of 95% CI = 1.04), indicating that unit increases in GPP in these lakes yielded, on average, greater than unit increases in respiration. At least two explanations for these surprising results seem possible. First, they may represent Type I errors; in constructing 25 confidence intervals at the 95% level to test the null hypothesis that β_1 should be ≤ 1, one or two false positives could reasonably be expected. Alternatively, greater-than-unit increases in respiration with GPP could result from metabolic 'priming' of heterotrophs by autotrophs, whereby labile autochthonously produced organic matter enables degradation of otherwise recalcitrant allochthonous organic matter (Guenet et al. 2010; Townsend et al. 2011). Indeed priming effects could be occurring in the other lakes as well, but would not be detectable by our analysis except when they push the slope of respiration on GPP up over 1. Priming effects would tend to bias our estimates of background respiration (β_0) towards lower values, because they would cause respiration of allochthonous and slow autochthonous pools to look like respiration of fast autochthonous pools in our analysis.

Our estimates of β_1 provide an empirical test of a simple lake and river carbon cycle model put together by Caraco and Cole (2004). The Caraco and Cole model calculates a quantity similar to our β_1, which we will call $\beta_{1\text{-CC}}$. Specifically, for a given TP and water load, their model calculates GPP, burial, and export from empirical equations; calculates the respiration of autochthonous production (R_{aut}) as the difference between GPP and the sum of export and burial; and then calculates the proportion of autochthonous production that is respired as R_{aut}/GPP = $\beta_{1\text{-}}$

$_{CC}$. This quantity should be somewhat greater than β_1 because it accounts for respiration of autochthonous organic matter within both the fast and slow pools, while β_1 accounts for only the fast pool.

Estimates of $\beta_{1\text{-}CC}$ from Caraco and Cole's (2004) model were close to 1 in oligotrophic and mesotrophic lakes, decreasing with water load to a minimum of ~ 0.9 at the highest water loads typical of lakes. In eutrophic systems, model estimates of $\beta_{1\text{-}CC}$ were slightly lower but still close to 1 across most of the range of lake-like water loads, although at high water loads there was a much more pronounced decrease in $\beta_{1\text{-}CC}$, to ~ 0.6, due to increased export.

In our study, TP concentrations spanned the oligotrophic to eutrophic gradient, and water loads (calculated as z_{mean} / residence time) ranged from 1 to 75 m yr^{-1}. Our results (Fig. 8) agreed with the predictions of the Caraco and Cole (2004) model in that β_1 was usually near 1 in low-TP systems. Lough Feeagh was an exception to this pattern, with β_1=0.71 and TP=7.3 μg L^{-1}; this may be because Feeagh has a high water load (31 m yr^{-1}) relative to its TP concentration, such that export of autochthonous production is probably high even though the concentration of autochthonous organic matter in the water column is not. Sparkling and Sunapee were also apparent exceptions to the pattern of high β_1 at low TP, but the β_1 estimates for these two lakes are probably invalid, as described in the Results. Our results also agree broadly with the model predictions in indicating that β_1 is lower at high TP concentrations. However, we identified a surprisingly low TP threshold above which considerable autochthonous production escapes immediate respiration; while the model predicts almost no difference in $\beta_{1\text{-}CC}$ between oligotrophic and mesotrophic lakes, we saw that many mesotrophic lakes with TP as low as 20 μg L^{-1} had β_1 considerably less than 1. This suggests that export and/or at least short-term burial (sedimentation) increase relatively quickly with TP, implying that the spatial division of total

R_{aut} among pelagic, benthic, and downstream compartments differs between oligotrophic systems and those that are naturally or culturally more eutrophic. Spatial displacement of respiration from the pelagic zones to other habitats may have important carbon cycle implications; for instance, organic matter that is degraded in the sediments is more likely to be anaerobically respired and returned to the atmosphere as methane than organic matter degraded in the water column (West et al. 2012). Another discrepancy between our results and the model predictions lies in the water load effect; we did not observe the predicted negative relationship between β_1 and water load, considering either all lakes together or the oligo-, meso-, and eutrophic lakes separately (data not shown).

Background respiration

The rates of background respiration that we estimated in this study were similar to those reported by previous studies that employed quite different approaches. In the following discussion we have converted rate estimates from their reported units to match the units used in this paper, assuming a respiratory quotient of 1 when necessary to convert from C to O currency. del Giorgio and Peters (1994) estimated average planktonic respiration and GPP in each of 20 Québec lakes, which had summer TP concentrations between 5 and 46 μg L^{-1} and DOC between 2.7 and 7.5 mg L^{-1}. They took the intercept of the across-lake regression of respiration on GPP as an estimate of a common background respiration rate equivalent to 0.07 mg O_2 L^{-1} d^{-1}. A later simulation model suggested four-fold variation in background respiration among this same set of lakes (del Giorgio et al. 1999). McCallister and del Giorgio (2008) estimated lake-specific background respiration in 8 Québec lakes, including some of those studied by del Giorgio and Peters (1994), via measurements of the δ^{13}C of respired C and a mass balance model. This approach allowed them to isolate the $R_{Hetero,Alloch}$ component of background respiration (Fig. 1), which varied between 0.05 and 0.12 mg O_2 L^{-1} d^{-1}. In the present study we estimated lake-specific background respiration in 25 lakes by calculating daily estimates of respiration using the free-water dissolved oxygen method and regressing them on daily estimates of primary production from the same method. Over a range of DOC and TP concentrations similar to those in the studies above, we observed background respiration between roughly 0.02 and 0.5 mg O_2 L^{-1} d^{-1}. Our estimates are thus similar to or slightly higher than those reported previously. The tendency for our approach to yield slightly higher estimates is expected because, unlike the bottle incubation or $\delta^{13}C$ methods, our approach incorporates some signal of sediment respiration in addition to water column respiration (Van De Bogert et al. 2007). Nonetheless, the similarity in rate estimates across these studies is striking, and suggestive of quite general controls on rates of background respiration in lakes.

The relationships that we observed between background respiration and $A_{watershed}$:V_{lake} (Fig. 9A) and between background respiration and respiration-GPP coupling (Fig. 9B) were consistent with the hypothesized response of background respiration to allochthonous and autochthonous inputs into a slow-turnover pool of organic matter. On the other hand, while $A_{watershed}$:V_{lake} is a good indicator of allochthonous organic matter loads (Canham et al. 2004), it is also correlated with nutrient loads (and therefore with TP; Table 2). This finding leads to asking whether the significant relationship between background respiration and $A_{watershed}$:V_{lake} might really be due to some nutrient-driven mechanism, rather than to allochthonous organic matter inputs. We assessed this possibility by fitting regression models including log-transformed TP, $A_{watershed}$:V_{lake}, or both as predictors of log-transformed background respiration, and comparing these models using AIC_c, the finite-sample corrected AIC (Burnham and Anderson 1998). This analysis indicated that $A_{watershed}$:V_{lake} by itself ($AIC_c = 59$) was a much better predictor of background respiration than was TP by itself ($AIC_c = 67$), although including both predictors improved the fit ($AIC_c = 55$). This suggests that an effect of nutrients on background respiration exists but that it is considerably weaker than the allochthonous inputs effect. In contrast, respiration-GPP coupling by itself was not as good a predictor of background respiration ($AIC_c = 79$) as TP by itself ($AIC_c = 67$), nor did adding respiration-GPP coupling to the TP model yield any improvement in fit ($AIC_c = 68$). This is consistent with our understanding of the autochthonous input mechanism indicated by the respiration-GPP coupling variable. Thus our results do seem to indicate that both allochthonous organic matter inputs from the watershed, and excess autochthonous production driven by nutrient enrichment, increase background respiration in lakes.

In what is to our knowledge the only other study to compare empirical background respiration estimates among lakes, McCallister and del Giorgio (2008) observed only a weak positive relationship between the planktonic bacterial respiration supported by allochthonous organic matter (roughly $R_{\text{Hetero,Alloch}}$; Fig. 1) and DOC concentration. Thus while they saw a substantial range of variation in total planktonic bacterial respiration (roughly $R_{\text{Hetero,Autoch-Fast}} + R_{\text{Hetero,Autoch-Slow}} + R_{\text{Hetero,Alloch}}$; Fig. 1), this variation was attributable chiefly to increasing $R_{\text{Hetero,Autoch}}$ in lakes with higher chlorophyll *a* concentrations, not to increasing $R_{\text{Hetero,Alloch}}$ in lakes with higher DOC concentrations. In contrast, to the extent that $A_{\text{watershed}}:V_{\text{lake}}$ is in fact an indicator of allochthonous organic matter loads independent of autochthonous primary production, our results suggest that $R_{\text{Hetero,Alloch}}$ may in fact vary appreciably with allochthonous inputs, just as $R_{\text{Hetero,Autoch}}$ varies with autochthonous primary production. Because loads and standing stocks are not necessarily strongly correlated, the $R_{\text{Hetero,Alloch}}$-DOC relationship that McCallister and del Giorgio (2008) observed and the background respiration - $A_{\text{watershed}}:V_{\text{lake}}$

relationship that we observed may be consistent descriptions of the same underlying processes. Future studies could explore these questions by coupling high-frequency measurements of respiration rates with direct measures of allochthonous loads and autochthonous primary production.

We did not find clear support for the hypothesized negative effect of organic matter recalcitrance on background respiration. While there was no significant linear or quadratic relationship between background respiration and a_{440}, the data are suggestive of a humped relationship in which background respiration at first increases with water color up to $a_{440} \sim 2$ m^{-1} and then decreases with water color beyond that point. This pattern could occur if weakly chromophoric terrestrial inputs provide labile substrates without strongly affecting light and heat profiles, while strongly chromophoric inputs provide recalcitrant substrates, reduce autochthonous inputs to the slow pool via shading of phytoplankton, and reduce the extent of warm oxygenated sediments via thermocline steepening. Our data may suggest a compensation point between these positive and negative effects at water colors around $a_{440} = 2$ m^{-1}. Alternatively, organic matter quality may be too complex to characterize adequately with a_{440} within the context of this study, or may interact with other lake characteristics such as residence time (Guillemette and del Giorgio 2011). Again, coupling our temporally intensive and geographically extensive approach with more detailed measures of allochthonous loads may be a productive avenue for further study.

Future directions

Taken as a whole, our results support and extend some long-standing conceptual models of aquatic ecosystem metabolism, such as the relationship between background respiration and allochthonous organic matter loads, while questioning others, such as the relationship between annual average respiration and DOC concentration. Data sets like the one that we used here are expanding rapidly, and will continue to provide novel research opportunities for years to come. As we have highlighted repeatedly here, one of the most productive avenues for such research is likely to be the combination of automated sensor data with other methodologies that have different inferential strengths, such as large-scale experimentation and ‘traditional’ manual measurements of rates and concentrations that are not measurable by automated sensors. Work in this vein promises to continue to extend our descriptive and predictive understanding of metabolism and carbon cycling in aquatic ecosystems.

Literature cited

Ask, J., J. Karlsson, and M. Jansson. 2012. Net ecosystem production in clear-water and brown-water lakes. Global Biogeochem. Cycles **26:** GB1017, doi:10.1029/2010gb003951

Baldocchi, D., E. Falge, L. H. Gu, R. Olson, D. Hollinger, S. Running, P. Anthoni, C. Bernhofer, K. Davis, R. Evans, J. Fuentes, A. Goldstein, G. Katul, B. Law, X. H. Lee, Y. Malhi, T. Meyers, W. Munger, W. Oechel, K. T. P. U, K. Pilegaard, H. P. Schmid, R. Valentini, S. Verma, T. Vesala, K. Wilson, and S. Wofsy. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Amer. Meteorol. Soc. **82:** 2415-2434.

Batt, R. D., and S. R. Carpenter. 2012. Free-water lake metabolism: Addressing noisy time series with a Kalman filter. Limnology And Oceanography: Methods **10:** 20-30.

Britton, C. M., and J. D. Dodd. 1976. Relationships of photosynthetically active radiation and shortwave irradiance. Agr Meteorol **17:** 1-7.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer.

Canham, C. D., M. L. Pace, M. J. Papaik, A. G. B. Primack, K. M. Roy, R. J. Maranger, R. P. Curran, and D. M. Spada. 2004. A spatially explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes. Ecological Applications **14:** 839-854.

Caraco, N. F., and J. J. Cole. 2004. When terrestrial organic matter is sent down the river: Importance of allochthonous C inputs to the metabolism in lakes and rivers, p. 301-316. *In* G. A. Polis, M. E. Power and G. Huxel [eds.], Food webs at the landscape level. University of Chicago Press.

Carignan, R., D. Planas, and C. Vis. 2000. Planktonic production and respiration in oligotrophic Shield lakes. Limnol. Oceanogr. **45:** 189-199.

Chatfield, C. 2004. The analysis of time series. Chapman and Hall.

Cole, J. J., and N. F. Caraco. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6. Limnol. Oceanogr. **43:** 647-656.

Cole, J. J., M. L. Pace, S. R. Carpenter, and J. F. Kitchell. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. **45:** 1718-1730.

Cole, J. J., Y. T. Prairie, N. F. Caraco, W. H. Mcdowell, L. J. Tranvik, R. G. Striegl, C. M. Duarte, P. Kortelainen, J. A. Downing, J. J. Middelburg, and J. Melack. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems **10:** 171-184.

Coloso, J. J., J. J. Cole, P. C. Hanson, and M. L. Pace. 2008. Depth-integrated, continuous estimates of metabolism in a clear-water lake. Can. J. Fish. Aquat. Sci. **65:** 712-722.

Coloso, J. J., J. J. Cole, and M. L. Pace. 2011a. Difficulty in discerning drivers of lake ecosystem metabolism with high-frequency data. Ecosystems **14:** 935-948.

Coloso, J. J., J. J. Cole, and M. L. Pace. 2011b. Short-term variation in thermal stratification complicates estimation of lake metabolism. Aquatic Sciences **73:** 305-315.

del Giorgio, P. A., J. J. Cole, N. F. Caraco, and R. H. Peters. 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. Ecology **80:** 1422-1431.

del Giorgio, P. A., and R. H. Peters. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnol. Oceanogr. **39:** 772-787.

del Giorgio, P. A., and P. J. L. B. Williams. 2005. The global significance of respiration in aquatic ecosystems: from single cells to the biosphere, p. 267-303. *In* P. A. del Giorgio and P. J. l. B. Williams [eds.], Respiration in aquatic ecosystems. Oxford University Press.

Duarte, C. M., and S. Agusti. 1998. The CO balance of unproductive aquatic ecosystems. Science **281:** 234-236.

Gelda, R. K., and S. W. Effler. 2002. Metabolic rate estimates for a eutrophic lake from diel dissolved oxygen signals. Hydrobiologia **485:** 51-66.

Guenet, B., M. Danger, L. Abbadie, and G. Lacroix. 2010. Priming effect: bridging the gap between terrestrial and aquatic ecology. Ecology **91:** 2850-2861.

Guillemette, F., and P. A. del Giorgio. 2011. Reconstructing the various facets of dissolved organic carbon bioavailability in freshwater ecosystems. Limnol. Oceanogr. **56:** 734-748.

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. **48:** 1112-1119.

Hanson, P. C., S. R. Carpenter, N. Kimura, C. Wu, S. P. Cornelius, and T. K. Kratz. 2008. Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. Limnology and Oceanography: Methods **6:** 454-465.

Hanson, P. C., D. P. Hamilton, E. H. Stanley, N. Preston, O. C. Langman, and E. L. Kara. 2011. Fate of allochthonous dissolved organic carbon in lakes: A quantitative approach. PLoS One **6:** e21884, doi:10.1371/journal.pone.002188.

Holtgrieve, G. W., D. E. Schindler, T. A. Branch, and Z. T. A'mar. 2010. Simultaneous quantification of aquatic ecosystem metabolism and reaeration using a Bayesian statistical model of oxygen dynamics. Limnol. Oceanogr. **55:** 1047-1063.

Laas, A., P. Nõges, T. Kõiv, and T. Nõges. 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia **694:** 57-74.

Lauster, G. H., P. C. Hanson, and T. K. Kratz. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Can. J. Fish. Aquat. Sci. **63:** 1130-1141.

Lloyd, J., and J. A. Taylor. 1994. On the temperature dependence of soil respiration. Functional Ecology **8:** 315-323.

Mccallister, S. L., and P. A. del Giorgio. 2008. Direct measurement of the $\delta^{13}C$ signature of carbon respired by bacteria in lakes: Linkages to potential carbon sources, ecosystem baseline metabolism, and CO_2 fluxes. Limnol. Oceanogr. **53:** 1204-1216.

Mulholland, P. J., C. S. Fellows, J. L. Tank, N. B. Grimm, J. R. Webster, S. K. Hamilton, E. Marti, L. Ashkenas, W. B. Bowden, W. K. Dodds, W. H. Mcdowell, M. J. Paul, and B. J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshw. Biol. **46:** 1503-1517.

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. **1:** 102-117.

Pace, M. L., and Y. Prairie. 2005. Respiration in lakes, p. 103-121. *In* P. A. del Giorgio and P. J. l. B. Williams [eds.], Respiration in aquatic ecosystems. Oxford University Press.

Prairie, Y. T. 2008. Carbocentric limnology: Looking back, looking forward. Can. J. Fish. Aquat. Sci. **65:** 543-548.

Prairie, Y. T., D. F. Bird, and J. J. Cole. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnol. Oceanogr. **47:** 316-321.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems **10:** 588-606.

Sadro, S., C. E. Nelson, and J. M. Melack. 2011. Linking diel patterns in community respiration to bacteriplankton in an oligotrophic high-elevation lake. Limnol. Oceanogr. **56:** 540-550.

Sand-Jensen, K., and P. A. Staehr. 2007. Scaling of pelagic metabolism to size, trophy and forest cover in small Danish lakes. Ecosystems **10:** 127-141.

Staehr, P. A., L. Baastrup-Spohr, K. Sand-Jensen, and C. Stedmon. 2012a. Lake metabolism scales with lake morphometry and catchment conditions. Aquatic Sciences **74:** 155-169.

Staehr, P. A., J. P. A. Christensen, R. D. Batt, and J. S. Read. 2012b. Ecosystem metabolism in a stratified lake. Limnol. Oceanogr. **57:** 1317-1330.

Staehr, P. A., and K. Sand-Jensen. 2007. Temporal dynamics and regulation of lake metabolism. Limnol. Oceanogr. **52:** 108-120.

Staehr, P. A., K. Sand-Jensen, A. L. Raun, B. Nilsson, and J. Kidmose. 2010. Drivers of metabolism and net heterotrophy in contrasting lakes. Limnol. Oceanogr. **55:** 817-830.

Townsend, S. A., I. T. Webster, and J. H. Schult. 2011. Metabolism in a groundwater-fed river system in the Australian wet/dry tropics: tight coupling of photosynthesis and respiration. J. N. Am. Benthol. Soc. **30:** 603-620.

Tranvik, L. J., J. A. Downing, J. B. Cotner, S. A. Loiselle, R. G. Striegl, T. J. Ballatore, P. Dillon, K. Finlay, K. Fortino, L. B. Knoll, P. L. Kortelainen, T. Kutser, S. Larsen, I. Laurion, D. M. Leech, S. L. Mccallister, D. M. Mcknight, J. M. Melack, E. Overholt, J. A. Porter, Y. Prairie, W. H. Renwick, F. Roland, B. S. Sherman, D. W. Schindler, S. Sobek, A. Tremblay, M. J. Vanni, A. M. Verschoor, E. Von Wachenfeldt, and G. A. Weyhenmeyer. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol. Oceanogr. **54:** 2298-2314.

Tsai, J. W., T. K. Kratz, P. C. Hanson, J. T. Wu, W. Y. B. Chang, P. W. Arzberger, B. S. Lin, F. P. Lin, H. M. Chou, and C. Y. Chiu. 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. Freshw. Biol. **53:** 1929-1941.

Van De Bogert, M. C., D. L. Bade, S. R. Carpenter, J. J. Cole, M. L. Pace, P. C. Hanson, and O. C. Langman. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol. Oceanogr. **57:** 1689-1700.

Van De Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnology and Oceanography: Methods **5:** 145-155.

Weiss, R. F. 1970. Solubility of nitrogen, oxygen and argon in water and seawater. Deep-Sea Res **17:** 721-735.

West, W. E., J. J. Coloso, and S. E. Jones. 2012. Effects of algal and terrestrial carbon on methane production rates and methanogen community structure in a temperate lake sediment. Freshw. Biol. **57:** 949-955.

Table 1. Description of the lakes and data sets used in this analysis. Lat and Long give latitude and longitude in decimal degrees, positive values indicate north latitudes and east longitudes. Elev is the surface elevation of the lake above sea level (asl). z_{max} and z_{mean} are the maximum and mean depth of the lake. A_{lake} and A_{wtrshd} are the area of the lake and its watershed. τ is the water residence time. TP, TN, Chl *a*, DOC, and a_{440} are mean summer epilimnetic values for total phosphorus, total nitrogen, chlorophyll *a*, dissolved organic carbon, and water color measured as absorbance at 440 nm. Δ_T is the time interval between measurements of dissolved oxygen concentration. z_{DO} is the depth at which the dissolved oxygen was measured. z_T is the depths at which water temperature was measured; notation like (1-7, 2) indicates that the temperature was measured every 2 m from 1 to 7 m inclusive. h_{wind} is the height above the lake surface at which wind speed was measured. Dates is the date range over which data were collected for this study. Notes contains references to footnotes describing data post-processing steps, in addition to those described in the main text, that were necessary in one or more lakes. na indicates data not available.

Lake	Lat	Long	Elev (m asl)	z_{max} (m)	z_{mean} (m)	A_{lake} (km^2)	A_{wtrshd} (km^2)	τ (years)	TP ($\mu g\ L^{-1}$)	TN ($mg\ L^{-1}$)	Chl *a* ($\mu g\ L^{-1}$)	DOC ($mg\ L^{-1}$)	a_{440} (m^{-1})	Δ_T (min)	z_{DO} (m)	z_T (m)	h_{wind} (m)	Dates	Notes
Acton	39.575	-84.744	263	8	4	2.53	259	0.249	114	5.84	55.7	3.59	1.48	5	1.5	(1-7, 2)	4.9	22 Jul 2008 04 Nov 2008	[1, 2]
Annie	27.207	-81.351	3.7	21	9	0.365	11	2	4.3	0.24	2.3	7.68	1.11	15	1.35	(0-18, 1)	10	01 Mar 2008 27 Feb 2009	
Balaton (southwest basin)	46.717	17.245	103	4	2	38.0	2750	0.25	72	1.66	17.7	7.7	1.38	10	1	var[3]	3	13 Jun 2008 11 Oct 2008	[4, 5]
Crampton	46.210	-89.473	510	19	5	0.257	na	na	8.9	0.32	2.6	3.8	0.55	5	1	1 3 5 8 9	2	01 Jun 2005 09 Sep 2005	[1, 6]
Crystal Bog	46.008	-89.606	503	2.5	2	0.005	0.08	1.7	27	0.68	19.2	11.5	5.1	10	0.25	(0-2.25, 0.25)	2	30 May 2008 05 Nov 2008	[6]
Feeagh	53.948	-9.575	0	45	14	4.00	8.3	0.47	7.3	0.13	1.8	7.8	3.96	2	1	(2-14, 3) (16-22, 2) 27 32 40	1.5	01 Jan 2006 30 Dec 2006	
Fredriksburg Slotsø	55.933	12.303	10	9	3	0.223	9.2	0.5	102.1	1.74	64.5	5.4	2.2	30	1	1 2 4 5 6 7	1.3	11 Apr 2006 21 Nov 2006	[7]

Hampensø	56	9.3333	79	14	4	0.76	9.2	1.4	22.7	0.58	5.3	3.1	0.48	30	1	0.5 1 2 3 4 5 7 9 11	1.3	19 Apr 2007 30 Sep 2007	[7]
Kentucky	36.739	-88.109	109	18	6	970	104117	0.079	47	0.79	16.8	3.00	na	15	1[8]	var[9]	10	01 Jan 2008 30 Dec 2008	[1, 2]
Mendota	43.099	-89.652	259	25	13	39.4	604	4.5	85	0.96	3.8	5.24	0.75	1	0.4	0 0.5 1 1.5 (2-20, 1)	2	10 Jul 2008 03 Nov 2008	[4, 6]
Mirror	41.807	-72.247	177	1.2	0.7	0.020	0.71	0.03	53	na	17.6	na	2	30	var[10]	var[11]	2	20 Mar 2003 15 Oct 2003	[4]
Müggelsee	52.438	13.648	34	7.7	5	7.46	7000	0.11	105	0.91	33.5	8.01	na	60	1	(0.5-5, 0.5)	4	11 Mar 2008 07 Dec 2008	[4, 12]
Onondaga	43.089	-76.208	110	19	11	12.0	642	0.25	35	na	17	3.6	1.7	60	3[13]	(1-6, 1)[14]	2.5	05 May 2001 27 Oct 2001	
Pontchartrain	30.316	-90.283	0	1.9	1.7	1603	12473	1.37	30	na	na	6.9		15	1	1	13	21 Mar 2008 31 Dec 2008	
Rotoiti	-38.039	176.428	279	125	31	34.6	123.7	1.5	30.3	0.29	4.2	1.35	0.20	15	1	0.5 2 4 6 9 12 15 18 19	1.5	25 Jul 2008 23 Jul 2009	[4, 6]
Rotorua	-38.066	176.266	280	24	11	79.8	520.54	1.2	32.7	0.48	14.3	2.3	0.23	15	1	(0.5-20.5, 2)	1.5	13 Jul 2007 12 Jul 2008	[4, 6]
Sparkling	46.008	-89.701	497	20	11	0.64	1.1	10.4	10	0.23	1.3	3.2	0.5	10	0.5	(0-5, 0.5) 6 7 (8-12, 0.5) 13 15	2	09 May 2008 26 Oct 2008	
St Gribsø	55.983	12.3	50	12	5	0.10	1.2	2.1	69	0.70	30.3	12.8	6.5	30	1	0.5 1 2 3 4 5 7 10	1.3	12 Apr 2006 23 Nov 2006	[7]
Sunapee	43.383	-72.033	333	32	10	16.7	123.23	3.2	5.3	0.17	1.9	2.36	na	10	1	(0-4, 0.5) (5-14, 1)	2	01 May 2008 30 Oct 2008	
Taihu	31.287	120.202	3	3	2	2338	36985	0.9	186	3.60	46	5.6	1.08	10	0.3	(0.3-1.8, 0.5)	5	09 Oct 2007 30 Oct 2008	[4]
Trout	46.029	-89.665	495	36	15	16.1	47	4.6	13	0.20	1.7	2.8	1	10	0.5	(0-19, 1)	2	30 May 2008 10 Nov 2008	[15, 16]
Trout Bog	46.041	-89.686	495	7.9	6	0.011	0.14	5.6	29	0.63	15	17.3	13.1	10	0.25	(0-3, 0.5) 4 5	2	30 May 2008 10 Nov 2008	[6, 17]
Vedstedsø	55.167	9.333	25	12	5	0.09	0.32	4.6	19.5	0.55	41.2	4.8	1.1	30	1	1 2 4 5 7 9 11	1.3	14 May 2008 30 Nov 2008	[7]
Võrtsjärv	58.317	26.013	34	6	3	270	3374	1	39.7	0.90	51.0	12.5	8.25	15	0.5	0.5	10	01 May 2009 11 Aug 2009	
Yuan Yang	24.583	121.4	1670	4.5	1.7	0.036	3.74	0.1	6.4	1.88	11.6	8.41	5.29	10	0.25	(0-1, 0.25) (1.5-3, 0.5)	2	25 Jan 2007 15 Dec 2007	[18]

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[1] Time stamps of z_T (temperature profile) measurements were adjusted by 0-2 minutes to align profile at a single time point.

[2] PAR data measured at a coarser time scale were interpolated to match Δ_T.

[3] Variable. One thermistor was at depth of 0.1 m, the others at fixed heights (0, 0.15, 0.40, 0.65 m) above bottom. These heights were converted to depths based on water level data.

[4] PAR derived from solar flux according to Britton and Dodd (1976).

[5] Temperature profile: 4 of 5 thermistors were deployed at fixed heights above bottom; for each time point these heights were converted to depths based on water level data.

[6] Some or all of PAR data was taken from a weather station < 10 km away from the buoy.

[7] DO: data recorded as % saturation, converted back to concentration following Weiss (1970).

[8] The depth of the DO sonde varied from 0.3-3.1 m (mean 0.9, SD 0.5); we assumed a constant depth of 1 m when fitting the metabolism model.

[9] Variable. The shallow thermistor ranged from 0.3-3.1 m (mean 0.9, SD 0.5). The deep thermistor ranged from 2.1-5.6 m (mean 3.1, SD 0.7).

[10] The depth of the DO sonde was changed periodically, and varied from 0.35-0.65 m.

[11] Variable. The depths of the thermistors were changed periodically. In all periods thermistors were deployed at 5-8 depths between 0.05 and 1.10 m.

[12] Wind speed and PAR data were aggregated to an hourly time step to match Δ_T.

[13] DO measurements were made with a profiling autosampler, and the depth of the DO measurement varied from 0.8 – 5.0 m (mean 3.0 SD 0.3). We assumed a constant depth of 3 m when fitting the metabolism model.

[14] Water temperature measurements were made with a profiling autosampler. The depths at each time point varied slightly around the indicated 1, 2, 3, 4, 5, and 6 m.

[15] No water temperature data at z_{DO}; used water temperature from 1 m depth.

[16] DO data were shifted down 3.02 mg L^{-1} over the entire data set based on calibration data.

[17] No water temperature data at z_{DO}; used water temperature from 0.5 m depth.

[18] PAR values were shifted down 120 μmol m^{-2} s^{-1} to correct consistent nighttime offset from 0.

Table 2. Correlations (Spearman's ρ) among lake descriptor variables. Only correlations significant at α=0.10 (without adjustment for multiple tests) are shown. Abbreviations for descriptor variables follow Table 1, plus WL (=z_{mean}/τ) is water load and V_{lake} (=$z_{mean} \bullet A_{lake}$) is lake volume.

	z_{mean}	A_{lake}	TP	DOC	a_{440}	τ	WL
A_{lake}	-						
TP	-	-					
DOC	-0.56	-0.38	-				
a_{440}	-0.48	-0.45	-	0.88			
τ	0.38	-	-0.54	-	-		
WL	-	-	-	-	-	-0.77	
A_{wtrshd}:V_{lake}	-0.77	-	0.49	0.40	0.46	-0.70	-

Table 3. Mean daily net ecosystem productivity (NEP; mg O_2 L^{-1} d^{-1}) in the 25 study lakes. Means were calculated over the entire period of record (Annual) or over the summer period only (Summer; 01 June through 31 August in the northern hemisphere, 01 December through 02 March in the southern hemisphere). In either case *n* indicates the number of days of data used.

	Annual		Summer	
Lake	NEP	*n*	NEP	*n*
Acton	2.20	81	4.45	30
Annie	-0.06	356	-0.05	92
Balaton	-0.85	39	-0.97	21
Crampton	-0.02	52	-0.03	43
Crystal Bog	-0.19	147	-0.41	80
Feeagh	-0.13	339	-0.24	83
Fredriksburg Slotsø	1.59	211	3.80	83
Hampensø	-0.01	165	0.17	92
Kentucky	-0.43	357	-0.88	91
Mendota	1.33	98	1.95	39
Mirror	-0.38	138	0.18	48
Müggelsee	0.59	223	1.75	79
Onondaga	-0.26	142	0.14	69
Pontchartrain	-0.68	232	-0.42	88
Rotoiti	-0.46	82	-0.68	43
Rotorua	-0.33	310	-0.43	77
Sparkling	0.03	125	0.08	63
St Gribsø	0.03	226	0.41	92
Sunapee	0.33	175	0.68	92
Taihu	0.43	245	0.64	91
Trout	-0.05	153	-0.07	80
Trout Bog	-0.15	153	-0.14	80
Vedstedsø	0.34	201	1.03	92
Võrtsjärv	0.04	45	0.01	30
Yuan Yang	-0.38	301	-0.15	91

Table 4. Parameter estimates for nominal fits of autoregressive models (Eq. 4) to the maximum likelihood estimates of respiration and primary production for each lake. Values in parentheses are standard errors. The parameters are α (first-order autoregressive parameter), β_0 (intercept, mg O_2 L^{-1} d^{-1}), β_1 (slope of respiration on primary production), and σ^2 (error variance).

	α	β_0	β_1	σ^2
Acton	-0.01 (0.15)	1.21 (0.47)	0.20 (0.10)	7.31
Annie	0.31 (0.05)	0.07 (0.02)	0.90 (0.07)	0.02
Balaton	0.05 (0.22)	1.17 (0.28)	0.85 (0.10)	0.86
Crampton	0.04 (0.16)	0.02 (0.06)	1.01 (0.15)	0.02
Crystal Bog	0.38 (0.08)	0.04 (0.14)	1.06 (0.09)	0.55
Feeagh	0.01 (0.07)	0.30 (0.04)	0.68 (0.07)	0.37
Fredriksburg Slotsø	0.32 (0.07)	0.90 (0.35)	0.51 (0.06)	5.56
Hampensø	0.29 (0.08)	0.40 (0.14)	0.76 (0.08)	0.41
Kentucky	0.00 (0.06)	0.21 (0.06)	1.09 (0.03)	0.69
Mendota	0.28 (0.10)	0.33 (0.19)	0.29 (0.07)	0.85
Mirror	0.63 (0.07)	2.62 (0.68)	0.58 (0.10)	5.95
Müggelsee	0.22 (0.07)	1.02 (0.18)	0.36 (0.04)	3.18
Onondaga	0.20 (0.09)	0.44 (0.15)	0.93 (0.07)	1.09
Pontchartrain	0.39 (0.06)	0.77 (0.12)	0.78 (0.05)	0.92
Rotoiti	0.59 (0.09)	0.60 (0.20)	0.76 (0.17)	0.62
Rotorua	0.43 (0.06)	0.23 (0.06)	1.15 (0.05)	0.22
Sparkling	0.37 (0.09)	0.12 (0.02)	0.12 (0.09)	0.02
St Gribsø	0.17 (0.07)	0.66 (0.10)	0.67 (0.05)	0.48
Sunapee	0.34 (0.09)	0.35 (0.06)	-0.21 (0.09)	0.13
Taihu	0.45 (0.06)	0.49 (0.16)	0.55 (0.04)	1.44
Trout	0.18 (0.08)	0.05 (0.02)	1.09 (0.11)	0.02
Trout Bog	0.23 (0.08)	0.20 (0.10)	1.00 (0.06)	0.66
Vedstedsø	0.59 (0.07)	0.54 (0.21)	0.57 (0.09)	0.63
Võrtsjärv	-0.23 (0.17)	0.56 (0.24)	0.65 (0.12)	0.60
Yuan Yang	0.74 (0.04)	0.51 (0.16)	1.08 (0.13)	0.58

Table 5. Reported relationships between respiration and DOC concentration. Respiration is a volumetric pelagic rate unless otherwise noted.

Reference	Study system	DOC range (mg L^{-1})	Relationship of respiration to DOC
1. del Giorgio and Peters 1994	20 lakes southern Québec	3 – 8	none
2. Carignan et al. 2000	12 Canadian Shield lakes, Québec	2 – 7	negative or none
4. Hanson et al. 2003	25 lakes northern Wisconsin	2 – 25	positive
5. Pace and Prairie 2005	63 mostly north temperate lakes, including studies 1 and 2	~ 2 – 12	positive
6. Sand-Jensen and Staehr 2007	64 small lakes, Denmark	na[1]	positive[1]
7. Ask et al. 2012	15 lakes northern Sweden	~ 1 – 17	positive (pelagic), negative (benthic) [2]
8. Staehr et al. 2012a	25 lakes Denmark	3 - 46	positive (volumetric), none (areal)
9. This study	25 lakes globally	1 – 17	none

[1] This study used measured colored dissolved organic matter (CDOM, absorbance at 360 nm) and reported that CDOM was correlated with DOC concentration. CDOM ranged from 3 to 258 m^{-1}.

[2] Relationships between respiration and DOC are for DOC expressed per area, as g m^{-2}

Figure captions

Figure 1. Ecosystem respiration can be conceptualized as the sum of several components reflecting respiration of different substrates by different organisms (del Giorgio and Williams 2005). The components are: $R_{Auto,}$ respiration by autotrophs; $R_{Hetero,Autoch\text{-}Fast}$, respiration by heterotrophs of autochthonously-produced labile organic matter; $R_{Hetero,Autoch\text{-}Slow}$, respiration by heterotrophs of autochthonously-produced recalcitrant organic matter; and $R_{Hetero,Alloch}$, respiration by heterotrophs of allochthonous terrestrial organic matter.

Figure 2. Examples of metabolism model input data and fits, for four consecutive days in Lake Annie. Data are photosynthetically active radiation (PAR), wind speed, mixed layer depth (z_{Mix}), and dissolved oxygen concentration (DO). For DO, points are observed values and line is the model fit.

Figure 3. Daily temperature-corrected gross primary production (GPP_{20}) and respiration (R_{20}) for St. Gribsø, demonstrating the determination of background respiration (β_0) as the intercept and respiration-GPP coupling (β_1) as the slope of the relationship between R_{20} and GPP_{20} in a regression model that accounts for temporal autocorrelation (Eq. 4).

Figure 4. Rates of gross primary production (gray points) and respiration (black points, plotted on negative scale to facilitate viewing) estimated at a daily scale in 25 lakes. Data are point estimates only; confidence intervals not shown. Lakes are positioned from top left to bottom right in order of increasing maximum daily GPP. Note that for the two southern hemisphere

lakes (Rotoiti and Rotorua), the x-axis labels should be shifted by 6 months to read ‘Jul’, ‘Jan’, ‘Jul’.

Figure 5. (A, B) Average annual gross primary production and respiration in the 25 study lakes were strongly related to total phosphorus concentration ($p<0.0001$), (D, E) but not to dissolved organic carbon concentration ($p>0.28$). (C, F) Net ecosystem production was ranged from slightly negative to slightly positive in most lakes, but was very positive in high-TP, moderate-DOC lakes.

Figure 6. Point estimates and bootstrapped 95% confidence intervals for respiration rates in two representative lakes. In lakes where confidence intervals are often narrow, as in Lough Feeagh, significant day-to-day differences in rates are common. In lakes where confidence intervals are usually wide, as in Kentucky Lake, it is more difficult to assess whether day-to-day differences in point estimates of rates are biologically meaningful. Confidence intervals for day i and day i+1 are non-overlapping on 50% of days in Feeagh and on 12% of days in Kentucky.

Figure 7. Comparison of fitted and observed rates of respiration (mg O_2 L^{-1} d^{-1}, corrected to 20°C) in 25 lakes. Observed rates are the maximum likelihood estimates from the metabolism model (Eqs. 1-3). Fits are from first-order autoregressive models which included rates of primary production as a predictor (Eq. 4). The R^2 of the model for each lake is indicated below the lake name. Solid lines indicate the 1:1 relationship.

Figure 8. Coupling of respiration to primary production at a daily scale (β_1) is strong in oligotrophic and dystrophic lakes, and weaker in eutrophic lakes. β_1 is estimated as the slope of a regression of respiration on primary production after temperature correction (Eq. 4). Boxes show the 25th, 50th, and 75th percentiles of 10,000 bootstrap estimates of β_1 for each lake. Gray boxes indicate lakes for which β_1 estimates may not be valid (*see* main text).

Figure 9. Background respiration, β_0, varies with (A) allochthonous input, indicated by the ratio of watershed area to lake volume, which has units km^{-1}; (B) input of autochthonous organic matter to the slow-turnover pool, indicated by the β_1 parameter; low β_1 equates to high inputs to the slow pool; (C) recalcitrance of dissolved organic matter, indicated by water color measured as absorbance at 440 nm. Background respiration is the portion of total community respiration that is not directly tied to autotrophic production, and is estimated as the intercept of a regression of respiration on primary production after temperature correction (Eq. 4). Boxes show the 25th, 50th, and 75th percentiles of 10,000 bootstrap estimates of β_0 for each lake. In one case (Lake Taihu) only the 50th and 75th percentile are plotted because the 25th percentile was negative. (B) Gray boxes indicate lakes for which β_1 estimates may not be valid (*see* main text).