Depth-integrated, continuous estimates of metabolism in a clear-water lake

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Abstract: High-frequency dissolved oxygen (DO) measurements have been used for estimating gross primary production (GPP) and respiration (*R*) in lake ecosystems. Most researchers have determined GPP and *R* only in surface waters, a practice that may underestimate *R* in general and GPP in clear-water lakes in particular. We deployed oxygen sondes at multiple sites and depths in a clear-water lake. Rates of GPP or *R* were similar horizontally over the surface waters of the lake. Diel DO signals weakened with depth; however, removing noise from the data, by either wavelet transforms or moving averages, enhanced our ability to resolve diel metabolic signals. While GPP declined sharply with depth, *R* was unrelated to depth. The majority of GPP and *R* occurred in the upper mixed layer, but deeper water accounted for 14%–28% of GPP and 20%–43% of *R*, depending on the statistical filtering technique used. GPP and *R* were nearly in balance in the surface waters, but for the entire lake *R* exceeded GPP, and net ecosystem production was negative. Deployment of oxygen sondes in various habitats and at multiple depths allows for a more complete estimate of whole-lake metabolism and a better understanding of the spatial and temporal complexity of lakes.

Résumé : Des mesures d'oxygène dissous (DO) répétées à haute fréquence servent couramment à estimer la production primaire brute (GPP) et la respiration (*R*) dans les écosystèmes lacustres. La plupart des chercheurs mesurent GPP et *R* seulement dans les eaux superficielles, ce qui peut sous-estimer *R* de façon générale et GPP particulièrement dans les lacs à eau claire. Nous avons installé des sondes à oxygène dans plusieurs sites et à diverses profondeurs dans un lac à eau claire. Les taux de GPP et de *R* sont semblables à une même profondeur sur toute l'étendue du lac. Les signaux journaliers de DO s'affaiblissent en profondeur; cependant, le retrait du bruit des données, soit par des transformations en ondelettes ou des moyennes glissantes, nous permet d'interpréter les signaux métaboliques journaliers. Alors que GPP diminue fortement en profondeur, *R* est indépendante de la profondeur. La plus grande partie de GPP et de *R* se produit dans la couche de mélange supérieure, mais les eaux profondes sont responsables de 14–28 % de GPP et de 20–43 % de *R* selon la technique de filtrage statistique retenue. GPP et *R* sont presque en équilibre dans les eaux superficielles, mais dans l'ensemble du lac, *R* est plus importante que GPP et la production nette de l'écosystème est négative. L'installation de sondes d'oxygène dans divers habitats et à plusieurs profondeurs permet ainsi une estimation plus complète du métabolisme du lac entier et une meilleure compréhension de la complexité spatiale et temporelle des lacs.

[Traduit par la Rédaction]

Introduction

In situ sondes fitted with sensitive and accurate oxygen probes have become a useful tool for estimating lake ecosystem metabolism (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006). By continuously measuring in situ changes in dissolved oxygen (DO) at high frequency, automated sondes enable the estimate of net ecosystem production (NEP), which is the balance between gross primary production (GPP) and respiration (*R*) (Odum 1956; Lovett et al. 2006).

The sonde method provides an alternative to more traditional methods of measuring metabolism that only use discrete samples. Two approaches have typically been used to estimate lake metabolism: bottle incubations that measure changes of metabolic components in a closed system and free water methods that measure changes of gasses in an open system. Bottle incubations estimate primary production by measuring the change in DO (Carignan et al. 2000) or the uptake of ^{14}C (Peterson 1980; del Giorgio and Peters 1994) that occurs in a contained sample over a specific amount of time and usually under controlled temperature and light conditions. Free water methods estimate GPP and *R* by measuring in situ changes in dissolved gases and include both continuous (sondes) and discrete sampling approaches (Odum 1956; Howarth et al. 1996; Bachmann et al. 2000). Estimates of lake metabolism based on discrete samples (from either incubations or free water approaches) could lead to erroneous conclusions about the trophic status of a lake because important dynamics are missed by limited sam-

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pling (Staehr and Sand-Jensen 2007). Continuous sampling by sondes overcomes many of the limitations of discrete samples and make it possible to measure metabolism in a wide variety of systems (Caraco and Cole 2002; Gelda and Effler 2002; Hanson et al. 2003).

Most previous studies using sondes in lakes have deployed them only at a central station in the upper mixed layer. Estimates from these deployments are representative of surface water metabolism only. Researchers have either avoided trying to measure metabolism in deeper water or assumed that the single sonde samples water that is representative of the entire surface layer and that the majority of lake metabolism occurs in the upper mixed layer (Cole et al. 2000; Hanson et al. 2003). Recently, there has been an increased focus on measuring the relative importance of littoral habitats as contributors to whole-lake processes, including primary production (Lodge et al. 1998; Vadeboncoeur et al. 2001, 2002). Several studies have deployed sondes in various sites in the surface waters and found that littoral metabolism can vary greatly from that of the pelagic, suggesting that metabolism estimates made in pelagic surface waters may miss a large portion of whole-ecosystem metabolism (Caraco and Cole 2002; Lauster et al. 2006; Van de Bogert et al. 2007). While these recent studies moved beyond the tradition of using one central pelagic sonde and explored spatial heterogeneity in surface waters, the observations were, nevertheless, still restricted to the upper mixed layer.

In clear-water lakes, light often penetrates well below the mixed layer, so that there is considerable primary production in deeper water. For a variety of clear-water lakes, the chlorophyll *a* maxima often occur below the mixed layer, extending even to regions of light as low as 1% of surface irradiance (Fee 1976; St. Amand and Carpenter 1993). These deep chlorophyll maxima indicate that there may be substantial primary production below the mixed layer, which would not be sampled by surface water sondes. Primary production has long been measured over depth using the ^{14}C bottle technique, and many earlier studies measured substantial production in deeper water (e.g., Saunders et al. 1962; Megard and Smith 1974; Carpenter et al. 1986). While results from ^{14}C methods indicate there is significant, measurable net primary production in deep waters, prior studies using these techniques could not measure in situ high-frequency variation in production and could not measure *R*, GPP, or NEP as is possible with DO sondes. Automated devices have been developed to profile the water column using DO sondes (Betts 1998; Branco et al. 2005), but few studies have used these devices to estimate lake metabolism at multiple depths. A notable exception was a study that used an automated DO profiler to calculate metabolism at 1 m intervals to depths up to 8 m. However, all of the estimates in this work were made within the mixed layer (Gelda and Effler 2002). Rarely have studies used sondes to explore metabolism below the upper mixed layer.

There are, however, possible problems with using sondes below the mixed layer. Strong temperature and density gradients establish a series of small layers within the metalimnion that have high relative thermal resistance to mixing. Because the water below the mixed layer is not necessarily well mixed (MacIntyre 1993), it may be difficult to determine what portion of the water column is actually represented by the oxygen measured by the sonde. Additionally, the strong oxygen and temperature gradients within the metalimnion have the potential to cause substantial noise in the sonde data if seiches or other processes cause different water masses to move past the probes. This noise could obscure the diel DO signal associated with metabolism, especially if the diel signal weakens with depth as light decreases.

In this study, we use DO sondes to investigate how metabolism changes horizontally within the mixed layer and vertically over depth in a north temperate, clear-water lake. Additionally, we integrate our estimates over depth and across the entire volume of the lake to produce a whole-lake estimate of metabolism and examine the relative contributions of each depth to the entire system. We also employ both moving averages and wavelet transforms to filter our DO time series to reduce non-diel noise and improve resolution of the metabolic signal.

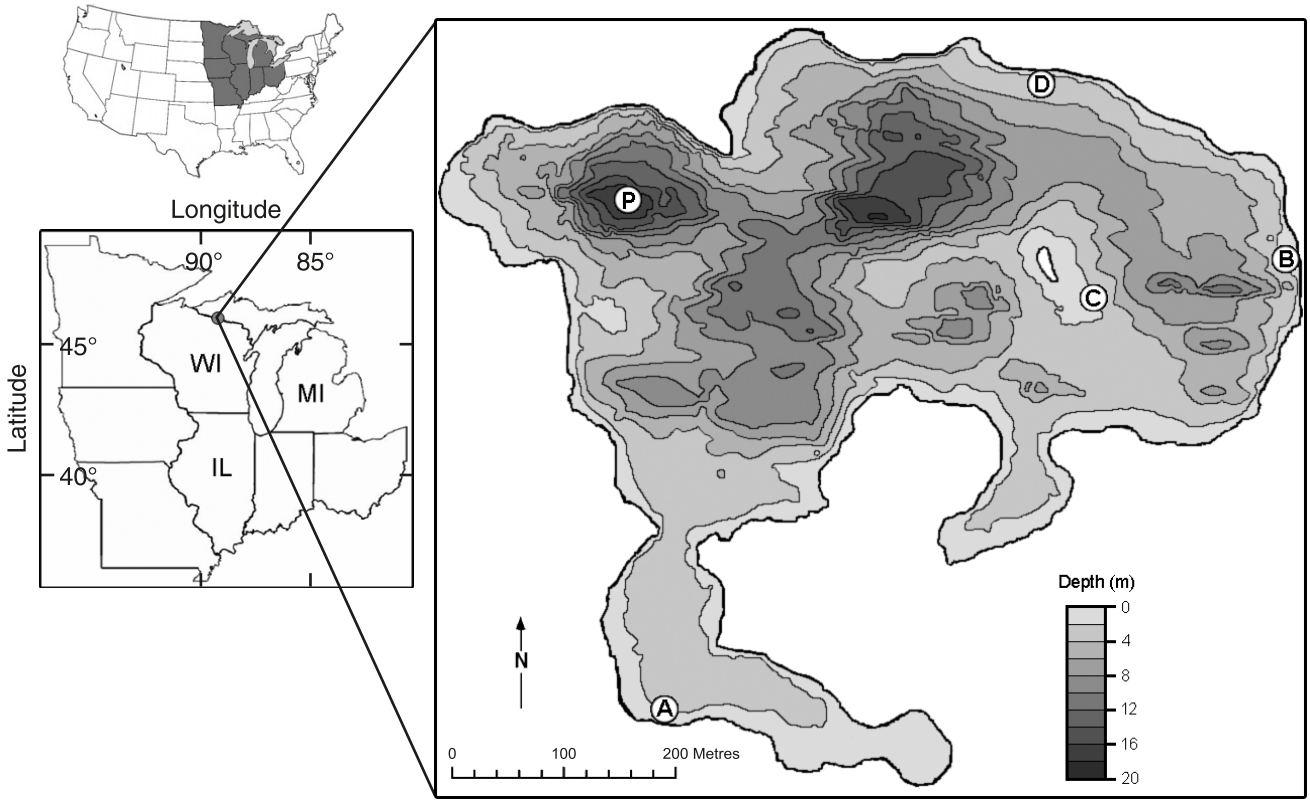
Materials and methods

We sampled Crampton Lake, located at the University of Notre Dame Environmental Research Center in Land O' Lakes, Wisconsin (46°12′N, 89°28′W), from 1 June to 1 September 2005. Crampton is a 25.7 ha, clear-water lake that strongly stratifies during the summer, with an average upper mixed layer depth of ~4 m. The maximum depth is 18.7 m, and the average depth is 5 m.

We deployed sondes at eight sites throughout the lake in both littoral and pelagic waters to measure free water DO and temperature at 5 min intervals for the duration of the study. Four littoral sondes were deployed at a depth of 1 m below the surface where the lake was about 2 m deep (Fig. 1). All littoral sites had similar organic substrates and sparse or no macrophytes. Macrophytes that were present consisted of mainly *Sparganium* spp. and *Eriocaulon aquaticum*. Four other sondes were deployed in the pelagic waters from a buoy moored at the deepest part of the lake. These sondes were deployed at depths of 1, 3, 5, and 8 m. We used YSI 600XLM, 6000UPG, and 6920 sondes fitted with rapid pulse oxygen probes (models 6562, 6030, and 6562, respectively) and temperature probes. All sondes were calibrated in water-saturated air prior to deployment and checked in water-saturated air upon recovery. Each week the sondes were removed for maintenance and recalibration. Calibrations before and after deployments were used to correct for electrode drift, with the assumption that it was linear. We used nine sondes for the eight sites so that we could get continuous measurements at the pelagic 1 m site by using the ninth sonde during the maintenance and calibration period. The placement of sondes was randomized among lake sites to remove any bias from differences in individual sondes.

Profiles of temperature and DO were taken weekly with a YSI model 58 DO meter, and the depth of the mixed layer (Z_{mix}) was determined to occur at the point where temperature changed more than 1 °C per half metre. Weekly light profiles were taken using LI-COR photosynthetically active radiation (PAR) sensors (models LI-190 and LI-193) and an LI-1000 datalogger. A profile of chlorophyll *a* concentration was made each week using a horizontal Van Dorn sampler to

Fig. 1. Crampton Lake bathymetry. Contour lines show depth at 2 m intervals. Letters indicate sonde locations. Littoral sites are denoted by letters A–D, while the pelagic site is denoted by P.



collect water at depths of 100%, 50%, 25%, 10%, 5%, and 1% surface irradiance as calculated from the light profiles. Samples were filtered, frozen, and later analyzed with a fluorometer after methanol extraction (Holm-Hansen and Riemann 1978; Marker et al. 1980). Wind speed at 2 m above the water surface and PAR were sampled every 5 min from a buoy deployed at the pelagic site.

Metabolic calculations are based on those outlined in Cole et al. (2000) and will only be described here briefly. These calculations were made using a program written by the authors in MATLAB (version 7.3, The Mathworks Inc., Natick, Massachusetts). The change in DO over a 5 min interval at any one sensor is assumed to result from three processes: net ecosystem production (NEP = GPP – R), diffusive exchange with the atmosphere (D), and other inputs and outputs of DO (A) such as flux between thermal layers and lateral flows.

$$\Delta\mathrm{DO} = \mathrm{NEP} + D + A \quad (1)$$

For this calculation, we assumed that each depth layer was a closed system (except for atmospheric exchange in the mixed layer) such that there were no other inputs or outputs of DO (i.e., $A = 0$). Previous studies have indicated that diffusive exchange between depth layers is minimal (Cole and Pace 1998; Gelda and Effler 2002). It is possible that processes, such as internal waves, could alter the DO signal measured by the sondes. We assumed these components of the DO signal, which occur at frequencies much higher than diel, are noise, and we reduced or removed these effects through filtering (see below). The consequences of our assumption are discussed below.

Diffusion with the atmosphere is governed by the departure of the DO concentration in the water from atmospheric equilibrium ($\mathrm{DO_{sat}}$), and the gas piston velocity for oxygen (k) at a given temperature.

$$D = k(\mathrm{DO_{sat}} - \mathrm{DO}) \quad (2)$$

D can be either positive (addition of DO to system) or negative (removal of DO from system). We used wind speed measured on the lake to predict k_{600} from the equations of Cole and Caraco (1998) at 5 min intervals. k was calculated from k_{600} using the Schmidt number equations of Jahne et al. (1987). Once atmospheric exchange is calculated, we can estimate NEP at any given time in the surface water. Since the sondes in the metalimnion and hypolimnion were isolated from the atmosphere, we assumed $D = 0$; thus the change in oxygen is equal to NEP for those layers. Because there is no GPP at night, we assume nighttime R equals nighttime NEP. R was measured from 1 h past sunset until 1 h before sunrise. During the day, NEP is a result of the balance between GPP and R. NEP was calculated from sunrise to sunset. We cannot directly measure R during the day, but if we assume that the daytime rate of R is equal to that of nighttime R (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006), then we can estimate GPP by adding daytime NEP and R. It is likely that daytime R exceeds nighttime R (Pace and Prairie 2005; Tobias et al. 2007), which would underestimate the magnitudes of GPP and R, but would not have an effect on NEP (Cole et al. 2000). The 5 min estimates of GPP, R, and NEP were accumulated over each 24 h period during the deployment, and these daily values were then averaged over

the entire season. For ease of comparison and to emphasize the aspects of oxygen production and consumption during metabolism, we present GPP values as positive and *R* values as negative.

The metabolism estimates from the four pelagic sondes were used to calculate a depth-integrated estimate of whole-lake metabolism. To do this, we defined boundaries to represent the layers of the lake each sonde was measuring. The 1 m sonde was assumed to measure the water from the surface to the depth of the mixed layer (Z_{mix}), as has been done in previous studies of surface water metabolism (Cole et al. 2000; Hanson et al. 2003; Lauster et al. 2006). However, below the mixed layer there are no clear boundaries to define what each sonde measured. We partitioned the remaining water column such that the 3 m sonde measured from Z_{mix} to 4 m, the 5 m sonde measured from 4 to 6.5 m, and the 8 m sonde measured from 6.5 m to the bottom. The consistency in assigning the depth layers was complicated by the deepening of Z_{mix} from 2.5 m at the beginning of the study to 6.5 m at the end. This caused the 3 and 5 m sondes to reside in the mixed layer along with the 1 m sonde for portions of the sampling period. On days when the mixed layer contained more than one sonde, the metabolism values from those sondes were averaged. Therefore, specific results presented below for the 3 and 5 m depth layers only include days when these depths were not part of the mixed layer. Volumetric metabolic rates were calculated daily for each layer and multiplied by the daily volume of that layer as determined from a hypsometric table and the daily value of Z_{mix}. The estimates from each layer were added to give daily values of whole-lake metabolism, which were then averaged over the entire season. The whole-lake values were divided by the lake area to obtain areal rates of metabolism. In this study, "whole-lake" refers to a depth-integrated, volume-corrected estimate of metabolism for the entire lake.

Variations in DO due to advection and other physical factors can obscure the GPP and *R* signals, which vary on a diel basis with light, and cause erroneous interpretations of the results. To clarify the diel components of the pelagic DO data, we used two different approaches to filter all DO time series prior to calculating metabolism. The first approach used a wavelet transform; the second approach used a more basic moving average. Although wavelet transforms have not been frequently used to filter ecological data, this technique is well-established in other fields and is particularly useful for analyzing and filtering noisy signals with intermittent or no periodicities (Addison 2002). We employed a Symlet wavelet transform using MATLAB software (version 7.4) to remove the noise from the DO data. We tested wavelet transforms at 160 and 320 min scales, but chose to remove noise at the 160 min scale based on visual inspection, because it appeared to remove high-frequency variability while preserving most of the diel signal. Although an analysis of specific wavelet and filter scale selection was beyond the scope of this paper, we suggest this as an area of further exploration. Because wavelets are fairly new to ecology, we also used a simple alternative, the moving average, to filter the DO data for comparison. We tested moving averages of 1, 2, and 4 h (i.e., 12, 24, and 48 DO observations). Based on visual inspection, the 2 h moving average removed the most noise while still maintaining a good fit with the test data, so we used this filter on all data. A robust comparison of the two filtering techniques is beyond the scope of this study, but we make limited comparisons below.

Results

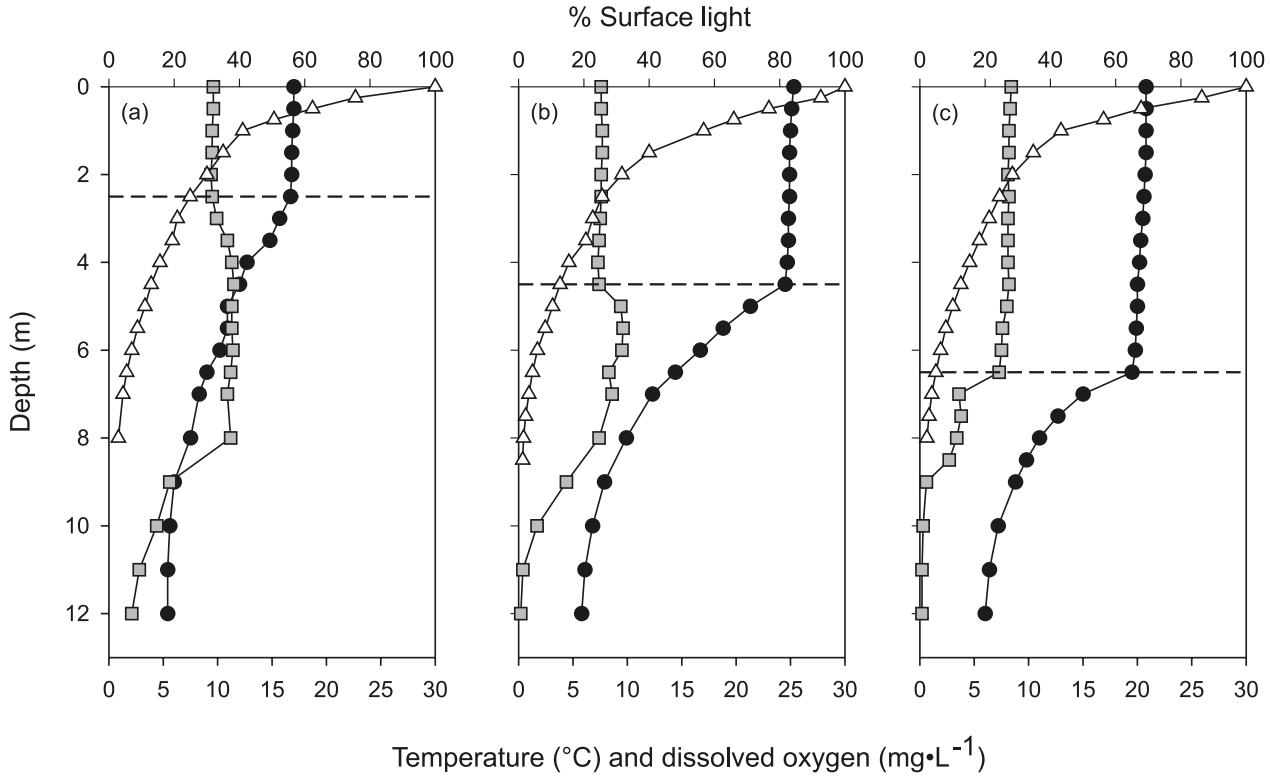
Temperature and DO profiles revealed clear stratification of the water column for the entire study period and a deepening of the mixed layer over the course of the summer (Fig. 2). The DO peak occurred below Z_{mix} for much of the season (60% of deployment days). Light penetration extended well beyond the mixed layer, especially before Z_{mix} began to deepen later in the summer (Fig. 2). Z_{mix} ranged from 2 to 6.5 m and averaged 4 m over the course of the season. On average, 14% of surface irradiance reached Z_{mix}, and 1% of surface irradiance reached 8.9 m. When we averaged the weekly chlorophyll *a* profiles, the average chlorophyll *a* maximum occurred below the mixed layer at 6.3 m (at the 5% light depth) and ranged from 2.6 to 9 m.

DO concentrations and diel patterns were similar across the surface waters, but showed increasing noise with depth. The four littoral sondes and the pelagic 1 m sonde had clear diel DO signals that corresponded with PAR, which is a strong indication of metabolism. However, the diel signal weakened with depth and was obscured by noise (i.e., other factors changed DO) at 8 m (Fig. 3).

Volumetric rates of metabolism were similar across the surface waters of the lake (Fig. 4). While GPP tended to be similar between the littoral sites (A–D) and the pelagic 1 m site (P), *R* was more variable between sites with littoral rates both higher and lower than pelagic rates. Those sites with the highest rates of GPP also had the highest rates of *R*, resulting in rates of NEP that were in balance or slightly negative. The sites with the lowest rates of GPP also had the lowest rates of *R* and positive rates of NEP. To compare these rates among sites, daily values of metabolism from the four littoral sites were each compared with site P using paired *t* tests. Each of the littoral sites had at least one gap in the daily series due to sonde malfunctions (n ranged from 50 to 64 days). Because of the gaps, the sites were compared only on days when both had data. There were no significant differences in GPP or NEP between any of the littoral sites and site P (p ranged from 0.07 to 0.81). Sites A and D both differed significantly from site P in the rates of *R* (paired *t* tests: $n = 64$, $p = 0.02$; $n = 62$, $p = 0.03$, respectively). The result at site D is surprising because the differences do not appear significant in Fig. 4. This is caused by the gaps in the data, which resulted in an elevated mean rate of *R* at site P for this comparison. Although the significant result at site D may be spurious, we conclude there was some modest spatial heterogeneity in rates of *R* across the surface waters in Crampton Lake.

While surface estimates of GPP were similar over space, the rates of GPP decreased dramatically with depth (Fig. 5). Rates ranged from 12.1 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ in the mixed layer to 4.2 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ at 8 m. The mean rate of GPP from the 3 m depth layer was nearly equal to that of the mixed layer. There was no trend with *R* and depth. The highest *R* occurred at 3 m, while the lowest was at 5 m (–18.1 and –10.64 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$, respectively). Estimates of NEP for the entire season varied

Fig. 2. Temperature (solid circles), dissolved oxygen (shaded squares), and light (open triangles) profiles for Crampton Lake on (*a*) 31 May, (*b*) 25 July, and (*c*) 9 September 2007. Broken lines indicate the depth of the mixed layer (Z_{mix}).



across the layers but were always negative and ranged from –0.4 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ in the mixed layer to –10.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$ at 8 m. Although the seasonal estimates of NEP were negative, the daily NEP estimates at 5 m were positive for many days early in the season. Daily rates of metabolism had no strong seasonal trends and were increasingly variable with depth. The standard deviations of the daily rates of GPP at 1 and 3 m were about equal to the mean. At 5 m, the standard deviation was more than twice as large as the mean, and at 8 m the standard deviation was more than 10 times the mean of the daily GPP values.

Of the 91 days of deployment, the mixed layer included the 3 m sonde for 69 days; the 5 m sonde was only in the mixed layer for 17 days. While in the mixed layer, the mean volumetric estimate of GPP from the 3 m sonde was similar to the mean estimate from the 1 m sonde (12.5 and 13.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$, respectively), but the estimate from the 5 m sonde was lower (7.8 mmol $O_2 \cdot m^{-3} \cdot day^{-1}$), suggesting that the deeper portions of the apparent upper mixed layer are not as well mixed.

The depth-integrated whole-lake estimate of metabolism (±95% confidence interval) was 51.4 ± 9.9, –66.6 ± 8.9, and –15.2 ± 7.5 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$ for GPP, *R*, and NEP, respectively. The mixed layer comprised a majority of both GPP and *R* (72% and 57%, respectively); however, that meant 28% of GPP and 43% of *R* occurred below the mixed layer (Fig. 6). The contribution of each layer to whole-lake metabolism changed over the course of the season. Early in the season, the depths below the mixed layer contributed an even larger portion. In June, 48% of GPP and 69% of *R* occurred below the mixed layer. These contributions declined over the course of the season, which was mainly the result of the deepening of the mixed layer to include the 3 and 5 m layers.

Our two approaches to filtering the DO time series were able to reduce noise and helped capture the diel signal (Fig. 3). Visual inspection of the filtered data indicated that the wavelet filter was better than the moving average at removing the high level of noise at 8 m while still maintaining the diel signal at 1 m where there was less noise. The two filtering approaches resulted in different estimates of whole-lake metabolism (Fig. 6, Table 1). However, comparisons of the daily estimates from all filters in Table 1 for each individual layer showed no significant differences among the mean GPP, *R*, or NEP values (Table 2). Both filter types reduced the estimates of GPP and *R* primarily by reducing the rates for the 8 m layer. The moving average produced a reasonable estimate of *R*, but it caused the estimate of GPP at 8 m to become substantially negative. This result (negative GPP) is related to the poorer fit and high noise present at the 8 m depth. Since GPP cannot be negative, we assumed for this analysis that it was zero at 8 m. The wavelet filter was better at reducing the noise at 8 m and caused reduced rates of GPP and *R*. The rates of the 3 m layer were also reduced by filtering, especially using the moving average. Both filters resulted in slight increases in mixed layer GPP over the unfiltered estimates, while the rates of *R* remained the same in the mixed layer after wavelet filtering and increased with application of the moving average filter. Interestingly, estimates for the 5 m layer remained mostly unchanged by both filtering approaches. Like the unfiltered data, the filtered data from the moving average resulted in negative NEP,

Fig. 3. Dissolved oxygen (DO) data at (*a*) 1 m, (*b*) 3 m, (*c*) 5 m, and (*d*) 8 m during a time when the mixed layer only contained the 1 m sonde. Gray lines show the raw, unfiltered DO data, and black lines show filtered data using wavelet transforms. (*e*) Photosynthetically active radiation measurements are shown from the central buoy.

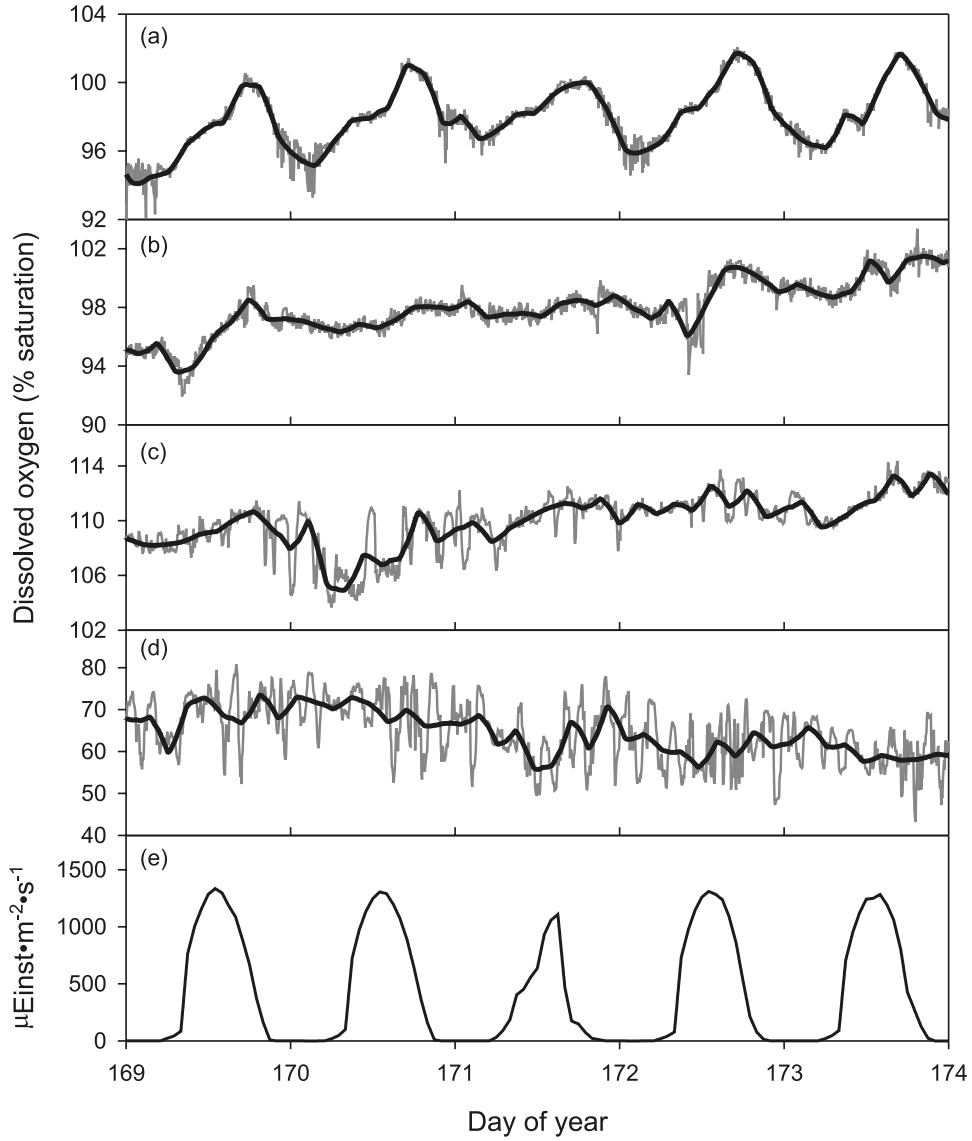


Fig. 4. Mean daily metabolism for the four littoral sites (A–D) and the 1 m pelagic site (P). Results are from the raw, unfiltered data. Error bars show 95% confidence intervals. GPP, gross primary production; *R*, respiration; NEP, net ecosystem production.

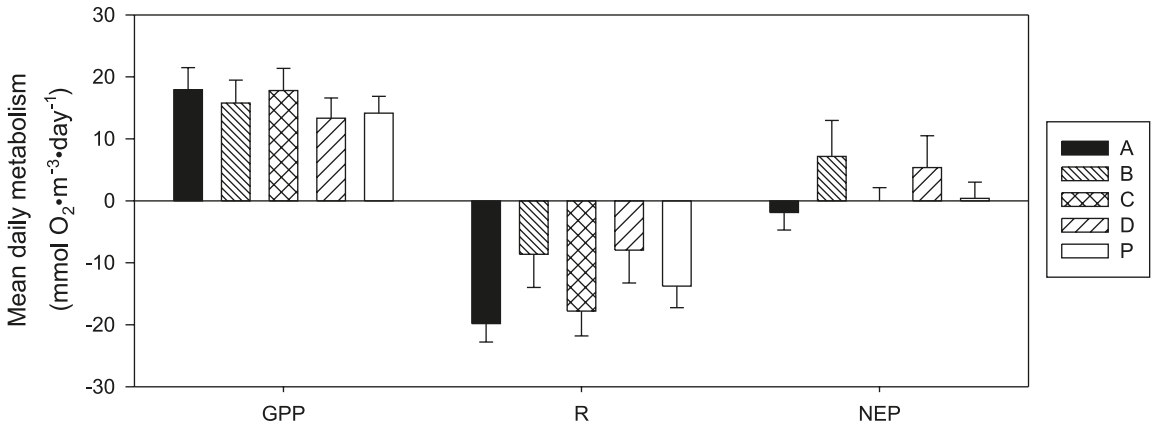


Fig. 5. Mean daily volumetric rates of gross primary production (GPP, open bar), respiration (*R*, solid bar), and net ecosystem production (NEP, crosshatched bar) for each depth layer in the pelagic zone. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Results are from the raw, unfiltered data. Error bars represent standard error.

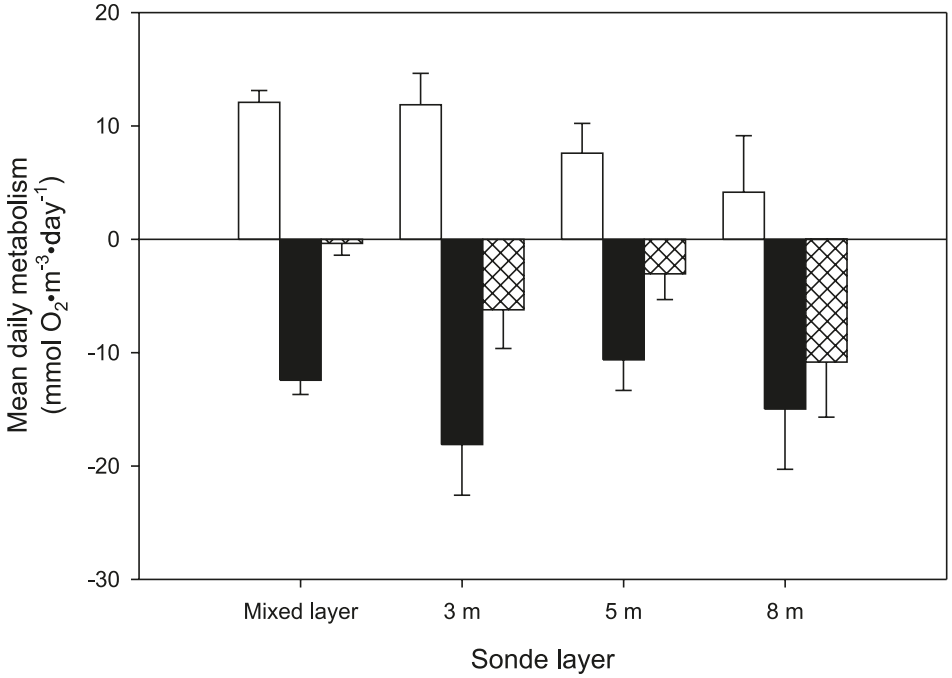


Fig. 6. Depth-integrated whole-lake estimates of metabolism showing contributions from the mixed (solid bars), 3 m (crosshatched bars), 5 m (hatched bars), and 8 m (open bars) layers. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Results are shown from the raw, unfiltered data as well as from data filtered by a wavelet transform (160 min scale) and a moving average (2 h scale). The moving average produced a negative rate of gross primary production (GPP) at 8 m, which we assumed to be zero. Error bars indicate 95% confidence intervals of the total whole-lake estimates. *R*, respiration; NEP, net ecosystem production.

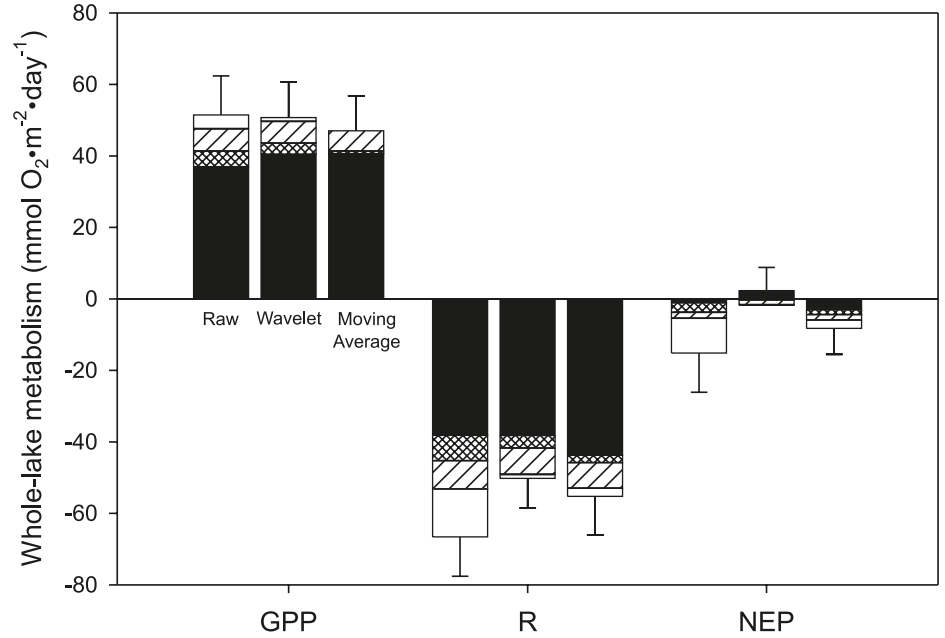


Table 1. Mean daily whole-lake metabolism estimates (mmol $O_2 \cdot m^{-2} \cdot day^{-1}$) from each depth layer using unfiltered data; moving average filtered data at 1, 2, and 4 h timescales; and wavelet-transformed data at 160 and 320 min timescales.

		Moving average			Wavelet transform	
Depth layer	Unfiltered	1 h	2 h	4 h	160 min	320 min
Total						
GPP	51.4 (11.1)	41.2 (9.6)	45.0 (9.9)	41.4 (8.9)	50.7 (10.0)	55.1 (9.4)
R	–66.6 (11.1)	–47.8 (9.8)	–55.0 (11.0)	–52.1 (9.5)	–50.2 (9.1)	–59.1 (7.5)
NEP	–15.2 (11.1)	–6.6 (8.5)	–9.9 (7.4)	–10.7 (6.7)	0.5 (7.7)	–3.9 (7.2)
Mixed layer						
GPP	37.0 (6.0)	37.0 (6.7)	40.7 (6.4)	37.8 (6.7)	40.5 (6.4)	42.6 (6.2)
R	–38.2 (7.1)	–38.5 (7.1)	–43.8 (7.5)	–43.0 (7.6)	–38.2 (6.0)	–42.8 (5.0)
NEP	–1.2 (5.7)	–1.5 (4.6)	–3.1 (4.7)	–5.2 (4.6)	2.3 (4.9)	–0.2 (5.1)
3 m layer						
GPP	4.5 (2.7)	2.6 (2.5)	0.8 (2.3)	1.0 (2.2)	3.1 (2.7)	2.6 (2.0)
R	–7.1 (4.7)	–4.6 (3.3)	–2.1 (2.7)	–2.6 (2.7)	–3.5 (3.4)	–3.9 (2.8)
NEP	–2.6 (2.9)	–2.0 (2.4)	–1.3 (1.6)	–1.6 (1.4)	–0.4 (1.7)	–1.3 (1.7)
5 m layer						
GPP	6.3 (3.8)	6.2 (3.8)	5.6 (4.2)	4.7 (4.1)	6.1 (3.6)	6.5 (4.3)
R	–7.9 (3.8)	–7.8 (2.8)	–7.2 (2.7)	–6.8 (2.6)	–7.3 (2.4)	–8.7 (2.5)
NEP	–1.6 (3.3)	–1.6 (2.7)	–1.6 (2.8)	–2.1 (2.7)	–1.1 (2.7)	–2.2 (3.3)
8 m layer						
GPP	3.7 (8.9)	–4.7 (6.0)	–2.0 (5.6)	–2.1 (5.0)	1.0 (6.7)	3.5 (5.9)
R	–13.5 (9.5)	3.1 (7.6)	–2.0 (6.6)	0.3 (4.9)	–1.2 (5.3)	–3.7 (4.4)
NEP	–9.7 (8.7)	–1.6 (3.1)	–3.9 (4.9)	–1.8 (3.9)	–0.2 (4.8)	–0.2 (4.1)

Note: The total values are from the whole lake and are the sum of each layer. The mixed layer includes data from the 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer. Values in parentheses are 95% confidence intervals. In all cases, $n = 84$. GPP, gross primary production; *R*, respiration; NEP, net ecosystem production.

while the wavelet filter resulted in a NEP near zero (0.48 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$). As a result of filtering, the portion of GPP and *R* estimated to occur below the mixed layer was respectively reduced from 28% and 43% to 20% and 24% for the wavelet filter and to 14% and 20% for the moving average filter.

Discussion

Rates of metabolism were similar across the surface waters of the lake, although there were some differences in rates of *R* between some of the littoral sites and the single pelagic site. These differences were small and opposing, with sites significantly higher and lower than the pelagic site, and may have averaged out over the entire littoral zone. The effect of any disparity between the littoral and pelagic zones is relatively unimportant at the whole-lake scale because the littoral zone is small in volume relative to the pelagic zone. Therefore, for our analysis, the rates of metabolism from the littoral sites were not included in our whole-lake estimate.

The lack of strong spatial heterogeneity in the surface water metabolism of Crampton Lake deviates from the large differences that both Lauster et al. (2006) and Van de Bogert et al. (2007) found between the pelagic and littoral habitats in other lakes as well as from differences for similar habitats documented by Caraco and Cole (2002) in a large river. Crampton Lake does not have dense, submerged macrophyte beds, and this may be one reason why any differences between littoral and pelagic rates were small. In both the Lauster et al. (2006) and Caraco and Cole (2002) studies, the largest differences were observed in systems or areas with dense macrophyte beds. Mixing caused by wind is another possible reason for the lack of spatial differences in surface water metabolism. Van de Bogert et al. (2007) found that wind acts as a homogenizing force, such that pelagic and littoral signals are indistinguishable on days when the average wind speed at 2 m (above the lake surface) exceeds a threshold of 2.75 $m \cdot s^{-1}$ for an hour. The wind on Crampton Lake reached this threshold on 70% of the days during our study. Site A was the most sheltered from the wind, as wind was predominantly from the southwest, and rates of metabolism at this site were the most different from the pelagic site.

Sondes reliably captured the diel changes in oxygen below the mixed layer at 3 and 5 m. The diel signals at these depths were weaker than those in the mixed layer, but they were still resolvable by our metabolism model, as it produced reasonable estimates of GPP and *R*. In addition, filtering the data enhanced our ability to resolve metabolic (i.e., diel) signals by removing the non-diel (i.e., nonbiological) variability in the DO signal. DO data from the 8 m sonde was not as clear, as high levels of noise made it difficult for our model to resolve the metabolic signal. The moving average filter was unable to reduce the noise at 8 m and recover reasonable metabolic estimates, as GPP tended to be negative using this approach. The wavelet transform was able to reduce the non-diel noise, and this transformation resulted in greatly decreased rates of metabolism at 8 m. This result

Table 2. Results of analysis of variance (ANOVA) tests comparing daily estimates over 84 days of gross primary production (GPP), respiration (*R*), and net ecosystem production (NEP) from the moving average (1, 2, and 4 h) and the wavelet transform (160 and 320 min) filters.

Depth layer	Source	SS	df	MS	*F*	*p*
Total						
GPP	Filter	11 712	4	2928	1.49	0.20
	Error	816 266	415	1967		
R	Filter	6 320	4	1580	0.83	0.51
	Error	791 674	415	1908		
NEP	Filter	7 583	4	1896	1.57	0.18
	Error	502 214	415	1210		
Mixed layer						
GPP	Filter	1 658	4	414	0.46	0.77
	Error	376 646	415	908		
R	Filter	2 638	4	659	0.68	0.61
	Error	402 485	415	970		
NEP	Filter	2 888	4	722	1.48	0.21
	Error	202 202	415	487		
3 m layer						
GPP	Filter	386	4	96	0.80	0.53
	Error	50 136	415	121		
R	Filter	350	4	87	0.46	0.77
	Error	79 485	415	192		
NEP	Filter	113	4	28	0.41	0.80
	Error	28 691	415	69		
5 m layer						
GPP	Filter	150	4	38	0.11	0.98
	Error	143 389	415	346		
R	Filter	166	4	42	0.29	0.89
	Error	60 076	415	145		
NEP	Filter	64	4	16	0.09	0.99
	Error	73 802	415	178		
8 m layer						
GPP	Filter	3 054	4	764	1.04	0.39
	Error	306 113	415	738		
R	Filter	2 017	4	504	0.68	0.61
	Error	308 311	415	743		
NEP	Filter	834	4	208	0.42	0.80
	Error	207 885	415	501		

Note: The total values are from the whole lake and are the sum of each layer. The mixed layer includes data from 1, 3, and 5 m sondes whenever they were present in the mixed layer. The 3 and 5 m layers only include data when those sondes were not in the mixed layer. The 8 m layer was always below the mixed layer.

suggests that much of the changes in DO at 8 m were primarily caused by physical rather than biological processes and for the most part did not reflect metabolism.

A complete mass balance of oxygen for any given layer is described in eq. 1, where *A* is the exchange, production, or consumption of oxygen by other physical–chemical processes. In our analyses, we have assumed *A* to be negligible compared with other terms in the equation. To test this assumption, we can estimate the vertical flux of DO between layers that may occur because of large concentration gradients. A large oxygen gradient occurs in Crampton Lake below the oxygen maximum, which is typically at 5 m. The difference in DO between sonde locations at 5 and 8 m during midsummer is approximately 2 $mg \cdot L^{-1}$. Assuming a coefficient of vertical diffusion (K_v) of 0.02 $cm^2 \cdot s^{-1}$, we can estimate the cross-gradient flux of oxygen using standard equations (Jassby and Powell 1975). The flux was 3.6 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$, which was quite small relative to the average whole-lake GPP and *R* estimates of 51.4 and –66.6 mmol $O_2 \cdot m^{-2} \cdot day^{-1}$, respectively. While there are mechanisms of oxygen consumption and production associated with *A*, these appear to be small fluxes relative to metabolic rates. An exception might be for deeper layers, such as the 8 m layer, where metabolic rates are lower so that these fluxes may have a larger impact, especially during episodic mixing events (Ostrovsky et al. 1996). These mixing phenomena may contribute to the considerable noise observed in the 8 m DO data. While inclusion of these fluxes into our oxygen budget may have some effect on our estimates of metabolism for each layer, our estimate of whole-lake metabolism, which includes all layers, may not be affected, since any oxygen lost by a layer through vertical exchange is gained by another layer. If there was a flux of oxygen from 5 to 8 m, then we would have overestimated metabolism in the 5 m layer, but we would also have underestimated metabolism in the 8 m layer by the same amount. Thus, the whole-lake estimate of metabolism would remain the same.

Because both GPP and *R* vary strongly with depth, estimates based on the surface water alone will underestimate whole-lake metabolism. This result is well known from early discrete sampling studies of primary production (Fee 1980), but it is useful to evaluate the degree of underestimation using the sonde approach where daily values of GPP, *R*, and NEP are generated. For example, had we only used the pelagic 1 m sonde in this study, we would have overestimated seasonal rates of GPP and *R* in the upper mixed layer by 13% and 3%, respectively, and underestimated whole-lake GPP by 18% and *R* by 41%.

Our study revealed that rates of metabolism were not constant throughout the apparent upper mixed layer, but were lower in the deeper portions. Our assessment of the depth of the mixed layer is based only on weekly temperature profiles and is too coarse to capture shorter-term dynamics in changes in the mixing regime that others have observed at a number of time scales (MacIntyre et al. 1999). While we do have high-frequency temperature data from each of the sondes, the data does not have enough vertical resolution to assess these short-term dynamics in thermal structure. The fact that the 5 m sonde on days we assessed it to be in the mixed layer gave different results than those at 1 and 3 m is probably indicative of this dynamic variation in mixing.

At the deepest site (8 m), DO did not vary on an obvious diel cycle with or without statistical filtering. It is possible that the estimates of GPP and *R* for this depth layer were spurious, and variations in DO were caused by either water movements or other processes. Additionally, we overestimated the contribution of the 8 m layer to whole-lake GPP because we extrapolated the 8 m results to the bottom of the lake, even though GPP is probably zero below 10 m. This error, however, is small (~2% of the unfiltered, total whole-lake GPP estimate) because the rate of GPP at 8 m is small, and the volume of water at 10 m and below is only about 5% of the lake volume. Nevertheless, even if we were to disregard GPP and *R* from the 8 m layer, the 1 m sonde alone would still have underestimated whole-lake GPP (through

the 5 m depth) by 12% and *R* by 26%. Furthermore, we would have falsely concluded that NEP for the mixed layer (and thus the whole lake) was positive if we had only used the pelagic 1 m sonde. Because *R* was not trended with depth and GPP decreased with depth, it is likely that NEP estimates would be lower in many lakes if depth-integrated values were used.

A single surface sonde is unable to accurately measure metabolism of the whole lake or even of the apparent mixed layer. Using multiple sondes deployed both horizontally and vertically within a lake is essential to accurately estimating whole-lake metabolism. Exactly how many sondes are required for robust estimates is unknown and likely depends on the heterogeneity of the system being studied. The results of this study suggest that thermal partitioning of the water column relates to the biological activity, as expressed in rates of metabolism. Even though past studies have assumed the epilimnion to be well mixed, our DO data from sondes placed near the top and bottom of the epilimnion yield different metabolism estimates, suggesting a certain degree of partitioning within the epilimnion, as has been found elsewhere (Eckert et al. 2002). Although the influence of short-term dynamics in thermal structure on the metabolic rates in the water column is beyond the scope of this study, further investigation of that relationship may prove fruitful.

Ecosystem-level processes are complex and difficult to estimate. The use of automated sensors is greatly enhancing our ability to estimate rates over broader time and space scales. These instruments allow researchers to collect considerably more data at scales that would be impossible using traditional techniques. Sensors are able to continuously sample at intervals of minutes rather than of days or weeks with traditional methods. Simultaneous high-frequency measurements from multiple sensors deployed in various locations allowed us to gauge the relative importance of different habitats and depth layers to whole-lake metabolism. With these advances in observation technology come challenges in signal processing and ecosystem modeling, especially as we begin scaling up estimates from multiple sensors to the whole ecosystem. High-frequency measurements allow for more temporally dense metabolism estimates, but also yield patterns at multiple time scales that can confound our ability to separate the desired signal from noise. Wavelet transforms are one type of filtering that shows promise for separating signals by scale. Furthermore, a tighter coupling between physical and biological processes in our models will help us better understand the relationships among thermal stratification, metabolism, and gas flux. As these techniques are applied to the diversity of aquatic ecosystems, we are sure to appreciate more fully the spatial and temporal complexity of lakes.

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References

Addison, P.S. 2002. The illustrated wavelet handbook: applications in science, engineering, medicine and finance. Institute of Physics Publishing, London, UK.

Bachmann, R.W., Hoyer, M.V., and Canfield, D.E. 2000. Internal heterotrophy following the switch from macrophytes to algae in Lake Apopka, Florida. Hydrobiologia, **418**: 217–227.

Betts, K.S. 1998. Technology update: all-weather water quality monitor. Environ. Sci. Technol. **32**: 85A.

Branco, B., Torgersen, T., Bean, J.R., Grenier, G., and Arbige, D. 2005. A new water column profiler for shallow aquatic systems. Limnol. Oceanogr.: Methods, **3**: 190–202.

Caraco, N.F., and Cole, J.J. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. Ecol. Appl. **12**: 1496–1509.

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

Carpenter, S.R., Elser, M.M., and Elser, J.J. 1986. Chlorophyll production, degradation, and sedimentation: implications for paleolimnology. Limnol. Oceanogr. **31**: 112–124.

Cole, J.J., and Caraco, N.F. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF_6. Limnol. Oceanogr. **43**: 647–656.

Cole, J.J., and Pace, M.L. 1998. Hydrologic variability of small northern Michigan lakes measured by the addition of tracers. Ecosystems, **1**: 310–320.

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

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

Eckert, W., Imberger, J., and Saggio, A. 2002. Biogeochemical response to physical forcing in the water column of a warm monomictic lake. Biogeochemistry, **61**: 297–307.

Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. Limnol. Oceanogr. **21**: 767–783.

Fee, E.J. 1980. Important factors for estimating annual phytoplankton production in the experimental lakes area. Can. J. Fish. Aquat. Sci. **37**: 513–522.

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

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

Holm-Hansen, O., and Riemann, B. 1978. Chlorophyll *a* determination: improvements in methodology. Oikos, **30**: 438–447.

Howarth, R.W., Schneider, R., and Swaney, D. 1996 Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. Estuaries, **19**: 848–865.

Jahne, B., Munnich, K.O., Bosinger, R., Dutzi, A., Huber, W., and Libner, P. 1987. On parameters influencing air–water gas exchange. J. Geophys. Res. **92**: 1937–1949.

Jassby, A., and Powell, T. 1975. Vertical patterns of eddy diffusion during stratification in Castle Lake, California. Limnol. Oceanogr. **20**: 530–543.

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

Lodge, D.M., Blumenshine, S.C., and Vadeboncoeur, Y. 1998. Insights and applications of large-scale, long-term ecological observations and experiments. *In* Experimental ecology: issues and perspectives. *Edited by* W.J. Resetarits, Jr., and J. Bernardo. Oxford University Press, New York. pp. 202–207.

Lovett, G.M., Cole, J.J., and Pace, M.L. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? Ecosystems, **9**: 152–155.

MacIntyre, S. 1993. Vertical mixing in a shallow, eutrophic lake: possible consequences for the light climate of phytoplankton. Limnol. Oceanogr. **38**: 798–817.

MacIntyre, S., Flynn, K.M., Jellison, R., and Romero, J.R. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. Limnol. Oceanogr. **44**: 512–529.

Marker, A.F.H., Crowther, C.A., and Gunn, R.J.M. 1980. Methanol and acetone as solvents for estimating chlorophyll *a* and phaeopigments by spectrophotometry. Arch. Hydrobiol. Beih. Ergebn. Limnol. **14**: 52–69.

Megard, R.O., and Smith, P.D. 1974. Mechanisms that regulate growth rates of phytoplankton in Shagawa Lake, Minnesota. Limnol. Oceanogr. **19**: 279–296.

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

Ostrovsky, I., Yacobi, Y.Z., Walline, P., and Kalikhman, I. 1996. Seiche-induced mixing: its impact on lake productivity. Limnol. Oceanogr. **41**: 323–332.

Pace, M.L., and Prairie, Y.T. 2005. Respiration in lakes. *In* Respiration in aquatic ecosystems. *Edited by* P.A. del Giorgio and P.J. le B. Williams. Oxford University Press, Oxford, UK. pp. 103–121.

Peterson, B.J. 1980. Aquatic primary productivity and the ^{14}C–CO_2 method: a history of the productivity problem. Annu. Rev. Ecol. Syst. **11**: 359–385.

Saunders, G.W., Trama, F.B., and Bachman, R.W. 1962. Evaluation of a modified ^{14}C technique for shipboard estimation of photosynthesis in large lakes. Univ. Michigan Great Lakes Res. Div. No. 8.

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

St. Amand, A.L., and Carpenter, S.R. 1993. Metalimnetic phytoplankton dynamics. *In* The trophic cascade in lakes. *Edited by* S.R. Carpenter and J.F. Kitchell. Cambridge University Press, London, UK. pp. 210–224.

Tobias, C.R., Böhlke, J.K., and Harvey, J.W. 2007. The oxygen-18 isotope approach to measuring metabolism in high-productivity waters. Limnol. Oceanogr. **52**: 1439–1453.

Vadeboncoeur, Y., Lodge, D.M., and Carpenter, S.R. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology, **82**: 1065–1077.

Vadeboncoeur, Y., Vander Zanden, M.J., and Lodge, D.M. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience, **52**: 44–54.

Van de Bogert, M.C., Carpenter, S.R., Cole, J.J., and Pace, M.L. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnol. Oceanogr.: Methods, **5**: 145–155.