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Assessing pelagic and benthic metabolism using free water measurements

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Abstract

Automated in situ sensors for measuring changes in dissolved oxygen (DO) at high frequency have facilitated estimates of gross primary production (GPP) and respiration (R) in aquatic systems. Lake researchers usually rely on a single sensor for these estimates, but such point measurements may miss important spatial heterogeneity in within-lake processes and may not accurately represent systemwide values of metabolism. Here we combine simultaneous measurements of metabolism using DO sensors along transects from the shore to the center of a lake with a spatial model to better understand the underlying heterogeneity in processes contributing to whole-lake epilimnetic metabolism. We use this model to achieve better estimates of epilimnetic GPP and R and to determine the relative contributions of benthic-littoral vs. pelagic processes to these estimates. We compared the spatially explicit process-based model to estimates of metabolism from both a single sensor at the lake's center and a spatially explicit averaging of multiple sensor sites. Estimates of both GPP and R varied on average 2.5- to 3.2-fold from site to site within the same lake, whereas variations were sometimes as high as 6- to 7-fold. Estimates of GPP and R near the perimeter of lakes were on average greater than measurements in the middle of the lake. Our model estimates that benthic-littoral processes accounted for ~40% of epilimnetic GPP and R. A single, centrally located sensor often misses a significant component of this benthic metabolism and accounts for only ~81% of lakewide GPP and R.

Introduction

When Odum (1956) introduced the concept and first measurements of whole-ecosystem primary production and respiration from diel "free-water" changes in dissolved oxygen concentrations, a tremendous effort (and usually a sleepless night) was required to obtain a metabolic estimate for even a single day. The advent of affordable instruments that continuously and reliably measure dissolved gases such as O_2 or CO_2 now allow researchers to acquire long series of high-frequency data for estimating whole-system metabolism (Langdon 1984; Uehlinger and Naegeli 1998; Mulholland et al. 2001; Hanson et al. 2003). Free-water methods have considerable advantages over incubation approaches in either light and dark bottles or benthic chambers. Container effects including enclosure in bottles, sediment chambers, and various other devices can be significant, and comparison among container studies is difficult because many studies fail to report key details of the containers used (Petersen et al. 1997; Petersen et al. 1999). Additionally, container approaches suffer from problems of scale (Gerhart and Likens 1975; Chen et al. 2000). Heterogeneity of the benthos (e.g., substrate, macrophyte and periphyton density, incident solar radiation) makes scaling from chambers to the whole system uncertain. Free-water techniques, on the other-hand, offer the promise of integrating a signal over the entire benthic-littoral region in much the same way that a terrestrial gas-flux tower is used to integrate gas-fluxes over a region (Valentini et al. 1996).

As the use of free-water techniques has expanded, new insights and new difficulties have emerged (McCutchan et al. 1998). Even if the free-water method perfectly represented whole-system gross primary production (GPP) and respiration (R), one is often really interested in the separate contributions

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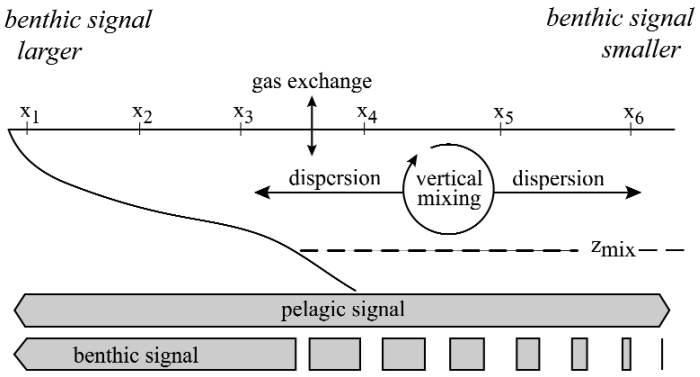

Fig. 1. Conceptual diagram of a spatial sonde deployment. At each sonde site (x_i) the sensor detects changes in dissolved O_2 due to an unknown mixture of benthic and pelagic processes occurring in the mixed layer of the lake. In the absence of horizontal dispersion, in shallow water (where $z < z_{mix}$) both benthic and pelagic processes would affect the local sensor. In deep water (where $z > z_{mix}$) only pelagic processes would affect the local sensor. At all sites horizontal dispersion tends to homogenize the O_2 signals. Under the right conditions the spatial profiles of dissolved oxygen changes over a transect of sonde sites (x_1 to x_6) can be used to separately compute the benthic contributions to GPP and R.

of benthic and pelagic habitats to this whole (Vadeboncoeur et al. 2003). These contributions are sometimes obtained by measuring the metabolism of the whole and one of the parts (using bottles or chambers and their associated uncertainties) and inferring the other component by difference (Naegeli and Uehlinger 1997; Fellows et al. 2001; Carpenter et al. 2005). However, it is not clear whether free-water techniques actually measure the metabolism of the whole system or some part of it. To date, most estimates of whole-system metabolism have relied on single sensors in the middle of the pelagic region. However, dissolved oxygen sensors placed in different habitats in both rivers (Caraco and Cole 2002) and lakes (Lauster et al. 2006) yield estimates of metabolism that vary with location. In both of those studies, oxygen concentrations were more dynamic in shallow, littoral habitats than in open water. If a single measurement location were able to provide a complete integration of whole-ecosystem processes, we would not expect to see different estimates among sites.

Lauster et al. (2006) found that differences in bottle (planktonic) estimates of metabolism between pelagic and littoral habitats were relatively small, suggesting that planktonic metabolism was nearly evenly distributed throughout the epilimnion. They also found that although differences were greatest near-shore, free-water metabolism estimates were greater than bottle estimates for both the littoral and pelagic habitats. Lauster et al. (2006) attribute the higher estimates of pelagic metabolism using the free-water method to benthic sources which are not accounted for by bottle methods. Therefore, a free-water estimate of metabolism from the center of a lake may include some portion (but not necessarily all) of the benthic-littoral signal. Although the free-water method integrates all signals that reach a sensor, the challenge is determining how much of the benthic or pelagic signals reach any given location.

If localized benthic-littoral processes contribute to whole-lake metabolism in addition to spatially less variable planktonic processes, metabolism as measured by free-water methods should be greatest near shore (planktonic and benthic processes) and lowest at the center of the lake (planktonic processes plus advection of some portion of the benthic signal) (Fig. 1). The degree to which measurements near shore are higher than measurements at the center depends on the magnitude of the benthic signal as well as the degree of horizontal mixing. Given time-series of measurements at only two locations, even if one is near shore and the other at the center of the lake, it is not possible to determine how much of the metabolic signal is derived from benthic sources because there are two unknown factors: the magnitude of benthic metabolism and the degree of advection from the littoral zone to the pelagic. Several series of measurements along a transect, however, might allow one to simultaneously estimate the rate of horizontal advection and partition the metabolism signal into benthic and pelagic sources. Here we use continuous free-water measurements of dissolved oxygen at several locations along a littoral-pelagic transect to (1) assess the variation in metabolism estimates among measurement locations, (2) estimate whole-lake epilimnetic metabolism based on spatially explicit volume-weighted averages of individual measurements, and (3) develop a spatially explicit model of whole-lake epilimnetic metabolism that partitions the whole-lake estimate into benthic and pelagic components.

Materials and procedures

Data for this study were collected from Peter Lake, located at the University of Notre Dame Environmental Research Center (UNDERC) near Land O'Lakes, Wisconsin, USA, over the course of two summers (2002 and 2003). Peter Lake is a 2.5-ha circular lake with a mean depth of 6 m, a maximum depth of 19 m, and an upper mixed layer during summer stratification of approximately 3 m (Carpenter and Kitchell 1993). In 2002, Peter Lake was fertilized with nitrogen and phosphorus to increase primary production (Carpenter et al. 2005). As a consequence of the added nutrients, average phytoplankton biomass increased 10-fold in 2002 relative to other years. We present data for both 2002 (fertilized) and 2003 (not fertilized).

Dissolved oxygen and temperature were measured using YSI model 600XLM multiparameter sondes calibrated in vapor-saturated air before each deployment. Each deployment consisted of 4 to 6 sondes placed within the epilimnion along a linear transect from the shore to the middle of the lake. Approximately half of the sondes from any deployment were within the littoral zone and half in the pelagic. The sonde closest to shore was placed at a distance from shore where the water depth was approximately 1 m. Measurements of temperature and dissolved oxygen were recorded every 5 min at a

depth of 0.7 m. Deployments lasted from 5 to 10 days, after which the sondes were brought back to the lab to be cleaned and prepared for the next deployment.

We followed YSI's guidelines for deployment and calibration (YSI Environmental, Technical Note #610, www.ysi.com). Briefly, our procedures were as follows. Before each deployment we reconditioned the surface of the probe (if necessary) and replaced the dissolved oxygen membrane. Proper probe functioning was tested using YSI's suggested diagnostics. The probe was initialized to log every 5 min and placed in water-saturated air to allow the membrane to relax to a stable state. After the membrane had relaxed (4–8 h, verified by stable dissolved oxygen readings), we calibrated the sensor to the ambient barometric pressure. Sondes were kept in the laboratory while logging data for a minimum of 2 additional hours in water-saturated air. These predeployment data were used to verify, and correct if necessary, the initial calibration. Upon retrieval (5–10 days later), probes were again placed in water-saturated air and allowed to log an additional 2–4 h at a stable temperature. These postdeployment data were used to determine the drift of the sensor. We corrected the data assuming any drift occurred linearly over the course of the deployment. On average, sonde drift (± 1 SD) was 0.043 ± 0.042 mg L^{-1} d^{-1}.

Before deploying the transects, we assessed sonde-to-sonde variability by allowing all 6 sondes to simultaneously collect data from the center of Peter Lake for 5 days. These data were independently corrected for drift and used with the models described below to obtain daily estimates of metabolism (GPP and R) for each sonde. These estimates were used to determine baseline sonde-to-sonde variability.

Because the oxygen sensors were located within the epilimnion of a strongly stratified lake, we assume they did not measure metabolism occurring below the mixed layer. This assumption is supported by tracer additions in Peter Lake and calculations of a vertical mixing coefficient based on heat flux calculations. In a previous study, lithium bromide (LiBr) added to the epilimnion of Peter Lake in May of 1993 was not detectable below the thermocline over the entire summer stratified season (Cole and Pace 1998). Calculation of mass transfer of oxygen across the thermocline based on the equations of Chapra (1997) indicates that 3.5 mg O_2 m^{-2} d^{-1} may be lost to the hypolimnion. This amounts to approximately 0.04% of the standing stock per day and is less than 0.50% of the magnitude of the daily change in epilimnetic dissolved oxygen concentration. Similarly, Gelda and Effler (2002) accounted for vertical transport of O_2 in their metabolism models and concluded that this component was unimportant and could be ignored. Therefore, we assume exchange across the thermocline over any given 24-h period is negligible, and for the purposes of our analyses, whole-lake metabolism refers to horizontal integration of benthic-littoral and pelagic processes within the epilimnion and not vertical integration of all stratification layers. This assumption is not valid for all lakes and all time periods; exchange of O_2 across the thermocline may need to be accounted for in other circumstances and could be incorporated into the modeling framework presented below.

Photosynthetically active radiation was measured using a mechanical pyranograph in 2002 and a Li-COR quantum sensor in 2003. The mechanical pyranograph provided estimates of total daily radiation, whereas the Li-COR sensor logged radiation every 5 min. To estimate PAR received every 5 min from the 2002 data, the total daily PAR values were partitioned according to the potential irradiance curve on a cloudless day using the equations of Iqbal (1983). In 2003, wind speeds at 2 m above the water surface were measured using an R.M. Young anemometer. Five-minute wind speed averages, as well as minimum and maximum values, were recorded with a Campbell Scientific 6250 data logger.

Site-specific metabolism—To estimate lake metabolism at each site, we fitted a simple model to the time series of dissolved oxygen concentration measured at 5-min intervals. For a single sonde at a given time, the rate of change of dissolved oxygen concentration is the result of metabolism and exchange with the atmosphere.

$$\frac{dY}{dt} = GPP - R + D \tag{1}$$

All symbols in this equation and below are defined in Table 1. Over a short interval, such as the 5-min interval between sonde measurements, the solution of equation 1 is approximately

$$Y_{t+1} = Y_t + (GPP - R + D)\Delta t \tag{2}$$

To estimate GPP and R from our data, we modified equation 2 to account for irradiance and diffusion rate in each 5-min time interval:

$$Y_{t+1} = Y_t + \frac{GPP24}{PAR24} \times PAR_t - R24\Delta t + D_t\Delta t + Z_t \tag{3}$$

Given estimates of the parameters GPP24 and R24, equation 3 predicts the next oxygen concentration using measurements of PAR_t and PAR24 and the exchange rate of oxygen with the atmosphere. For a 5-min time interval Δt, the diffusive flux D_t was computed as

$$D_t = \frac{k([O_2]_{SAT,t} - Y_t)}{z} \tag{4}$$

where $[O_2]_{SAT,t}$ is the concentration of dissolved oxygen in equilibrium with the atmosphere which was calculated at each time step from temperature data and the equation of Weiss (1970) and corrected for barometric pressure according to the equations in USGS Water Quality Technical Memoranda #81.11 and #81.15 (United States Geological Survey 1981a; 1981b). The coefficient k was computed from the Schmidt number (Sc) and the gas piston velocity corresponding to a Schmidt number of 600 (k_{600}).

$$k = k_{600}\left(\frac{Sc}{600}\right)^{-\frac{1}{2}} \tag{5}$$

The Schmidt number is dependent on water temperature and was calculated at each time step using the O_2-specific equation of Wanninkhof (1992). For this analysis, we used a

Table 1. Definition of symbols used in the models.

Symbol	Definition	Units
a	shape parameter (vertical stretch) for the inverse tangent function	dimensionless
A_B	ratio of benthic area to lake surface area	dimensionless
b	shape parameter (horizontal shift) for the inverse tangent function	dimensionless
D	instantaneous rate of diffusion between lake and atmosphere	mmol m^{-3} d^{-1}
GPP	instantaneous rate of gross primary production	mmol m^{-3} d^{-1}
GPP24	daily rate of gross primary production	mmol m^{-3} d^{-1}
GPP_b	daily rate of benthic gross primary production	mmol m^{-2} d^{-1}
GPP_p	daily rate of planktonic gross primary production	mmol m^{-3} d^{-1}
k	coefficient of gas exchange	m d^{-1}
k_{600}	coefficient of gas exchange for a gas with a Schmidt number of 600	m d^{-1}
m_x	proportion of metabolism (GPP or R) from benthic sources sensed by a sonde placed at distance x from shore	dimensionless
PAR	photosynthetically active radiation on the lake surface over a 5-min interval	µmol m^{-2} Δt^{-1}
PAR24	daily photosynthetically active radiation on the lake surface	µmol m^{-2} d^{-1}
R	instantaneous rate of whole ecosystem respiration	mmol m^{-3} d^{-1}
R24	daily rate of whole ecosystem respiration	mmol m^{-3} d^{-1}
R_b	daily rate of benthic respiration	mmol m^{-2} d^{-1}
R_p	daily rate of planktonic respiration	mmos m^{-3} d^{-1}
t	time	d
Y	dissolved oxygen concentration	µM
z_x	depth of water in the epilimnion at location x	m
Z	autocorrelated model error	µM
Δt	small interval	d
ε	model error corrected for autocorrelation	µM
φ	autocorrelation coefficient	dimensionless

constant value for k_{600} of 0.4 m d^{-1}, which is within the range of estimates based on wind, CH_4 flux measurements, and an SF_6 addition to this lake (Bade and Cole 2006). Finally, the areal diffusive flux is divided by the epilimnion depth, z, to express the value in volumetric units.

The prediction error Z_t is autocorrelated, and an autocorrelation correction is computed as

$$Z_t = \varphi Z_{t-1} + \varepsilon_t \quad (6)$$

To estimate the parameters GPP24 and R24, we minimized the normal negative log likelihood of the Z_t (Hilborn and Mangel 1997). To determine the autocorrelation coefficient, φ, we then minimized the normal negative log likelihood of the ε_t.

Table 2. Steps in bootstrapping

Step	Description
1) Fit model $Y = f(X,\theta) + \varepsilon$	Determine nominal set of parameters, θ, by minimizing the normal negative log likelihood of the ε. Compute predictions as $\hat{Y} = f(X,\theta)$. Save $\hat{Y}$, θ, and ε.
2) Bootstrapping loop	
2a) Compute pseudo-observations	Randomly sample, with replacement, the ε as ε_R. Create pseudo-observations as $Y_P = \hat{Y} + \varepsilon_R$.
2b) Refit model	Find new set of parameters, θ_B, by minimizing the normal negative log likelihood of the ε_R. Save bootstrap estimates, θ_B.
2c) Repeat	Return to 2a and repeat 10,000 times.
3) Compute Statistics	Find mean, standard deviation, confidence intervals, covariance matrix, and so on, for bootstrap estimates of the parameters, θ_B.

Minimization was computed using the *fminsearch* function of Matlab (v. 7). We computed 95% confidence intervals of the parameters by bootstrapping with 10,000 iterations (Efron and Tibshirani 1993). Estimates of GPP24 and R24 were computed for each 24-h period beginning at sunrise as calculated from the latitude of Peter Lake and the declination of the sun on each day (Hartmann 1994).

Site-specific estimates of metabolism obtained by fitting equations 3 and 6 to the data make no assumptions about source (benthic or pelagic) of the metabolic fluxes. The estimates of GPP24 or R24 represent the sum of the processes affecting the concentration of oxygen at that location regardless of whether they are benthic or pelagic. We used these site-specific estimates in two ways. First, on all days, we calculated spatially explicit volume-weighted estimates of whole-lake GPP and R and compared these to estimates made by a single sensor at the middle of the lake. Second, we applied, when possible, a model of whole-lake metabolism to calculate the separate contributions of benthic and pelagic processes to GPP and R.

Spatially explicit volume-weighted estimate of whole lake metabolism—For each of the 40 dates on which we measured free-water metabolism, we applied the measured rates from each transect location to the volume of the epilimnion represented by that location. We first calculated the surface area of concentric rings divided at the midpoints between each sonde site and then calculated the volume of water within each concentric ring based on the hypsographic curve for the lake. Metabolic rates for each ring were multiplied by the appropriate volume of water and summed for the entire epilimnion.

Estimating rates of benthic and pelagic metabolism—Where metabolism changes monotonically from inshore to the center

of the lake, it is possible to partition metabolism between benthic and planktonic sources. Here "benthic" refers only to benthic processes occurring within the littoral zone (and thus within the mixed layer). In this analysis, we assume that the planktonic GPP and R are uniform in space and benthic metabolism only occurs where the bottom of the lake is within the upper mixed layer (>30% of the area of Peter Lake). To compute oxygen dynamics at any point x along a transect from shore to the center of the lake, we adapt equation 3 as follows:

$$Y_{x,t+1} = Y_{x,t} + m_x\left[\frac{GPPb}{PAR24}PAR_t - Rb\Delta t\right]\frac{1}{z_x} + \left[\frac{GPPp}{PAR24}PAR_t - Rp\,\Delta t\right] + D_{x,t} + Z_{x,t} \quad (7)$$

As in the site-specific model, prediction errors $Z_{x,t}$ are autocorrelated and can be corrected for autocorrelation using equation 6. Given a value of the spatial weighting function m_x (explained below), measurements of PAR24 and PAR_t, and estimates of D, equation 7 can be fitted to the data to estimate the parameters GPP_b, R_b, GPP_p, and R_p and their confidence intervals as described above for site-specific metabolism.

The value of m_x (which is a function of distance from shore) can be viewed as the proportion of the GPP or R produced in 1 m^2 of benthic habitat that is seen by a sensor at location x. A sensor directly above benthic sediment may "see" nearly all of the benthically derived metabolism produced there. A sensor near the boundary between the littoral and pelagic zone may see only a portion of the benthically derived metabolism because the signal may be diluted by water mixing between the zones. A sensor in the middle of the lake may see only a small portion of the metabolic signal produced near shore (see Fig. 1). The sum of the benthic signal seen at all locations cannot be more than the benthic area is capable of producing. Thus the mixing function is constrained by the area of benthic sediment in contact with the mixed layer. Two extreme, hypothetical examples illustrate this point. If there is no horizontal mixing of water, then 100% of the benthic signal would be measured in the littoral zone and 0% measured in the pelagic (Fig. 2a). On the other hand, if there were instantaneous mixing, the benthic signal would immediately be evenly spread out through the entire epilimnion (Fig. 2b). Intermediate scenarios are more likely, and a couple of examples are drawn in Fig. 2c. All of the intermediate scenarios can be described by an inverse tangent function transformed to have a range between 0 and 1:

$$m_x = \left(\tan^{-1}(ax+b) + \frac{\pi}{2}\right)\times\frac{1}{\pi} \quad (8)$$

The shape of the function is determined by the parameters a (vertical stretch) and b (horizontal shift). Because the area under each curve is constrained by the area of the lake where benthic-littoral metabolism can occur, the two parameters (a and b) can be reduced to one unknown by setting the integral of the function (equation 9) from 0 to 1 equal to the ratio of benthic area to lake area (equation 10).

$$\int m(x)dx = \frac{1}{\pi}\cdot\left\{\frac{1}{a}\cdot\left[(ax+b)\cdot\tan^{-1}(ax+b) - \frac{1}{2}\ln\left(1+(ax+b)^2\right)\right] + \frac{\pi}{2}\cdot x\right\} \quad (9)$$

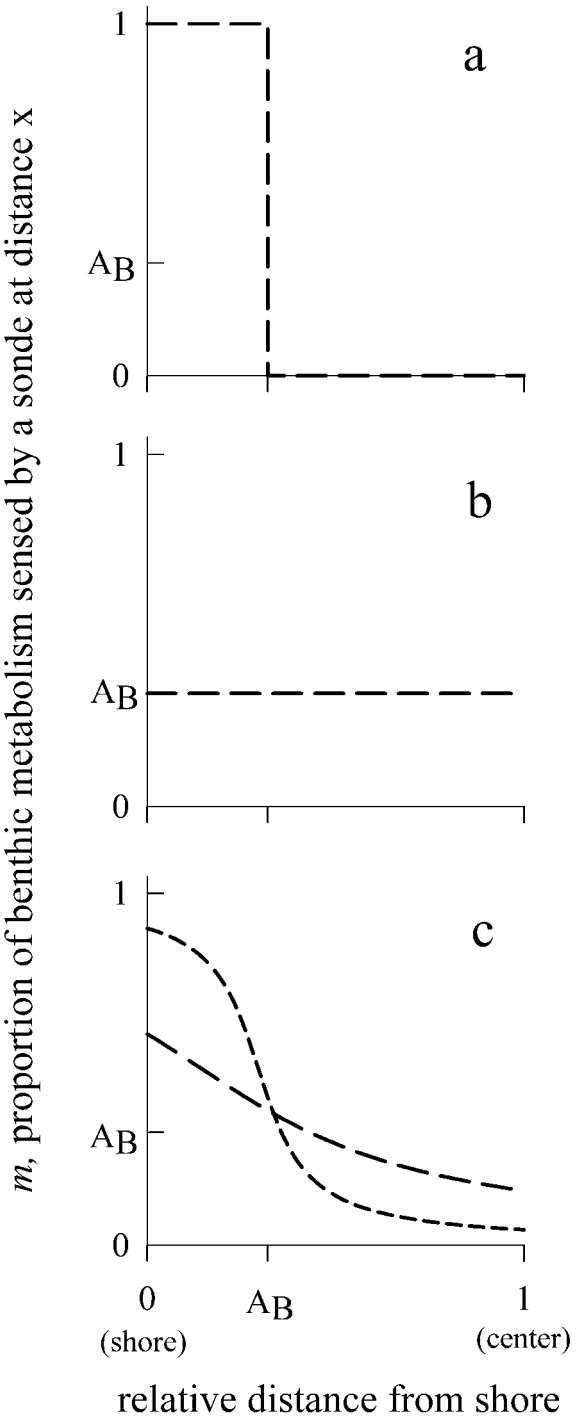

Fig. 2. Idealized models of the mixing function used to distribute the benthic metabolic signal along the transect. The *x*-axis is the ratio of the area of the lake from shore to distance *x* to the area of the entire lake. A_B is the ratio of benthic-littoral area to lake area. The *y*-axis represents the proportion of benthic-littoral metabolism detectable at a point *x*. In a, there is no mixing and the entire oxygen signal from benthic metabolism remains in the littoral zone. In b, there is perfect mixing, and the oxygen signal from benthic processes is evenly spread along the entire transect. Examples of intermediate cases are shown in c. In each case, the area under the curve is equal to A_B.

$$A_B = \int_0^1 m(x)dx = \frac{1}{\pi}\cdot\left\{\frac{1}{a}\cdot\left[(a+b)\cdot\tan^{-1}(a+b)-\frac{1}{2}\ln\left(1+(a+b)^2\right)\right]+\frac{\pi}{2}\right\} \quad (10)$$
$$-\frac{1}{\pi}\cdot\left\{\frac{1}{a}\cdot\left[(b)\cdot\tan^{-1}(b)-\frac{1}{2}\ln\left(1+b^2\right)\right]\right\}$$

The arbitrary parameter b can be expressed in terms of the value of m_x at shore by setting x equal to 0 and solving equation 8 for b.

$$b = \tan(m_0 \times \pi - \frac{\pi}{2}) \quad (11)$$

During the fitting process, a single value of the intercept (m_0) is estimated for all sensor locations on a given day. Given an estimate of m_0 and the ratio of benthic area to lake area, the value of b is calculated from equation 11 and the value of a can be solved numerically from equation 10 using the *fzero* function of Matlab 7.0, which finds the root of a continuous function of one variable.

Assessment

Sonde performance—We estimated 24-h GPP and R for each of 5 days and for all 6 sondes placed at the same location in the center of Peter Lake. Between-sonde variability was low for all days, and the pooled standard deviation between sondes was 3.35 mmol m^{-2} d^{-1}, or about 9% of the average metabolism estimates over the 5 days. In contrast, site-to-site variation in metabolism estimates when sondes were placed along transects was >3 times this amount, with a standard deviation of 10.5 mmol m^{-2} d^{-1}, or 38% of the average metabolism estimate over all transects.

Site-specific estimates of metabolism—Using equation 3, we analyzed 197 sonde-days to estimate GPP and R at each transect location. The model captured the diel pattern of dissolved oxygen dynamics with only the processes of GPP, R, and diffusion (Fig. 3a). The autocorrelation term improved the fit of the model and resulted in nonautocorrelated residuals, but did not change the estimates of the underlying processes (Fig. 3b). Estimates of metabolism for any given day varied based on the location of the measurement. For GPP, 40% of the days had a coefficient of variation (CV) <25% from site to site. For R, 20% of the days had a CV <25%, and for net ecosystem production (NEP = GPP – R), only 13% of days had a CV <25%. On average, the highest recorded GPP value was 2.5 times the minimum value (with a range of 1.1 to 6.1). For R, the average difference was 3.2-fold (with a range of 1.1 to 7.6).

Of the 40 days analyzed, 15 (37.5%) followed the hypothesized pattern of highest metabolism values near shore and lowest values near the center of the lake (e.g., Fig. 4a). The remaining days followed no discernable trend (30%), a U-shaped trend (25%), or an N-shaped trend (7.5%) (Fig. 4b–d). Despite the varied patterns observed, the average magnitude of metabolism values for all days still decreased as a function of distance from shore (Fig. 5).

Spatially explicit and center site estimates—For the 40 days and all sonde sites (197 sonde days), we compared the spatially explicit estimates of whole-lake 24-h GPP, R, and NEP to those obtained from the sonde in the center of the lake (Fig. 6). For GPP, the center sonde accounted for an average (± SD) of 81% ± 28% of whole lake GPP (Fig. 6a). For R, the center sonde accounted for 81% ± 65% (Fig. 6b). Because NEP can change sign, it is better to compare the actual values of the estimates from the center site (8.3 ± 18.5 mmol O_2 m^{-2} d^{-1}) to the spatially explicit estimate (8.4 ± 15.5 mmol O_2 m^{-2} d^{-1}). On 3 of the 40 dates, the sign of NEP was different between the single central sonde and spatially explicit estimates (Fig. 6c). On average, a sonde in the center of the lake tends to underestimate both GPP and R. The range (among individual days) in the ratio of an estimate from a single sonde in the center to the spatially explicit approach is large for all aspects of metabolism.

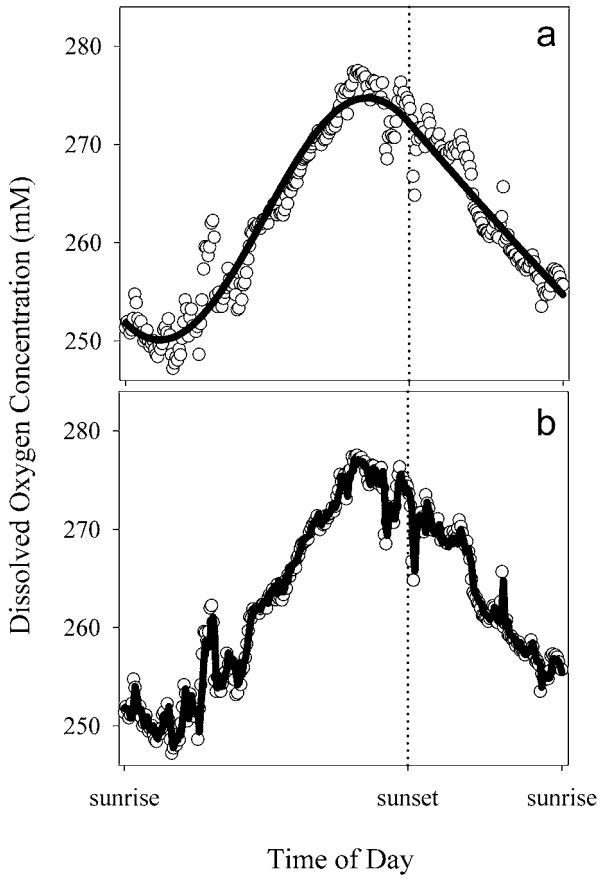

Fig. 3. Dissolved oxygen dynamics for a representative 24-h period from sunrise to sunrise. The data (points) and the process model fit (line) are shown in a. The first-order auto-regressive fit is shown in b.

Daily integrated estimates of benthic and pelagic metabolism—Because our model which partitions benthic and pelagic metabolism (equation 7) assumes pelagic metabolism is constant throughout the epilimnion and benthic-littoral metabolism only occurs near shore, and because the model only accounts for simple mixing along that gradient, it can work only for days when we see higher metabolism near shore and lower metabolism in the center of the lake. That is, the model does not have a mechanism to explain values of metabolism

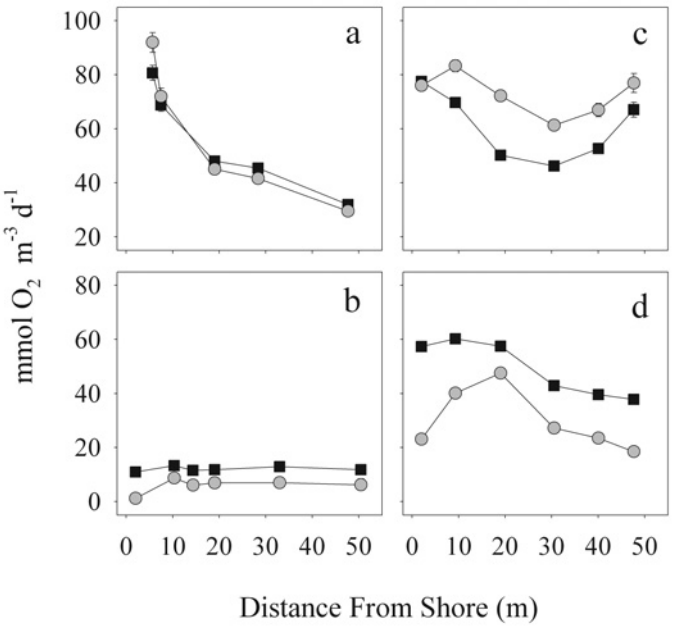

Fig. 4. Volumetric estimates of site-specific GPP (squares) and R (circles) with respect to distance from shore for 4 dates representative of the varying spatial patterns observed (a–d). Error bars represent bootstrapped 95% confidence intervals and may be obscured by the symbols.

that are higher away from shore. We therefore applied this model to only the 15 transects in which metabolism decreased from shore to the center of the lake. For 3 of these days, the model could not adequately fit the diel oxygen curve because of irregularities in the shape of the curve that could not be explained by our simple model. For the remaining 12 days, the simultaneously estimated oxygen curves fit as well or nearly as well as the fits for the individual sondes.

Estimates of whole-lake GPP and R based on this model were higher than estimates based on single sondes in the middle of the lake. Over the 12 days analyzed, whole-lake GPP ranged from 18.7 to 166 mmol O_2 m^{-2} d^{-1}, with a mean of 54.0 (Fig. 7a), whereas GPP estimated from a single sonde in the middle of the lake had a mean of 37.3 mmol O_2 m^{-2} d^{-1}, with a range of 8.82 to 134. Whole-lake R ranged from 17.9 to 129 mmol O_2 m^{-2} d^{-1}, with a mean of 52.5 (Fig. 7b). Estimates of R based on a single sonde in the middle of the lake had a mean of 34.6 mmol O_2 m^{-2} d^{-1}, with a range of 6.20 to 92.2. The estimates for whole-lake GPP and R were highest from the 3 transects we deployed in 2002 when the lake was fertilized.

Modeled rates of pelagic metabolism were lower than measurements of metabolism at the center of the lake: mean pelagic GPP was 32.2 mmol O_2 m^{-2} d^{-1} and mean pelagic R was 28.2 mmol O_2 m^{-2} d^{-1}. Rates of benthic metabolism were more than twice as high as pelagic metabolism when examined per unit area of littoral habitat, with mean benthic GPP and R of 66.5 and 75.0 mmol O_2 m^{-2} d^{-1}, respectively. When expressed in terms of whole-lake area, benthic GPP and R contributed slightly less (21.7 and 24.3 mmol O_2 m^{-2} d^{-1}, respectively) to

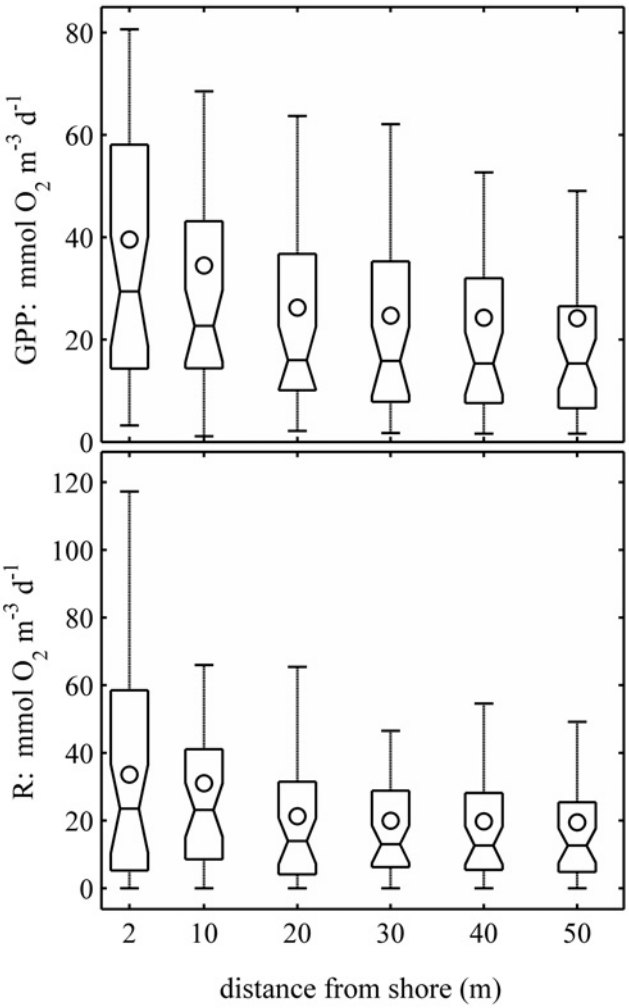

Fig. 5. Metabolism values as a function of distance from shore for all 40 days of samples on Peter Lake. Boxes represent middle 50% of the data, with the median shown as the center line. Circles show mean values and whiskers extend to the most extreme value within 1.5 times the interquartile range of the samples.

whole-lake metabolism than pelagic processes. On average, benthic processes made up 39% of whole-lake GPP and 42% of whole-lake R but varied considerably between days (Fig. 7).

Net ecosystem production also varied between habitats. Pelagic NEP ($NEP_p = GPP_p - R_p$) was more often positive (net autotrophic), whereas benthic NEP was more often negative (net heterotrophic). Mean pelagic NEP was 4.10 mmol O_2 m^{-2} d^{-1} (range of –8.60 to 40.9), whereas mean benthic NEP was –2.61 (range of –21.4 to 10.3). Whole-lake NEP was on average slightly positive, with a mean of 1.49 mmol O_2 m^{-2} d^{-1} (range of –13.8 to 37.4).

Wind as a homogenizing force—Between-site variation in daily metabolism estimates (GPP and R combined) was inversely related to the average wind speed (r^2 = 0.33, P < 0.002) and to the maximum recorded 5-min average wind speed (r^2 = 0.37, P < 0.0006) from the first 18 h of the day.

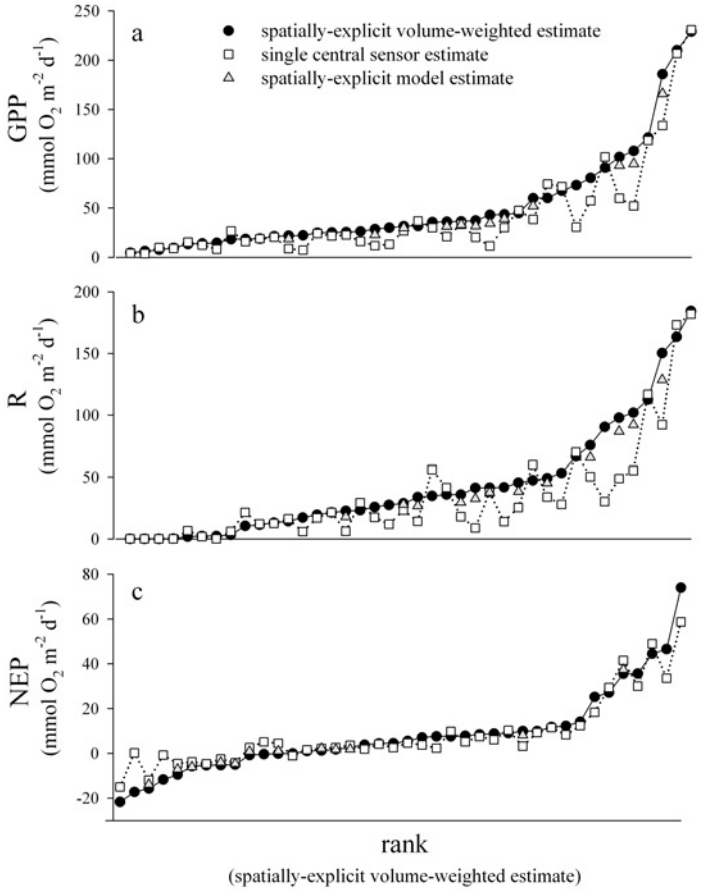

Fig. 6. Comparison of metabolism values based on 3 different methods. Estimates from the center of the lake are shown in squares, estimates based on volume-weighted averages of all sensor locations are shown in circles, and spatially explicit whole-lake model estimates for the 12 days when the model was run are shown with triangles. Estimates based on single, central sensors are often much lower than estimates which account for spatial variability in metabolism.

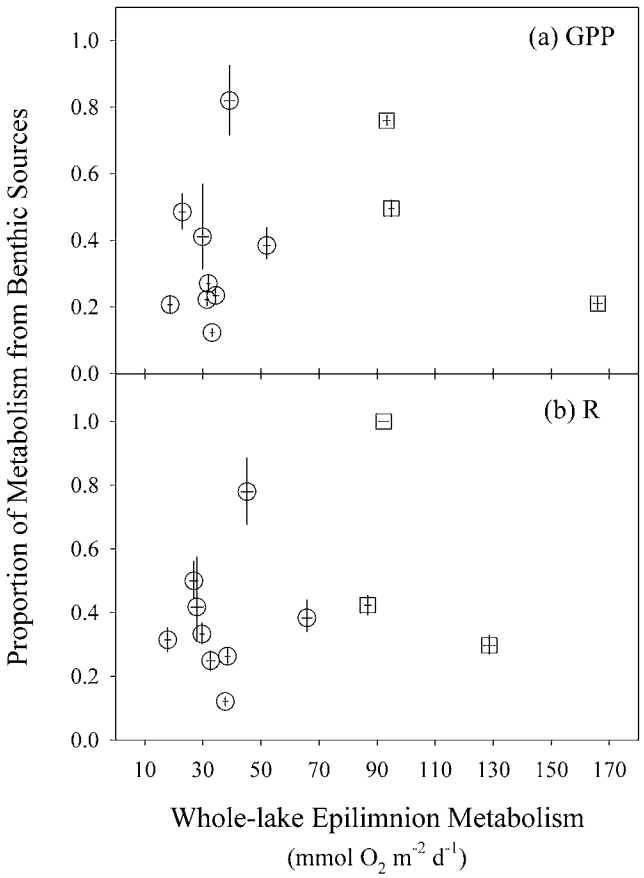

Fig. 7. Estimates of whole-lake GPP and R (mmol O_2 m^{-2} d^{-1}) and the benthic contribution of each based on the spatially explicit model. Error bars show 95% confidence intervals based on 10,000 bootstrap iterations. Data from 2002 (fertilized) are shown using squares and data from 2003 (not fertilized) are shown using circles.

When average 5-min wind speeds topped 2.75 m s^{-1} for more than a total of 1 of the first 18 h of a day (nearly half of all days studied in 2003), standard deviation in daily metabolism estimates among sites was <5 mmol O_2 m^{-2} d^{-1}—too low to detect significant differences. In contrast, when average wind speeds did not top this threshold, 73% of transects (11 of 15) showed standard deviations of metabolism estimates >5 mmol O_2 m^{-2} d^{-1} and of these, 9 displayed the hypothesized pattern of highest metabolism near shore and lowest at the center of the lake (Fig. 8).

Discussion

Models of dissolved oxygen at individual locations within a lake as well as simultaneous models of whole transects revealed that dynamics were not homogenous throughout space in our study lake. Indeed, severalfold differences in metabolism estimates from site to site were common. Although these differences did not always follow predictable patterns, on average an estimate based on a single, central location underestimated whole lake values.

Epilimnetic water circulation may be one factor that determines the degree to which a single sonde estimate of metabolism adequately represents whole-lake metabolism. Water circulation (and the differential rates and patterns of that circulation through time) can mask the real heterogeneity in underlying ecosystem processes which occur at slower rates. When circulation occurs quickly relative to the underlying biotic processes, measurements of metabolism will be similar regardless of location, and a single measurement location may provide a reliable estimate of whole-lake epilimnetic metabolism. When circulation occurs much more slowly relative to the biotic processes, site-to-site variation should occur in a predictable manner, with highest values near shore and lowest values in the center of the lake.

As a driver of water circulation, measurements of wind speed can provide one prediction of the degree of homogenization in metabolism estimates among sites. When wind speeds are high, metabolism estimates are quite similar between locations. Even short periods of high wind are enough to set cir-

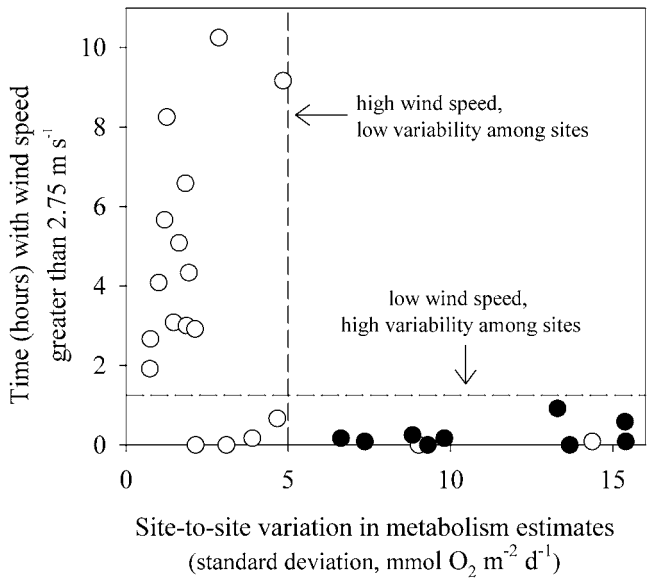

Fig. 8. Relationship between site-to-site variation in daily metabolism estimates (GPP and R combined) and the amount of time in the first 18 h of the day with 5-min average wind speeds greater than 2.75 m s^{-1}. Each point corresponds to one 24-h transect from 2003. Filled-in points denote days when metabolism was highest near shore and lowest in the center of the lake and are the days when we were able to partition benthic and pelagic metabolism.

culation patterns in motion that conceal the underlying heterogeneity in ecosystem processes. For Peter Lake, there appeared to be a threshold of 1 h with 5-min average wind speeds above 2.75 m s^{-1}: above this threshold, metabolism estimates were always similar among sites. This threshold is likely a function of the magnitude of the differences in underlying ecosystem processes. Larger differences between benthic and pelagic metabolism rates could raise this detection threshold. When wind speeds are low, other physical drivers (e.g., precipitation, convection currents) can provide homogenizing forces and may need to be considered.

Differences among lakes (e.g., size, morphometry, and trophic state) may also affect the degree to which a single sonde estimate of metabolism adequately represents whole-lake values (Fee 1979; Håkanson 2005). In large lakes with very steep littoral zones (and thus small littoral area relative to total lake area), pelagic metabolism may make up a larger proportion of the total. In this case, even if a sonde measures none of the benthic metabolism, the measurement should be closer to whole-lake values than one in a smaller lake with large littoral zones. The effect of lake size, however, is likely more complicated and in need of further study. It is reasonable to hypothesize, for example, that across a gradient of increasing lake size, central sondes will receive less and less signal from the littoral zone because the increased distance allows the littoral signal to be muted by atmospheric diffusion. The balance between this signal loss and its initial magnitude would likely determine how close a single estimate of metabolism in the center of lake approaches the true whole-lake value. In lakes smaller and shallower than Peter Lake, benthic metabolism may make up a greater proportion of the total. If benthic metabolism is not effectively measured by a central sonde, the measurement may be a more extreme underestimate of the true whole-lake value. Alternatively, if the shorter distance between the shore and center allows the benthic signal to reach the center of the lake without being muted by atmospheric diffusion, a single sensor may be able to accurately measure whole system metabolism. In any given case, an investigator can use the approach presented here to examine spatial heterogeneity in metabolism and design a deployment strategy suitable for capturing whole-lake metabolism.

In Peter Lake a sonde placed at a central location measured pelagic metabolism and an unknown portion of benthic-littoral metabolism. In the cases where we could apply the spatially explicit model, we found that a sonde in the center of the lake measured only an average of 75% of the whole-lake epilimnetic GPP and 73% of the whole-lake epilimnetic R. On these days, the central sonde only measured approximately 25% of the benthic GPP and R—the remaining portion was not detectable with a single sensor in the center of the lake. Because these days had the lowest rates of mixing as determined by wind speed, this estimate may be a lower bound on the proportion of benthic metabolism seen by the central sonde.

Ecologists often are more concerned with net ecosystem production than either GPP or R alone (Cole et al. 1994; 2000). The data presented here illustrate that NEP is also heterogeneous with pelagic metabolism tending toward net autotrophy and benthic processes tending toward net heterotrophy. In this case, inference based on a single measurement may lead to erroneous conclusions about a lake's trophic status. Similarly, Pace and Prairie (2005) report spatial variation in pCO_2 within lakes and surmise that this variation is also due to spatial heterogeneity in NEP.

Although we were only able to apply the spatial model on 12 of 40 days, the remainder of the deployments were still useful for measuring site-specific and volume-weighted epilimnetic metabolism. Furthermore, collecting data using automated samplers is fairly easy. There is not much difference in the work needed to collect data for 3 days vs. 10 days because the additional sampling costs only instrument time—not labor or money. What might be considered oversampling for answering the benthic-pelagic question is still useful for obtaining better estimates of whole-lake metabolism. The benthic-littoral portion can be inferred from days during the deployment when weather conditions (e.g., low wind speed) allow the use of the spatially explicit model presented in this article.

Comments and recommendations

The results of this study suggest that ecologists interested in whole-lake metabolism should recognize the potential for heterogeneity in within lake processes and acknowledge that single-site estimates may not represent whole-lake metabolism or

only pelagic metabolism, but rather something between these two endpoints. Determining whole-lake metabolism requires an evaluation of the spatial heterogeneity in one's study system: How large is the littoral zone—is it 1% or 50% of lake area? How different are simultaneous metabolism estimates from near shore and at the center of the lake? In larger lakes, are plankton patchy? Questions such as these should be addressed over a period encompassing a representative range of weather patterns (e.g., wind, solar radiation, precipitation), and the answers will help investigators decide whether pursuing measurements at higher spatial resolution is necessary or useful for their particular goals.

Although the cost of sensors is dropping, it is still significant. Thus, more work is needed to determine the minimum number needed for accurate estimates of whole-lake metabolism across systems. Our data show that on days with high wind speed, measurements are not significantly different across sites and therefore the only benefit of many sensors is to verify the uniformity of metabolism estimates. However, on days with low wind speeds, variation among sites may be high or low and is not predictable with the data we collected. On low wind days, this study shows that for lakes similar to Peter Lake, the number of sensors needed is >1 and will likely need to include enough to separately sample the littoral zone, the pelagic zone, and perhaps a few places along the gradient between. Although Peter Lake is small, we suspect these results will be applicable for many lakes given that 97% of the world's lakes are smaller than or equal to the area of Peter Lake and that lakes the same size or smaller account for 22% of the worldwide surface area of lakes (Downing et al. 2006). This study demonstrates the potential for in-lake heterogeneity to bias single-location estimates of whole-lake metabolism by underestimating benthic contributions. The degree to which similar bias occurs in larger lakes is a question that still needs to be studied.

Investigators interested in partitioning benthic and pelagic metabolism from whole-lake values will need to employ several sensors (4 to 6 were used in this study) along a littoral-pelagic gradient. Although this study did not address the optimal number of sondes needed to answer this question, we note that a minimum of 3 sensor locations is needed to be able to simultaneously estimate the two end members of metabolism and the rate of mixing along the transect.

The increased use of automated data acquired from sensors along with declining cost is leading to enhanced potential to measure ecosystem processes. Free-water oxygen measurements like those used in this study overcome many of the limitations of bottle and chamber methods, but there is still much to learn about these methods, particularly what types of sampling regimens are necessary to adequately capture ecosystem estimates of processes like metabolism. Without further evaluation of sensor-based methods, process estimates will suffer ambiguities similar to traditional techniques. For example, just as traditional ^{14}C primary productivity methods measure some unknown value between net and gross primary production (Peterson 1980), a single centrally located oxygen sensor may measure some unknown value between pelagic metabolism and whole-lake metabolism. These ambiguities may be reduced with improved sampling designs coupled with models that incorporate spatial heterogeneity in ecosystem processes.

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