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Lake metabolism and the diel oxygen technique: State of the science

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Abstract

Significant improvements have been made in estimating gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP) from diel, "free-water" changes in dissolved oxygen (DO). Here we evaluate some of the assumptions and uncertainties that are still embedded in the technique and provide guidelines on how to estimate reliable metabolic rates from high-frequency sonde data. True whole-system estimates are often not obtained because measurements reflect an unknown zone of influence which varies over space and time. A minimum logging frequency of 30 min was sufficient to capture metabolism at the daily time scale. Higher sampling frequencies capture additional pattern in the DO data, primarily related to physical mixing. Causes behind the often large daily variability are discussed and evaluated for an oligotrophic and a eutrophic lake. Despite a 3-fold higher day-to-day variability in absolute GPP rates in the eutrophic lake, both lakes required at least 3 sonde days per week for GPP estimates to be within 20% of the weekly average. A sensitivity analysis evaluated uncertainties associated with DO measurements, piston velocity (k), and the assumption that daytime R equals nighttime R. In low productivity lakes, uncertainty in DO measurements and piston velocity strongly impacts R but has no effect on GPP or NEP. Lack of accounting for higher R during the day underestimates R and GPP but has no effect on NEP. We finally provide suggestions for future research to improve the technique.

Measurement of diel, "free-water" changes in dissolved oxygen (DO) concentrations has become a widely accepted method to examine whole-ecosystem primary production and respiration in aquatic systems, particularly in lakes (Cole et al. 2000; Gelda and Effler 2002; Lauster et al. 2006; Staehr and Sand-Jensen 2007). Sargent and Austin (1949) were the first to take advantage of diel changes in oxygen to calculate rates of production and respiration in a coral reef system. However, it was not until the application by the Odum brothers in their studies of river, lake, and coral reef metabolism in the 1950s that the method became widely accepted and applied (Odum and Odum 1955; Odum 1956, 1957). Since then the method has been used extensively in a variety of aquatic ecosystems (e.g., Hall 1972; Smith and Key 1975; Kemp and Boynton 1980; Barnes 1983; Gattuso et al. 1993; D'Avanzo et al. 1996; Cole et al. 2000; Caffrey 2003; Hanson et al. 2003; Van de Bogert et al. 2007; Staehr et al. 2010; and many others), with samples measured at gradually increasing frequency through the decades.

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Recent developments in self-contained, automated, remote sensors have made it easy to continuously measure DO concentrations and relevant physical and chemical parameters accurately at time intervals of less than 1 min for periods from several days to much longer. Such data not only allow a detailed description of temporal variability in the measured variables, but also enable calculation of lake metabolism and extensive analysis of the drivers of metabolism. As the use of free-water techniques has expanded, however, new insights and new questions have emerged on the validity of the metabolic estimates (McCutchan et al. 1998; Staehr and Sand-Jensen 2007; Hanson et al. 2008), and the extent to which free-water measurements actually represent whole-lake metabolism (Lauster et al. 2006; Van de Bogert et al. 2007; Coloso et al. 2008). There is, therefore, a pressing need to evaluate the method by identifying critical assumptions and uncertainties and establishing a current best practice for measurement and calculation of lake metabolism. Here we identify key areas of uncertainty in the calculation of lake metabolism and suggest advances that need to be made.

The diel dissolved oxygen technique assumes that changes in oxygen concentration of a body of water reflect the biological balance between photosynthetic production and respiratory consumption as well as the physical exchange of oxygen between air and water. Production of DO via photosynthesis occurs only during daylight whereas consumption of DO occurs throughout the diel period and is the only metabolic process occurring at night. Thus, net ecosystem production (NEP), ecosystem respiration (R), and gross primary production (GPP) can be directly quantified by measuring temporal changes in DO concentration throughout a 24-h period.

Aquatic metabolism can be determined in a number of ways, all of which have their limitations and assumptions. In the past, metabolism has been measured in bottles and chambers incubated at varying irradiance levels, using either dissolved oxygen or carbon (as ^{14}C) as an elemental tracer. By extrapolating bottle rates to represent 24-h periods, it is possible to calculate depth- and time-integrated pelagic rates of GPP, NEP, and R; and when combined with sediment chamber incubations, it is possible to estimate GPP, NEP, and R of entire ecosystems (e.g., Kemp et al. 1997; Gazeau et al. 2005). While enclosing part of an aquatic system within bottles is attractive because it allows precise measurements with replication, incubations are significantly affected by "container effects," which hamper estimates of ecosystem level metabolism (Bender et al. 1987). The main uncertainty with the container approaches concerns problems of scale (Gerhart and Likens 1975; Chen et al. 2000) and is related to natural heterogeneity of the benthos and variability in accounting for the natural light conditions. Also, comparisons among container studies are difficult because many studies fail to report key details of the containers used (Petersen et al. 1997, 1999). In comparison, it was hoped that free-water techniques integrate a signal over the entire benthic-littoral and pelagic region in much the same way that a terrestrial gas-flux tower integrates gas-fluxes over a region (Valentini et al. 1996). However, free-water measurements suffer their own set of uncertainties, which to a large extent, remain unexplored.

Although there are several uncertainties associated with measuring lake metabolism using the diel DO technique, its advantages over other methods and the development of relatively inexpensive and reliable sensors, has promoted its continued and growing application at an increasing number of lakes around the world. Researchers and managers have come to realize that temporal dynamics obtained by a continuous monitoring approach have the potential to strengthen predictions of how changes in environmental conditions (e.g., climate, deforestation, and eutrophication) affect lakes (Hanson et al. 2006; Kratz et al. 2006; Tilak et al. 2007; Williamson et al. 2008). Although each lake is essentially unique, comparisons between lakes are still valuable for the evolution of our understanding of how lakes respond to external changes. To improve the reliability and reproducibility of metabolism estimates, as well as comparison among lakes and studies, it would be prudent to have a protocol that represents the best practices currently known and an awareness of the limitations of any given approach. Furthermore, information on the current best practices needs to account for diversity in equipment, sampling protocols, and the physical conditions defining the studied lakes. Data are collected in various ways for various reasons, and although technology is constantly evolving, some monitoring agencies have good reasons to stick to a local, perhaps no longer ideal, protocol to best maintain a long-term historical record of change. Nevertheless, we can identify strengths and weaknesses in common protocols for sonde-based measurements of metabolism and make some suggestions for improvement. Through an understanding of the uncertainties contributing to the metabolism estimates we can determine when estimates are comparable.

This article aims to provide some guidelines and cautions for applying the diel DO technique of calculating metabolism in lakes using continuous high-frequency data from sondes. More specifically, we A) present the governing equations and provide an overview of the data needed to compute lake metabolism; B) identify the assumptions and uncertainties of the approach; and C) propose a set of protocols that work as well as possible given these precautions. This includes advice on where and how frequent and how long time measurements should be made. Finally, we D) discuss the current research frontiers in lake metabolism to encourage research toward reducing uncertainties and better understanding of the embedded assumptions.

The concept behind the diel oxygen technique

Although one can calculate free water metabolism from measurement of either dissolved oxygen or dissolved carbon dioxide over the diel cycle, at the present time dissolved oxygen sensors are cheaper, more robust, less power demanding,

and therefore in more widespread use than dissolved carbon dioxide sensors (Hanson et al. 2003). As the DO method is more widely used, we will limit our discussion of free water metabolism to the use of dissolved oxygen measurements.

The governing equation for estimating free-water metabolism from measurements of dissolved oxygen was first established by Howard T. Odum (1956) and is typically written as:

$$\Delta O_2/\Delta t = GPP - R - F - A \quad (1)$$

where $\Delta O_2/\Delta t$ is the change in dissolved oxygen concentration through time, GPP is gross primary production, R is ecosystem respiration, F is the exchange of O_2 with the atmosphere, and A is a term that combines all other processes that cause changes in dissolved oxygen concentration at the sampling site (Fig. 1). These processes include, for example, horizontal or vertical advection within the lake, photochemical oxidation of organic matter, and non-aerobic consumption of oxygen during the time step. $\Delta O_2/\Delta t$ is measured from direct observation, F is typically modeled as a function of the concentration gradient between water and atmosphere with a wind-derived exchange coefficient, and A is often assumed to be negligible. GPP is assumed to be zero during the night, and therefore R can be estimated directly from night time changes in dissolved oxygen. By assuming that respiration during the day is equal to that at night, one can then calculate GPP from daytime changes in dissolved oxygen concentration. As we discuss later, this assumption needs closer consideration.

Although the equation is relatively simple, there are multiple ways to deal with the myriad assumptions and ancillary data required to determine free water estimates of lake metabolism. It is therefore possible that differing estimates of metabolism could be derived from identical measurements. In the following, we provide insight into the assumptions and uncertainties of the diel oxygen technique and give recommendations on how to manage them.

Where should I put my sondes?

Having obtained a sensor capable of logging DO frequently over an extended period, the first question arises: where

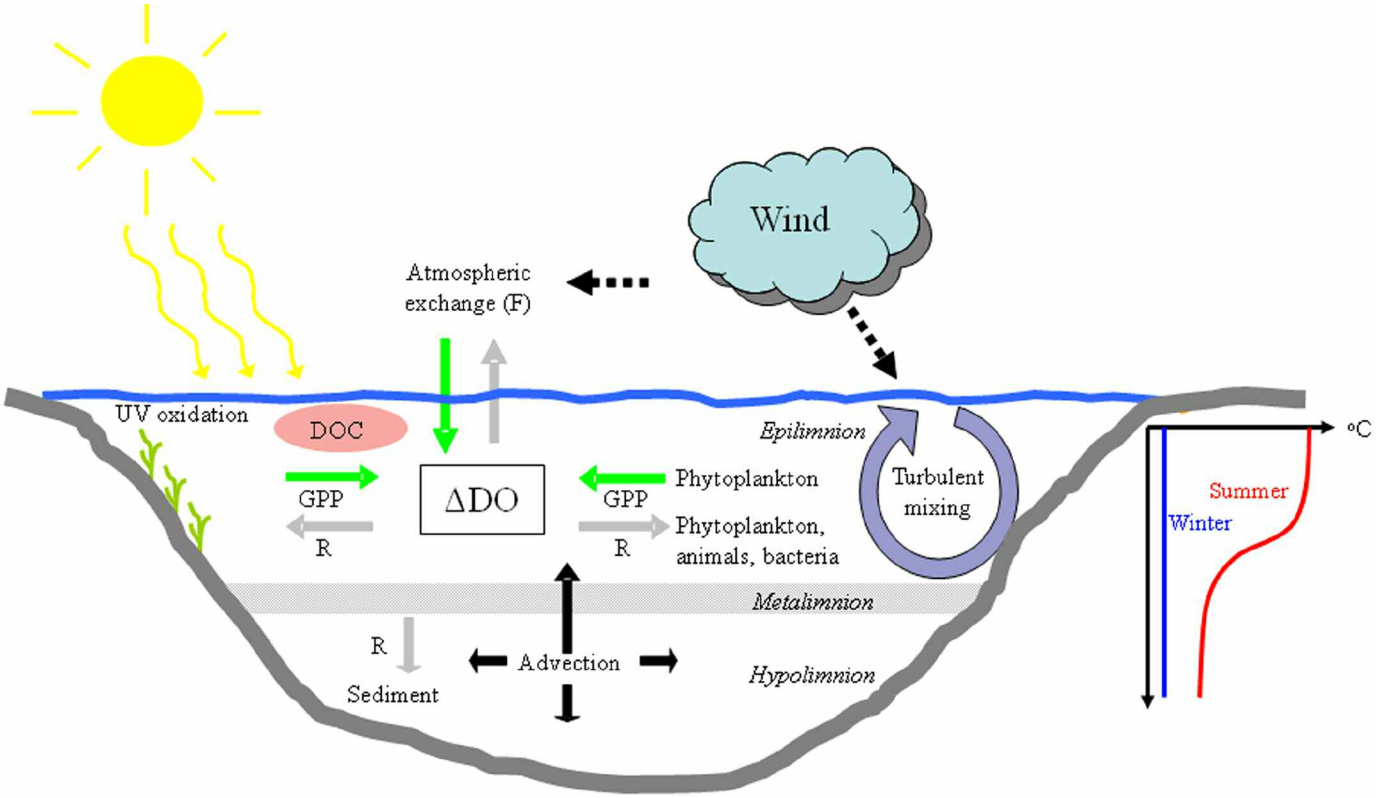

Fig. 1. Conceptual model of the biological and physical components contributing to variability in dissolved oxygen (DO) in a lake. Diel changes in DO occurs as a result of oxygen production during daylight by autotrophs (phytoplankton, macrophytes, benthic algae) and oxygen consumption (respiration) by all organisms in the ecosystem during the entire diel cycle. Furthermore photochemical UV oxidation and photoinhibition in surface waters by dissolved organic carbon (DOC) may significantly influence the measured DO concentration. Adding to this is an exchange of oxygen (F) between water and air, driven by a concentration gradient and physical mixing affected by wind. Other processes such as advective mixing across a thermal stratification layer (metalimnion) during summer and horizontal exchange of oxygen with shallow littoral zones may cause significant noise (A in Eq. 1) in the measured diel DO cycle. Thermal stratification occurs in deeper lakes during summer when density gradients caused by surface warming are strong enough to prevent water column mixing.

should I put my sonde? Although the generally accepted short answer is "in the upper 1/2-1 m at the central deep part of the lake," there are a number of assumptions and uncertainties associated with this recommendation that need consideration. Depending on the aim of the measurements and the characteristics of the lake, the central deep part may not be sufficient at all and significantly bias the interpretation and understanding of the variability and magnitude of lake metabolism.

Spatial and vertical heterogeneity of the DO signal is, in fact, an interesting topic, and we are just beginning to understand the causes behind this heterogeneity in lakes and the effects on estimates of lake metabolism. Here we review the conventional practices, recent research on horizontal and vertical heterogeneity of metabolism, potential consequences of ignoring the different kinds of heterogeneity and research opportunities.

The basic assumption behind and generally accepted advantage of the open water diel DO technique is that diel changes in DO in the water column is an integrated response to the metabolism of the entire ecosystem (all autotrophs and heterotrophs), thus avoiding exclusion of key components outside bottles or chambers (Fig. 1). Underlying this assumption is the premise that the DO sensor is placed such that it senses all sources and sinks of DO in the upper mixed layer of the lake, where in the absence of a deep chlorophyll maximum, most of the production is assumed to occur. Also, because gas exchange through the surface is highly variable and contributes substantially to epilimnetic gas flux, frequent gas measurements are required. In the layers that have water overlying them (meta- and hypolimnia), there is no gas exchange directly with the atmosphere, irradiance-driven primary production is low (except when production below metalimnion, see later), and exchange with other thermal layers is low (Coloso et al. 2008). Thus, coarser measurements through time may adequately characterize metabolism in those layers. Ideally, the sensor should be placed such that oxygen produced or consumed by the biological components at any given place in the lake will be carried on to the zone of measurement instantaneously. Recent research has shown that there is a zone of influence on the sensor and sensors in different locations within the same system can yield different estimates (Caraco and Cole 2002; Lauster et al. 2006; Van de Bogert et al. 2007).

Provided that the lake is small and shallow, such that the water column is well mixed (i.e., no thermal stratification), with steep banks and a small littoral zone with sparse or no benthic plant cover, the DO signal sensed by a centrally placed sonde is indeed likely to provide a measure of lake metabolism in the upper mixed layer. Most lakes, however, differ from this "ideal" lake. Oxygen produced in dense, submerged, emergent, or floating-leafed macrophyte beds in a shallow littoral zone in one part of the lake may not be sensed at a remote central part of the lake as the signal may be equilibrated with the atmosphere, or at least damped, before reaching the centrally located sensor. The extent to which this is of concern depends primarily on the horizontal water movement (dispersion). Therefore, the extent to which the underlying physical heterogeneity influences the validity of metabolism estimates using a single sonde depends on how quickly the metabolic signal is mixed through the lake to the location measurements are taken. This in turn is a function of A) the size and underlying physical/ecological heterogeneity of the system, B) the rate of atmospheric exchange (which is modeled as a function of wind speed), and (C) rate of horizontal mixing (which may also be a function of wind speed, among other things). Rapid water mixing may blur spatial differences in metabolism, but allow a better estimate of whole-lake metabolism with only one centrally located sonde. The extent to which this will bias whole lake metabolism estimates also depends on the relative metabolic rates of benthic versus pelagic communities. In a lake dominated by pelagic metabolism (phytoplankton, zooplankton, and bacteria) metabolism occurring at shallow depth in the littoral zone by benthic organisms (macrophytes, macro- and microalgae, invertebrates, microbes) becomes less of an issue. However, in lakes deep enough to experience vertical temperature stratification, the photic zone of clear water lakes may extend below the metalimnion, resulting in primary production that is not measured by a sonde in the upper mixed layer, thereby underestimating whole-lake areal gross primary production (Coloso et al. 2008). Light availability is, however, not sufficient to support pelagic primary production below the metalimnion in most stratified lakes. But because respiration occurs at all depths, and appears to be unrelated to depth (Coloso et al. 2008), calculation of areal rates using epilimnetic data only would significantly underestimate R. The extent to which this produces an uncertainty in whole-lake metabolism estimates depends on the duration and strength of the stratification as well as the volume of water in the hypolimnion. This is an issue in most tropical lakes more than a few meters deep, and a reoccurring problem in temperate lakes during summer, especially in sheltered, deep, and darkly stained lakes. The accuracy and/or validity of true whole lake metabolism estimates are accordingly strongly influenced by the physical template of the lake and to some extent by the trophic status of the lake (i.e., macrophytes versus phytoplankton dominated primary production).

General practice

As DO measured at a given place and time in the lake is a function of metabolism, degree of mixing, and exchange with the atmosphere, estimates of metabolism on 2 d of identical metabolic activity, but with differing rates of mixing, may result in different estimates of metabolism when non-metabolic processes are not accounted. Lakes exhibiting large horizontal and vertical heterogeneity in primary production ideally require deployment of multiple sondes in various habitats (Van de Bogert et al. 2007) and at multiple depths (Gelda and Effler 2002; Coloso et al. 2008) to obtain a more reliable esti-

mate of whole-lake metabolism. Although this seems logical, it is rarely done because the adequate number of sondes to deploy spatially and how the spatial data should be integrated are currently unknown. Furthermore, although sondes have become less expensive, more sensitive and require less calibration work than in the past (especially optical sensors), sondes do require maintenance, which can be expensive and time consuming.

It is therefore not surprising that the general practice has been to place one sonde in the upper mixed layer of the central or deep part of the lake. The rationale behind this approach is that in lakes sufficiently deep to stratify for longer periods, much of the productivity is pelagic and occurs in the upper mixed layer of the lake. Whereas this is true in some lakes, there are caveats to this approach that need consideration. For example, while the colder temperatures and lower light levels often constrain productivity in deeper waters, deep chlorophyll maxima may suggest the development of deep water phytoplankton populations that are many times those found in the surface waters (Saros et al. 2005). In addition to the limited ability of surface water oxygen measurements to include these deep water primary producers, the fate of these primary producers and subsequent development of hypoxia and anoxia in deeper waters needs to be considered more carefully in estimates of whole lake metabolism. Photochemical consumption of oxygen can also be substantial and varies strongly with dissolved organic carbon (DOC) concentrations (Lindell and Rai 1994; Reitner et al. 1997). As chromophoric DOC increases, increased absorption of incoming irradiance can reduce primary production and increase both photochemical and microbial oxygen consumption.

Frequency and duration of sonde measurements

In the early days of the diel O_2 technique, before the advent of automatically logging sondes, people would manually sample water at 1 to 3 h intervals throughout a few days, and measure DO using Winkler titrations until they became exhausted (Odum 1957). With the development of automatic DO sensors, measurements have become much less work intensive, and directed toward sonde calibration and data retrieval. Along with this development investigators have been provided a choice of logging frequency (minutes) and deployment duration (days). In this section, we address the questions: What is an appropriate sampling frequency and how long must I sample at that frequency? It is important to understand that these questions are scale-dependent, and here we answer them in the context of estimating the current metabolic condition of the lake (i.e., "What is metabolism today?," and not "How does metabolism change over a season?").

Logging frequency—Analysis of DO data spanning 20 y has shown that variability in DO is driven by multiple factors at different time scales (Hanson et al. 2006). According to this study, diel cycles of DO variability are controlled primarily by metabolism, exchange with the atmosphere, and temperature. Although it was recognized early that variability in DO at subdiel time scales is determined by changes in irradiance, wind driven gas exchange, and advective mixing (Odum 1956; Hanson et al. 2008), the nature and extent of DO changes at hourly and minute scales remains largely unexplored. Furthermore, Hanson et al. (2008) show that internal waves and short-term mixing events add variance to DO data at short time scales. To reduce this problem, measurements should therefore be made at a frequency similar to the time scale of internal waves (usually minutes to hours) and episodic mixing events that occur at the beginning and end of the day.

The choice of optimal measurement frequency is furthermore dependent on the strength of the DO signal driven by biological activity as opposed to changes in DO that result from physical and chemical processes. Changes in DO occurring over the diel scale clearly tend to be biologically driven, but sometimes noise contributed by nonbiological processes blurs even the diel biological signal, thus obscuring daily estimates of metabolism. According to the Nyquist theorem (Nyquist 1932), we must sample at twice the frequency of the signal. However, many processes contribute to the control of DO dynamics, and exogenous drivers, such as light and wind, can manifest their variability as noise in the DO signal. Analysis of changes in the DO signal in two lakes, however, showed that metabolism explains most of the diel changes (Hanson et al. 2008). In the following, we explore relationships between measurement period and our confidence in the metabolism estimate.

To investigate the importance of sampling frequency, we have chosen data from three different lakes, each of which shows diel pattern in dissolved oxygen (Fig. 2). This choice of data was made to assure that the conditions under which the assumptions of the diel curve techniques are met. Three lakes from northern Wisconsin, U.S.A. were chosen to provide contrast in size (1-194 ha), depth (3.4-10.9 m; mean depth), and trophic state (Little Arbor Vitae is eutrophic, Sparkling is oligotrophic, and Trout Bog is dystrophic). Measurements of DO, water temperature, light and wind speeds were recorded at the central deep hole of the lakes, during reasonably calm weather. Data were recorded every 10 min for 4 d, and subsampled to represent different time intervals of measurement, ranging from 10 min to 4 h. We call these time intervals 'sampling period.' For each possible sampling period, metabolism and atmospheric exchange (F_{atm}) were calculated according to Cole et al. (2000), resulting in metabolism distributions for each sampling period. We then conducted a power analysis to determine how many samples would be required at that sampling period to be assured we would be within 20% of the mean with a certainty of 80%. We then calculated the product of the "number of samples required" and the sampling period to obtain the "required duration (days)" at that measurement frequency.

All lakes had obvious diel changes in DO, however with large differences in the degree of DO saturation and the level

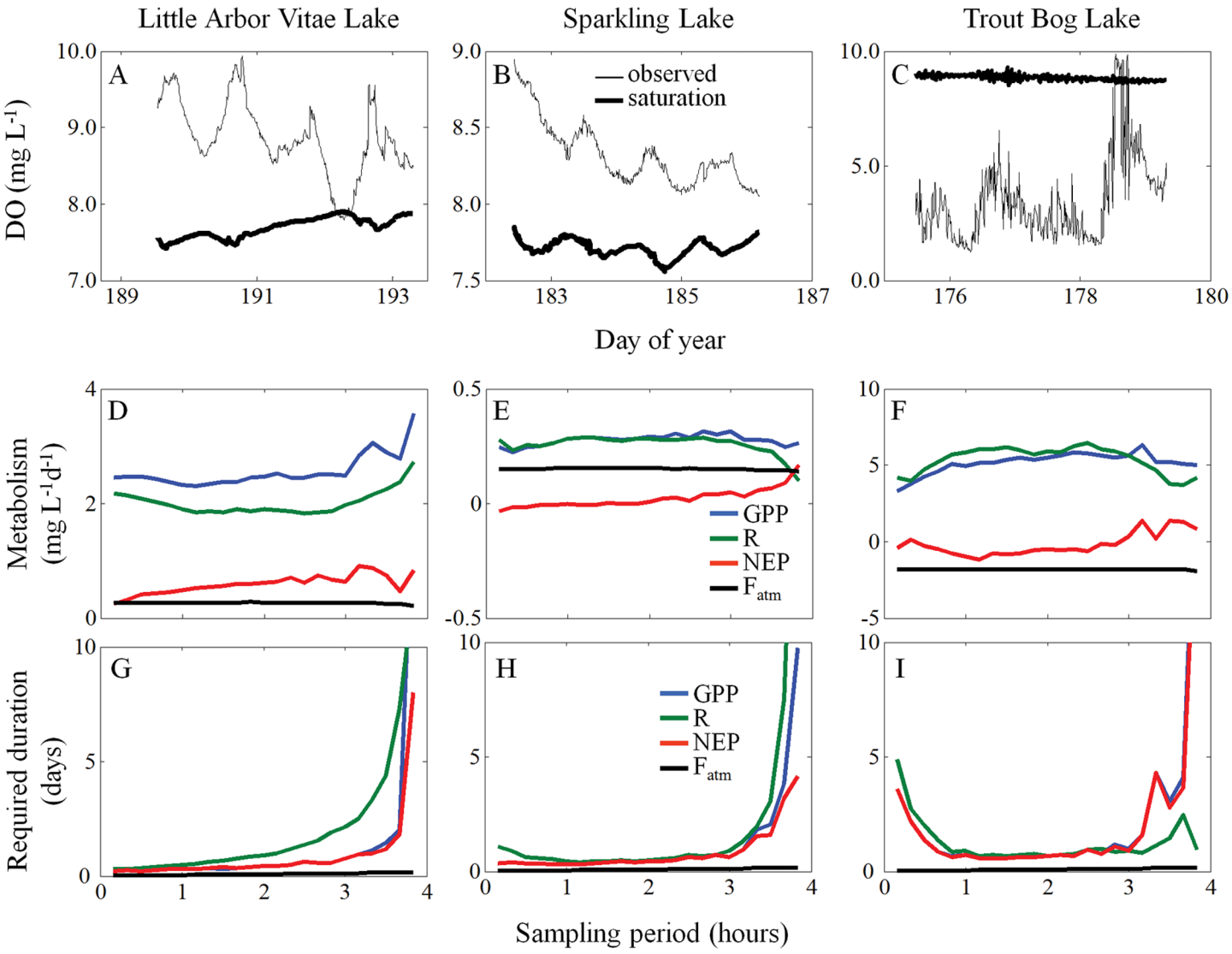

Fig. 2. Dissolved oxygen time series (A-C, note differing y axis scales), metabolism (D-F, note differing y axis scales), and required sample duration (G-I) in three study lakes (columns). Metabolism values are means calculated at different sampling periods. Required sample duration is the number of days required to sample at the specified sampling period to detect metabolism within 20% of the mean with a power of 80%.

of noise associated with the DO measurements (Fig. 2, A-C). Whereas Little Arbor Vitae was supersaturated by nearly 2 mg DO L^{-1}, Trout Bog was under-saturated by about 6 mg L^{-1}, and Sparkling was slightly supersaturated at about +0.5 mg DO L^{-1}. Calculation of metabolism and gas flux over different measurement intervals (Fig. 2, D-F) revealed large differences in the overall levels of GPP, R, and NEP between lakes, which relates to differences in the magnitude and variation in DO saturation. Thus, super-saturation of DO was associated with a positive NEP and high GPP in Little Arbor Vitae, sub-saturation mirrored negative NEP, and high R in Trout Bog, and close to saturation were related to near neutral NEP (NEP~0) in Sparkling Lake. Atmospheric flux on the other hand was nearly constant through time for all lakes. For sampling periods less than about 3 h, metabolic rates and atmospheric flux were almost constant across sampling periods. Above a period of about 3 h, the number of sampling days required to assure an accuracy of 20% in metabolic rates increased exponentially (Fig. 2, G-I). As expected, the required sampling duration was generally low at high sampling frequencies. For Trout Bog (Fig. 2, I), however, an unexplained increase in required duration at high sampling frequency was observed, which seemed to result from the high noise level (Fig. 2, C). Previous investigations suggest that such noise results from internal waves (Hanson et al. 2008). Smoothing the high-frequency samples would reduce estimate uncertainties (Coloso et al. 2008) and may flatten that tail of the graph. Based on this analysis, a minimum sampling frequency of one hour seems prudent.

Table 1. Characteristics of Crampton and Castle lakes. Mixing depth, Chl *a*, total phosphorus (TP), and gross primary production (GPP) are averages from June to August collected in Crampton lake in 2005 (Coloso et al. 2008) and Castle lake in 2004 (Staehr and Sand-Jensen 2007).

Parameter	Crampton lake	Castle lake
Location	46°N, 89°W	56°N, 12°E
Size (ha)	25.7	22.3
Max depth (m)	18.7	9.0
Mean depth (m)	5	3.5
Summer mixing depth (m)	4.0	4.3
Summer Chl *a* (μg L^{-1})	2.8	100.5
Summer TP (μg L^{-1})	8.7	156.7
Summer GPP (mmol O_2 m^{-2} d^{-1})	58	891

However, the caveats above suggest a slightly more conservative approach, so we recommend a minimum sampling frequency of 30 min to capture metabolism at the daily time scale. Higher sampling frequencies would allow you to capture additional pattern in the DO data, but these are more likely to be related to short-term changes in air-water gas exchange and variation in DO caused by physical mixing rather than metabolism.

Deployment duration

Sondes must be deployed for at least 24 h to obtain sufficient information to calculate daily rates of GPP, NEP, and R. Depending on the biological signal to physical mixing (noise) ratio, day-to-day differences in irradiance and rapid development of algal blooms, metabolic rates estimated from only 1 d may not necessarily resemble rates on the previous or following day. Despite this commonly observed problem, no guidelines exist as to how many sonde-days are required to obtain seasonally reliable metabolic estimates primarily related to the biological activity of the system rather than noise caused by, e.g., advective mixing. It was previously found in a eutrophic and very productive lake that productive summer periods are associated with a significantly higher day-to-day variability in GPP and R than less productive winter and fall periods, suggesting a seasonal influence in determining how many sonde-days are needed to obtain a reliable weekly or monthly estimate of GPP (Staehr and Sand-Jensen 2007).

To evaluate this further, we compared temporal variability in published GPP data for a eutrophic, turbid lake (Castle Lake) and an oligotrophic, clear-water lake (Crampton Lake; Table 1) that differed substantially in nutrient availability, phytoplankton biomass, and GPP but otherwise of comparable size, mixing depth and with sparse submerged macrophyte cover (Staehr and Sand-Jensen 2007; Coloso et al. 2008). Areal GPP was on average almost five times higher in Castle Lake with large day-to-day variability in absolute values of GPP (Fig. 3). However, comparing the number of

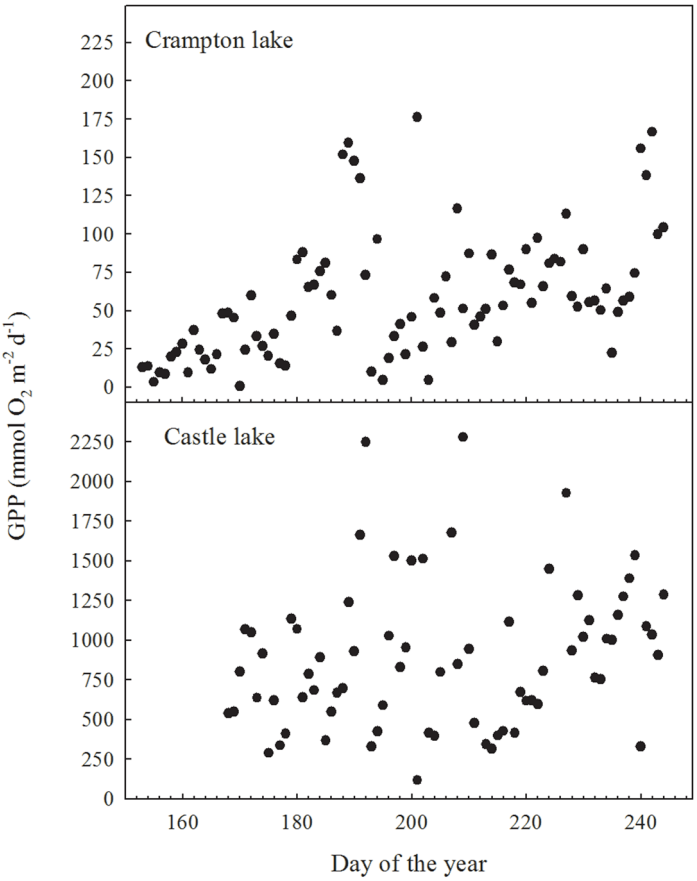

Fig. 3. Difference between weekly means of GPP in oligotrophic Crampton Lake and eutrophic Castle Lake. Values were obtained by averaging over 1 to 7 sampling days, for each week from June to August. Error bars represent 95% CL.

sonde-days required to attain a GPP estimate that was less than 20% of the weekly average, both lakes required at least 3 sonde days per week (Fig. 4). Also the coefficient of variation (%CV = SD/mean × 100) in GPP was similar for Crampton (60%) and Castle (51%) Lake. Thus, although Crampton Lake was much less productive than Castle Lake, our analysis indicates that they had similar variability in GPP, at least in relative units. For Castle Lake, a seasonally divided analysis of metabolic variability indicated a weaker coupling of GPP to environmental variables (light and temperature) during the highly productive, nutrient-poor, and stratified summer period than during spring and fall (Staehr and Sand-Jensen 2007). This was interpreted as exchange of organic and inorganic material, and injections of anoxic bottom water across the metalimnion during summer driving the variability in metabolic rates in the epilimnion. Other possible explanations include changes in the vertical distribution of productivity involving seasonal changes in transparency (Williamson et al. 2007), photochemical oxidation (Morris and Hargreaves 1997), or the development of a deep

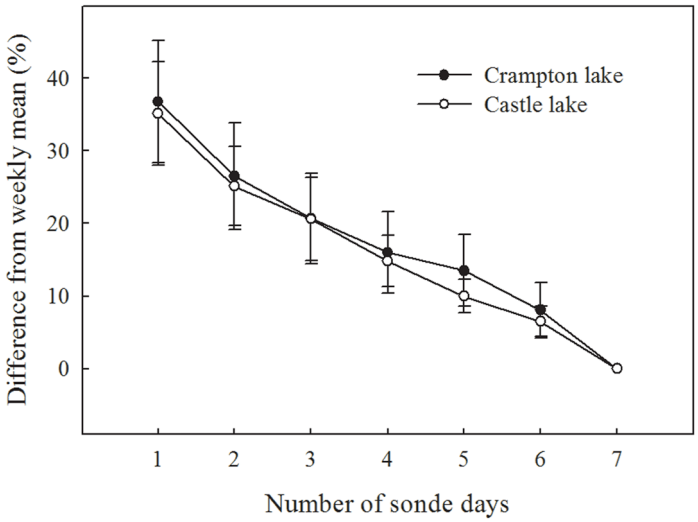

Fig. 4. Day-to-day variation in gross primary production (GPP) in oligotrophic Crampton Lake and eutrophic Castle Lake from June to August. Notice the 10-fold difference in GPP. Areal rates represent the upper mixed layer.

chlorophyll maximum (Saros et al. 2005). The extent to which the same phenomenon can account for the observed daily variability in GPP in Crampton Lake during summer is uncertain. However, because the lakes have somewhat similar physical conditions and benthic plant cover, and thus littoral production is of minor importance in both lakes, exchange of oxygen and matter across the metalimnion seems a likely candidate for the calculated GPP variability in Crampton Lake as well. Because sonde data have become more reliable and easier to obtain, the number of sonde days with high quality diel DO data have increased several fold over the years. This enables calculation of daily metabolic rates almost all year round, thereby improving our understanding of day-to-day variability as well as the credibility in seasonal and annual rates. Assuming that high daily variability in metabolic rates is a general phenomenon in lakes, it is highly recommendable to scale the duration of sonde measurements to the aim of the study.

How do I calculate metabolism from sonde data?

In the following, we give recommendations on how to proceed from raw data to estimates of daily GPP, R, and NEP values. Although our recommendations are aimed at a single, central sonde deployment, most of the steps would be similar for multiple site strategies. The number of steps one must go through depends to some extent on the number of variables being measured. In addition, the order in which the data are prepared does not necessarily have to follow our guidelines. The equations used to calculate metabolism are shown in Table 2, and their use is visualized in Fig. 5.

So here are the steps:

Mixing depth: The depth of the mixed layer (Z_{mix}) can be inferred from temperature profiles as the upper mixed zone where temperature remains relatively constant. Z_{mix} extends down to the beginning of the metalimnion, where temperature starts to decrease. Operationally, this can be defined as the depth where water temperature starts to decrease at a rate of 1°C m^{-1} or more. Traditionally, Z_{mix} is inferred from manual temperature profiles measured biweekly or less and interpolated linearly between measurements. With the advent of temperature data loggers (thermistors), frequent (e.g., 10 min) estimates of Z_{mix} can be determined and taken into account in calculations of hourly NEP (Staehr et al. 2010).

Calculate O_{2sat}: The oxygen concentration in water in equilibrium with the atmosphere at ambient temperature, and salinity can be computed according to Eq. 2 (Table 2). Furthermore, oxygen saturation must be corrected for barometric pressure or altitude using Eq. 3 (Table 2).

Calculate O_{2meas}: Using %DO and temperature data, calculate the actual DO concentration (mg L^{-1}) (Table 2; Eq. 4). Make sure to examine the DO data for drift and correct if necessary. A simple approach is to compare percent saturation of water sample saturated with air at the beginning and at the end of a deployment and correct for the difference assuming the drift to be linear during the period of deployment.

Calculate Schmidt number (Sc): The Schmidt number is required to determine the physical air-water oxygen exchange. Sc essentially denotes the ratio of kinematic viscosity, υ, to the diffusion coefficient, D, two molecular transport properties of a gas: $Sc = \upsilon/D$ (Jähne et al. 1987). Whereas υ is constant, the diffusion coefficient D is temperature dependent. Sc is therefore calculated as a function of temperature (Table 2; Eq. 5)

Calculate piston velocity (k): Piston velocity is calculated for each time step from the estimate of k_{600} and the ratio of Schmidt numbers (Table 2; Eq. 8). k_{600} is commonly estimated as a function of wind speed at 10 m above the lake surface (Table 2; Eq. 7). Whereas most meteorological stations measure wind at 10 m, it is generally recommended to use wind speeds measured on the studied lake, which is usually measured at only 1 to 2 m height. Therefore, an empirical relationship is used to relate wind speed (U) measured at a given height (z) to the wind speed at a height of 10 m (U_{10}) under the assumption of a neutrally stable boundary layer (Table 2; Eq. 6). Several similar equations exist. We show the most commonly used. It is acceptable, and even desirable to calculate k at the most frequent wind measurement available. Wind is much more variable than is DO, generally.

Calculate oxygen exchange with the atmosphere (F): F (g O_2 m^{-2} h^{-1}) is the physical exchange of gas with the atmosphere calculated from the difference in DO concentration from DO saturation multiplied by the piston velocity (k) (Table 2; Eq. 9). The easiest way to do this is to use units for k in m h^{-1}.

Determine Dayfraction: Dayfraction is the proportion of a 24-h period when it is light. Day length may be determined directly on-site by measuring the length of time that irradi-

Table 2. Equations used to calculate lake metabolism.

Parameter	Equation	Reference	Eq.
The governing equation	$\Delta O_2/\Delta t = GPP - R - F - A$	Odum 1956	1
Oxygen saturation as a function of temperature (T, kelvin) and salinity (S, ppt)	O_{2sat} (mg L^{-1}) = (e^{C}) × 1.423 mg O_2 mL^{-1}	Weiss 1970	2
	C (ml O_2 L^{-1}) = (–173.4292 + 249.6339 × (100 / T) + 143.3483 × ln(T / 100) – 21.8492 × (T / 100) + S × [–0.033096 + 0.014259 × (T / 100) – 0.0017000 × (T / 100)^2]		
Correction of $O2_{sat}$ for barometric pressure (BP, millibars) for altitude (m)	O_{2sat} (mg L^{-1}) corrected for pressure = O_{2sat} (mg L^{-1}) × correction factor	USGS memo #81.11 1981	3
	correction factor = (BP ×0.0987 - 0.0112)/100	USGS memo #81.15 1981	
	Correction factor = (0.0000005 × altitude^2 – 0.0118 × altitude + 99.979)/100		
Conversion of $\%O_2$ to O_2 concentration	O_{2meas} (mg L^{-1}) = (%DO 100) × O_{2sat} (mg L^{-1})		4
Schmidt coefficient, from water temperature (T, Celsius)	$Sc = 0.0476\ T^3 + 3.7818\ T^2 - 120.1\ T + 1800.6$	Wanninkhof 1992	5
Wind speed, at 10 m height (U_{10}) from wind speed at height z (U_z, m/s)	U_{10} (m s^{-1}) = $U_z \times \alpha$	Smith 1985	6
	$\alpha = 1.4125\ z^{-0.15}$		
Piston velocity	k_{600} (m h^{-1}) = (2.07 + 0.215 $U_{10}^{1.7}$)/100	Cole and Caraco 1998	7
	k (m h^{-1}) = k_{600}(m h^{-1})×([Sc/600]$^{-0.5}$)	Jähne et al. 1987	8
Physical gas flux	F (g O_2 m^{-2} h^{-1}) = k (O_{2meas} – O_{2sat})		9
Dayfraction light_hours determination from day of year (DOY) and latitude (lat, in radians)	dayfraction = light_hours/24 h		10
	rads = 2 × ≠ × DOY/365	Iqbal 1983	11
	dec = 0.006918 – 0.399912 × cos(rads) + 0.070257 × sin(rads) – 0.006758 × cos(2 × rads) + 0.000907 × sin(2 × rads) – 0.00297 × cos(3 × rads) + 0.00148 × sin(3 × rads)		
	x = [–1 × sin(lat) × sin(dec)]/[cos(lat) × cos(dec)]		
	SR = (3.14154 / 2) – atan{x/[ℊ(1 – ×^{2})]}		
	light_hours = SR (2/0.262)		
$NEP_{daytime}$	NEP_{hr} (g O_2 m^{-3} hr^{-1}) = ΔO_2 (g m^{-3} hr^{-1}) – F/Z_{mix}	Cole et al. 2000	12
	$NEP_{daytime}$ (g O_2 m^{-3} daylight period^{-1}) = mean NEP_{hr} during daylight × dayfraction × 24		13
R	R_{hr} (g O_2 m^{-3} h^{-1}) = mean NEP_{hr} during darkness		14
	$R_{daytime}$ (g O_2 m^{-3} daylight period^{-1}) = R_{hr} × 24 h × dayfraction		15
	R_{day} (g O_2 m^{-3} d^{-1}) = R_{hr} × 24 h		16
GPP	GPP (g O_2 m^{-3} d^{-1}) = $NEP_{daytime}$ + $R_{daytime}$		17
NEP	NEP (g O_2 m^{-3} d^{-1}) = GPP - R_{day}		18

ance is above 0 µmol photons m^{-2} s^{-1} (Table 2; Eq. 10) or from latitude and date of measurements (Table 2; Eq. 11).

Calculate hourly net ecosystem production (NEP) rate: NEP is calculated for each time interval according to Eq. 12 (Table 2). Because net production indicates oxygen gains from photosynthesis and oxygen depletion during respiration, NEP is

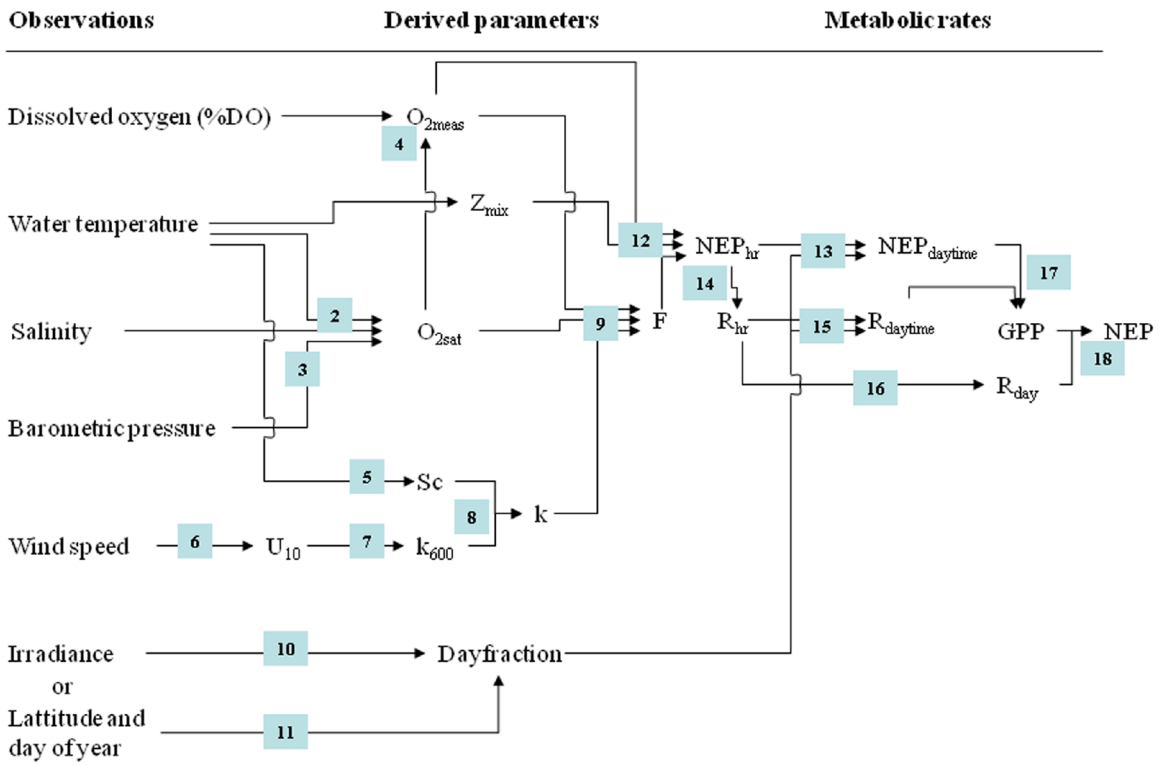

Fig. 5. Mapping measured data onto metabolic processes. Numbers refer to equations explained in Table 2, which also explains the abbreviations.

derived directly from observed changes in DO after accounting for the atmospheric exchange (*F*).

Calculate daytime NEP ($NEP_{daytime}$): Daytime NEP is the portion of NEP occurring while photosynthesis is taking place. Thus, $NEP_{daytime}$ is the mean hourly NEP rate occurring between sunrise and sunset extrapolated over Day Length (Table 2; Eq. 13).

Calculate respiration (R): Determination of R rests on two assumptions. First, we assume that at night there is no photosynthesis, so GPP = 0 and nighttime R is thus equal to nighttime NEP. Algal cells, charged with $NADPH_2$, can continue to fix C (and produce O_2) for some time after light is removed (Raven 1974). Many practitioners therefore calculate R for one hour post-sunset until dawn. Second, we assume that nighttime R is equal to daytime R (Odum 1956, Hanson et al. 2003; Lauster et al. 2006). 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 have no effect on NEP (Cole et al. 2000). Hourly respirations rates (R_{hr}), derived from nighttime DO changes are extrapolated over a 24-h period to determine respiration for the day (R_{day}). Respiration between sunrise and sunset ($R_{daytime}$) is calculated from R_{hr} extrapolated over Day Length (Table 2; Eqs. 14-16).

Calculate gross primary production (GPP): $NEP_{daytime}$ as the balance between GPP and $R_{daytime}$ and, thus, GPP is represented as the change in DO due to NEP plus that as a result of respiration (Table 2; Eq. 17). Noisy diel DO curves, often caused by advective mixing and other hydrodynamics, may sometimes result in GPP values below 0 because daytime NEP is negative or smaller than daytime R. Similarly advective transport of DO may cause net increases in hourly NEP during darkness leading to negative R-values. While smoothing solutions can be applied to remove this problem (Coloso et al. 2008), the general agreement is that this problem decreases in importance as the total number of days under investigation increases. Sondes enable a high frequency of easily obtained measurements and facilitate the calculation of metabolism for multiple days, months, or years. A distribution of all GPP estimates over multiple days may show some negative values that are theoretically erroneous (GPP cannot be negative). If the distribution is normally shaped then the high values of GPP would also be erroneous. This argument supports the strategy of making as many measurements over as many days as possible and using the mean values. Furthermore, empirical relationships between metabolic rates and driving variables (e.g., light, temperature, mixing) are stronger when analyzed on weekly rather than daily rates (Staehr and Sand-Jensen 2007).

Data presentation: By convention, GPP rates are plotted with a positive sign and R rates with a negative sign, whereas daily NEP, as it is the difference between GPP and R, can be both negative and positive depending on the magnitude of GPP and R (Eq. 18; Table 2). Volumetric metabolic rates (mg O_2 m^{-3} d^{-1} or mmol O_2 m^{-3} d^{-1}) can be turned into areal rates (g O_2 m^{-2} d^{-1} or mol O_2 m^{-2} d^{-1}) by multiplying by mixing depth

Table 3. Summary of variables important to calculate lake metabolism using the diel DO technique. Also shown are driving variables, which should be included when monitoring a lake.

Variable	Relevance
Required variables	
Dissolved oxygen	Produced and consumed by productive and respiratory metabolic processes, respectively
Water temperature	Influences oxygen solubility. When measured over several depths it can be used to determine variation in mixed layer depth
Mixed layer depth	The depth to which water is mixing as determined by differences in water density and available wind energy. Either assumed to equal average lake depth (shallow ~2-3 m deep lakes), determined biweekly from manual temperature profiles, or calculated from high frequency temperature loggers at several depths
Latitude and day of year	Used to calculate hours of daylight (i.e., dayfraction) in case of no irradiance data
Barometric pressure or altitude	Influences oxygen solubility. Usually taken into account by the sensor itself
Salinity	Influences oxygen solubility. Necessary to measure in lakes affected by saline inputs
Supportive variables	
Wind	Facilitates gas exchange between the water column and the atmosphere; supplies energy to mix the water column. If not measured on lake, then use data from a nearby meteorological station. Last resort is to assume a constant value.
Irradiance	Used to calculate hours of daylight (i.e., dayfraction)
Driving variables	
Irradiance	Driver of photosynthesis. Variability between days due to clouds is often the primary cause of day-to-day variability in GPP. When measured at several depths in the water column, it is possible to follow short-term changes in light attenuation (K_D), which relates to changes in particulate and dissolved organic matter. Parameters that strongly affects metabolism.
Dissolved organic carbon (DOC)	A supply of organic carbon that can influence respiration
Total phosphorus (TP)	Often the limiting resource of primary production in freshwater systems.
Chlorophyll *a* (Chl *a*)	A proxy for phytoplankton biomass, which often determines the magnitude of GPP, NEP, and R

(Z_{mix}, m). In theory, these rates represent the average metabolic rates per square meter of the entire lake, which multiplied by the lake area, gives an estimate of whole lake metabolism. The extent to which a single sonde will provide true "whole-lake" metabolism will, however, depend on the mixing regime and horizontal heterogeneity in benthic producers. It is important to remember that the free-water method of calculating metabolism represents metabolic activity occurring at the sensor and that horizontal and vertical scaling attempts should be considered thoroughly.

What else do I need to measure?

Besides dissolved oxygen and temperature, calculation of lake metabolism using the free-water diel dissolved oxygen method requires a number of variables that either need to be measured, can be assumed, calculated or obtained from nearby meteorological stations (Table 3). In this section, we discuss current practices involved in measuring that is either required or supportive, and measurement of variables that operate as drivers of aquatic metabolism.

Dissolved Oxygen. Modern methods of measuring DO typically use electronic membrane or optical sensors. Although less expensive, membrane DO sensors are susceptible to error at extremely low oxygen concentrations or very slow water movement because oxygen is consumed by the probe. Membrane sensors typically have more problems with signal drift than do optical electrodes. Drift can be estimated by measuring DO in water-saturated air at both the beginning and end to the deployment.

Water Temperature and Salinity. Water temperature and salinity are necessary to calculate the saturation concentration of DO, as well as any stratification properties of the aquatic system of interest (Table 2; Eq. 2). The thermistor accompanying the sonde is sufficient for determining O_2 saturation, but a vertical array of thermistors can be helpful in determine mixing depth, Z_{mix} (see Staehr et al. 2010). It is important to remember that Z_{mix}, which is the depth of mixing epilimnetic waters, may not be the same depth as the thermocline, which is the depth of greatest temperature change. Z_{mix} is thus always more shallow than the depth of the thermocline.

Barometric pressure. Barometric pressure influences oxygen solubility in water (Table 2; Eq. 3). If no data exists, a correction can be made from information on altitude (Table 2; Eq. 3).

Wind. Wind energy is a key driver of many lake functions including water circulation and exchange of dissolved gases with the atmosphere (Table 2; Eq. 7). Optimally, data should be collected from a mooring on the lake, because local wind may deviate from land based weather stations, and vary significantly between small protected and large open lakes. In

the absence of any wind data, a uniform reaeration constant (k; piston velocity) may be assumed. On small lakes, a value of 0.5 m d^{-1} is a reasonable guess in the absence of wind data. But see sensitivity analysis below.

Irradiance. The amount of light entering a lake ecosystem provides the primary source of heat to the water, drives the potential for the water column to be mixed with wind energy, and supplies photons to drive photosynthesis. Ambient light data and light extinction values (K_D) determine the light available for photosynthesis and can be important potential drivers of metabolic rates (Staehr et al. 2010). They are not directly involved in the metabolism calculations presented here, but can be used in models that parameterize diel changes in DO as a function of light (Hanson et al. 2008). It is essential to know the length of the photoperiod for each day that metabolism is calculated, and this information can be determined from local measurements (Table 2; Eq. 10) or calculated from latitude (Table 2; Eq. 11). At seasonally high irradiance levels, photoinhibition may be important in the surface waters of clear water systems (Hader et al. 1998), reducing the photosynthetic production of oxygen. Variations in the concentration of chromophoric dissolved organic matter (CDOM) may also alter the fate of incoming irradiance and the proportion that results in photosynthesis and oxygen production versus photochemical oxidation of CDOM and oxygen consumption (Lindell and Rai 1994).

Other Driving Variables. In general, it is useful for the researcher to simultaneously measure variables that are not used in metabolism calculations but may be linked to metabolic rates. For example, Hanson et al. (2003) showed that total phosphorus (TP) was correlated with GPP and that dissolved organic carbon (DOC) was linked to R across multiple lakes. In that study, the variables were used as correlates of mean metabolism for each lake but the researchers did not study how dynamics in TP and DOC relate to dynamics in metabolism. In addition, Chlorophyll *a* may also be strongly related to GPP (see Staehr et al. 2010) especially if the lake's ratio of pelagic to littoral production is high (i.e., production is dominated by phytoplankton). Other water quality, hydrologic, physical, or even anthropogenic factors may be influential drivers of metabolic rates for a given aquatic ecosystem, and the variables mentioned here are by no means exhaustive.

Sensitivity analysis

To evaluate the sensitivity of metabolic rates to errors associated with k, Z_{mix}, and the assumption of constant respiration, we created a model to simulate diel oxygen curves that roughly approximate metabolic conditions in the low productive Crampton Lake (Coloso et al. 2008) and the highly productive Castle Lake (Staehr and Sand-Jensen 2007). We modified parameters in the model to investigate their influence on estimates of GPP and R, compared with the known inputs of GPP and R in the underlying model. Estimated daily values of GPP, R, and NEP were calculated from the artificial oxygen data according to the guidelines previously described (Table 2).

For the base model, photoperiod was 12 h with a mixing depth (Z_{mix}) of 4 m and piston velocity (k) of 0.4 m d^{-1}. We assigned total daily R and GPP values to the model and R was held constant over a 24-hour period. To reduce complexity, the daily light-dependent changes in GPP were not modeled mechanistically, but approximated by reducing GPP during 2 h of dawn and dusk. We assigned 1/30 of the daily GPP rate to the first and 12th hour of daylight, 1/15 of the daily GPP rate to the second and 11th hour, and 1/10 of the daily GPP rate to each remaining 8 h. We evaluated the model after it ran for 50 d so that diel O_2 curves would reach a dynamic steady state (i.e., O_2 concentrations returned to nearly equal values in a given 24-h period). Assessing the model during steady state allowed the differences in true and estimated metabolism values to be attributed solely to the parameter being investigated and removed any influence of the initial conditions. As the sensitivity to the different parameters may depend on the metabolic condition of the lake, we tested the sensitivity at three levels of GPP and R to produce conditions of NEP that were positive, negative, and balanced.

We tested three key assumptions central to the method of calculating metabolism presented in this paper. First, we tested the sensitivity of metabolism to uncertainty in estimating the oxygen saturation concentration (Table 2; Eqs. 2 and 3). Second, we tested the sensitivity of metabolism to uncertainty in *k* (Table 2; Eq. 8). Last, we tested the assumption that daytime respiration is equal to nighttime respiration.

Uncertainties in O_{2sat}—We altered the original values of O_{2sat} by ± 1%, 5%, and 10% to test effects on metabolic calculations. Incorrect values of O_{2sat} could originate due to errors in temperature, barometric pressure measurements, or poor calibration. Errors of this sort would cause error in the oxygen flux term of the governing equation for oxygen dynamics. Whereas uncertainty in O_{2sat} influenced R, GPP was not affected because the flux error caused by an incorrect value of O_{2sat} is offset by the error it caused in estimating R. We therefore only show data for R (Table 4). As R increases the influence of O_{2sat} decreases, especially so in the less productive Crampton Lake. At a 10% overestimate in the value of O_{2sat} and our lowest input value for R (10 μmol O_2 L^{-1} d^{-1}), the calculated value of R was overestimated by nearly 30% in Crampton Lake. In comparison, a 10% overestimate in the value of O_{2sat} in the highly productive Castle Lake caused less than 2% overestimation of R. Therefore in lakes with low R, it is imperative that O_{2sat} be estimated accurately.

Uncertainties in k—We altered the value of k by ± 10%, 25%, and 50% from the assigned value of 0.4 m d^{-1}. This error would also influence the O_2 flux term, but in a different manner than error in O_{2sat}. Under balanced NEP conditions (NEP = 0), an incorrect estimate of k did not affect the estimates of GPP, R, or NEP regardless of the magnitudes of GPP and R used. When NEP is balanced, the diel O_2 curve cycles on either

Table 4. Sensitivity of respiration estimates to inaccuracy in estimating O_{2sat}. Sensitivity was examined at levels of GPP, R, and NEP (μmol O_2 L^{-1} d^{-1}) representative of summer means in the low productive Crampton Lake, and the highly productive eutrophic Castle Lake. Sensitivity is reported for estimates of respiration, as absolute rates, the difference from model input and as percent change from the model input.

Crampton Lake	GPP = 10, R = 15, NEP = –5			GPP = 10, R = 12.5, NEP = –2.5			GPP = 10, R = 10, NEP = 0			GPP = 12.5, R = 10, NEP = 2.5			GPP = 15, R = 10, NEP = 5		
	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%
% change in O_{2sat}															
1%	15.28	0.28	1.9%	12.78	0.28	2.2%	10.28	0.28	2.8%	10.28	0.28	2.8%	10.28	0.28	2.8%
5%	16.40	1.40	9.4%	13.90	1.40	11.2%	11.40	1.40	14.0%	11.40	1.40	14.0%	11.40	1.40	14.0%
10%	17.81	2.81	18.7%	15.31	2.81	22.5%	12.81	2.81	28.1%	12.81	2.81	28.1%	12.81	2.81	28.1%
Castle Lake	**GPP = 220, R = 230, NEP = –10**			**GPP = 220, R = 225, NEP = –5**			**GPP = 220, R = 220, NEP = 0**			**GPP = 225, R = 220, NEP = 5**			**GPP = 230, R = 220, NEP = 10**		
	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%
% change in O_{2sat}															
1%	230.24	0.24	0.1%	225.24	0.24	0.1%	220.24	0.24	0.1%	220.24	0.24	0.1%	220.24	0.24	0.1%
5%	231.37	1.37	0.6%	226.37	1.37	0.6%	221.37	1.37	0.6%	221.37	1.37	0.6%	221.37	1.37	0.6%
10%	232.77	2.77	1.2%	227.77	2.77	1.2%	222.77	2.77	1.3%	222.77	2.77	1.3%	222.77	2.77	1.3%

Table 5. Sensitivity of respiration estimates to inaccuracy in estimating piston velocity (k). Sensitivity was examined at various levels of NEP and combinations of GPP and R (μmol O_2 L^{-1} d^{-1}) representative of summer means in the low productive Crampton Lake, and the highly productive eutrophic Castle Lake. Uncertainties are reported for estimates of respiration, as absolute rates, the difference from model input and as percent change from the model input.

Crampton Lake	GPP = 10, R = 15, NEP = –5			GPP = 10, R = 12.5, NEP = –2.5			GPP = 12.5, R = 10, NEP = 2.5			GPP = 15, R = 10, NEP = 5		
	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%
% change in k												
10%	15.49	0.49	3.3%	12.75	0.25	2.0%	9.75	–0.25	–2.5%	9.50	–0.50	–5.0%
25%	16.24	1.24	8.3%	13.12	0.62	5.0%	9.38	–0.62	–6.2%	8.76	–1.24	–12.4%
50%	17.48	2.48	16.5%	13.74	1.24	9.9%	8.76	–1.24	–12.4%	7.51	–2.49	–24.9%
Castle Lake	**GPP = 220, R = 230, NEP = –10**			**GPP = 220, R = 225, NEP = –5**			**GPP = 225, R = 220, NEP = 5**			**GPP = 230, R = 220, NEP = 10**		
	est R	diff.	%	est R	diff.	%	est R	diff.	%	est R	diff.	%
% change in k												
10%	230.95	0.95	0.4%	225.46	0.46	0.2%	219.46	–0.54	–0.2%	218.96	–1.04	–0.5%
25%	232.44	2.44	1.1%	226.20	1.20	0.5%	218.71	–1.29	–0.6%	217.47	–2.53	–1.2%
50%	234.91	4.91	2.1%	227.43	2.43	1.1%	217.47	–2.53	–1.2%	214.98	–5.02	–2.3%

side of 100% saturation such that errors in O_2 flux from an incorrect estimate of k will offset and have no influence on metabolism estimates. When GPP > R (positive NEP), an overestimate of k resulted in an underestimate of R (Table 5). Under negative NEP conditions (NEP < 0; GPP < R; net heterotrophy) a positive correlation existed between the error in estimated k and the error in estimated R. The magnitude of error caused by uncertainty in k is related to the magnitude of NEP. At similar NEP values (e.g., NEP = 5), uncertainty in k causes a similar absolute error in estimated R, but relatively more error for the less productive Crampton Lake (Table 5). For both lakes, GPP was estimated correctly despite errors in k under both positive and negative NEP. This again is because the error in the flux term is offset by the error in estimated R when calculating GPP. We did not investigate variability in errors of k within or among days nor whether the independence of GPP to errors in k holds true under conditions that are not steady state.

Constant R—Last, we examined the assumption that daytime respiration is equal to nighttime respiration. We adjusted daytime respiration to be 1.1, 1.25, 1.5, and 2 times nighttime respiration, and calculated metabolism using the standard assumption that hourly respiration rates are similar during daytime and nighttime periods (Table 6). Using a 12:12 h dark:

Table 6. Sensitivity of GPP and R estimates for variation in daytime R, examined at various levels of NEP and combinations of GPP and R (μmol O_2 L^{-1} d^{-1}). For example, if nighttime R is 0.28 μmol O_2 L^{-1} h^{-1}, a 100% increase gives a daytime R value of 0.56 μmol O_2 L^{-1} h^{-1}. Because we calculate 24 h R-values from hourly night time R, any underestimation of daytime R will provide daily R and GPP values, which are lower than the true values. Analysis is performed on data representative of summer means in Crampton Lake.

	NEP = –5		NEP = –2.5		NEP = 0		NEP = +2.5		NEP = +5	
% increase in daytime R	GPP = 10	R = 15	GPP = 10	R = 12.5	GPP = 10	R = 10	GPP = 12.5	R = 10	GPP = 15	R = 10
10%	–7.2%	–4.8%	–6.0%	–4.8%	–4.8%	–4.8%	–3.8%	–4.8%	–3.2%	–4.8%
25%	–16.7%	–11.1%	–13.9%	–11.1%	–11.1%	–11.1%	–8.9%	–11.1%	–7.4%	–11.1%
50%	–30.0%	–20.0%	–25.0%	–20.0%	–20.0%	–20.0%	–16.0%	–20.0%	–13.3%	–20.0%
100%	–50.0%	–33.3%	–41.7%	–33.3%	–33.3%	–33.3%	–26.7%	–33.3%	–22.2%	–33.3%

light cycle, a model input of daily R of 12 μmol O_2 L^{-1} d^{-1} gives an hourly R rate of 0.5 μmol O_2 L^{-1} hr^{-1} throughout the entire day. Doubling daytime R compared with nighttime R implies an hourly nighttime R of 0.33 μmol O_2 L^{-1} h^{-1} compared with 0.66 μmol O_2 L^{-1} h^{-1} during the daytime period. Because we only use nighttime values in our calculation of daily R, using nighttime R-values that are lower than daytime R will systematically underestimate our 24-h respiration estimates. Because nighttime R was underestimated in this test, GPP was always underestimated. In theory, an incorrect assumption of daytime respiration rates will have no impact on estimated values of NEP even though the individual magnitudes of GPP and R will be incorrect.

Future research

Technological development has undoubtedly made it easier and more affordable to obtain continuous, high quality measurements of O_2 from which representative estimates of whole-lake GPP, NEP, and R can potentially be derived. Although the method has several advantages and avoids the caveats of bottle and chamber incubations (Gerhart and Likens 1975; Bender et al. 1987; Petersen et al. 1997, 1999; Chen et al. 2000), a number of uncertainties and assumptions are, however, also associated with the current application of the technique that need consideration (Table 7). Regardless of these issues, buoy-based data are being collected from an increasing number of lakes around the world, making it possible to investigate changes in metabolism over large gradients in time and space. Efforts should therefore be made to further improve the method and the validity of the metabolic estimates. In this section, we summarize what we see as interesting and compelling research issues related to the diel oxygen technique. As we see it, these fall into two broad groups: (1) Methodological studies of vertical, horizontal, and temporal heterogeneity, and (2) Studies that explore and develop better analytical tools for understanding variability in lake metabolism.

Problems of heterogeneity—As metabolic estimates derived from a single sensor are representative of an unknown zone of influence, recommendations on how to most efficiently reduce uncertainties associated with horizontal and vertical heterogeneity in measured DO is greatly needed. Although it is intuitively clear, and shown in a few lakes, that one sensor are often not sufficient to provide true "whole-lake" metabolism (Van de Bogert et al. 2007; Coloso et al. 2008), we need further studies on the extent to which this is a general problem, and what to do about it. More precisely, we need recommendations of how and when to perform depth-integrated determinations of lake metabolism using automatic profiling systems. Also we need recommendations of how and when to perform multiple sonde measurements of lake metabolism using horizontally distributed sondes. In general, we need lower uncertainties associated with horizontal and vertical heterogeneity, by which we can avoid labor intensive and expensive measurement programs.

Analytical considerations—High frequency measurements of DO are often noisy. Although, we have a basic understanding of what controls this variability over multiple temporal scales (e.g., Hanson et al. 2006), we need analytical solutions to help separate variation caused by physical and chemical processes from the biological processes that relate to metabolism. Examples of this include the use of wavelet functions to isolate patterns to scales at which biological process are the predominant drivers of the diel DO curve (Coloso et al. 2008) or by the use of other filters, such as simple moving average.

Another important issue concerns uncertainties associated with quantification of the air-water exchange term. Currently, we use wind speed as a proxy of micro-turbulence on the lake surface area to calculate piston velocity (k), although it is frequently stated that relationships between wind and k should be established for each lake due to local conditions, this is rarely done because it is rather time consuming and difficult. Optimally analytical methods and/or techniques should be made that enable continuous estimation of k as its control changes from, e.g., wind drivers to advective heating or cooling of the water column.

Also, a core assumption of the diel O_2 curve technique for estimating metabolism is that respiration measured during night time, resembles respiration during daylight. Previous investigations on respiration in ponds with dense phytoplankton communities, however, indicated higher respiration during daylight with a systematic decrease following sunset

Table 7. Advantages, uncertainties, and assumptions associated with the diel-oxygen technique.

Advantages	Uncertainties	Assumptions
Measures all system components	Air-water flux difficult to quantify	Equal respiration during light and darkness
Easy to collect data	O_2 method misses anaerobic R	Sensor detects changes in the entire mixed layer
Avoids bottle effects	Horizontal, vertical and temporal heterogeneity due to variable zone of influence on DO sensor	
Provide daily rates of GPP, R, and NEP	O_2:C conversion problems	
	Physics may obscure biology	

(Markager and Sand-Jensen 1989). The implication of this is that we may significantly underestimate respiration during daylight and thus GPP. The extent to which this occurs and what to do about it needs consideration.

Another issue that is related to analytical problems is the integration of dynamical lake models and high frequency lake measurements. Models should be able to continuously use the collected data, and then extrapolate from one or more sondes to the entire lake. Models should include information on lake meta-parameters. Here we should take advantage of the short time steps over which rates can now be determined. If combined with measurements of temperature, irradiance, algal biomass, and nutrients, etc. (e.g., Cole et al. 2000; Hanson et al. 2003; Staehr et al. 2010), we can achieve a wealth of strong empirical data to quantify in situ undisturbed processes and test the relations of GPP, NEP, and R to irradiance, temperature, nutrient availability, and food web structure. A most creative use of metabolism estimates has been estimation of nutrient recycling in the epilimnion of Lake Mendota (Kamarainen et al. 2009).

Whereas there still are several assumptions and uncertainties embedded in the diel DO technique for determining metabolic rates in lakes, its relative ease of application, improved quality of sonde data, and high temporal resolution of data obtained will continue to make the diel DO technique a suitable method for determining the magnitude and variability in metabolic rates in lakes. Application of a common protocol on measurements and data analysis will hopefully improve our ability to compare metabolic rates, understand the importance of different drivers, and the importance of lakes for carbon storage and release globally. A looming issue in the estimate of metabolism is the establishment of realistic estimates of uncertainty. Using a Bayesian framework in flowing waters, Holtgrieve et al. (2010) were able to put credible limits on GPP, R, NEP, and even gas flux. When this method is adapted for lakes, and if it works, it will likely be a significant step forward in both the estimate of metabolism, and more importantly, in the associated errors.

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