Depth-integrated estimates of ecosystem metabolism in a high-elevation lake (Emerald Lake, Sierra Nevada, California)

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Abstract

A series of vertical profiles of dissolved oxygen (DO) collected periodically over two consecutive ice-free seasons in an oligotrophic high-elevation lake (Emerald Lake, California) were used to investigate volumetric and areal rates of gross primary production (GPP), community respiration (CR), and net ecosystem production (NEP). Diel patterns in DO did not weaken with depth in this lake, where the entire 10-m water column was within the euphotic zone and where a deep chlorophyll a (Chl a) maximum was common during periods of thermal stratification. During stratification, both GPP and CR increased with depth, and heterotrophy (NEP < 0) tended to occur below the thermocline in association with higher Chl a and particulate matter concentrations. With the onset of autumn mixing each year, vertical gradients in metabolism weakened or disappeared and the entire water column was autotrophic. Net autotrophy over the growing season was confirmed using three methods of estimating whole-lake metabolism. During periods of stratification, flux across the thermocline, where eddy diffusivities were near molecular, was small (4% of total epilimnetic fluxes), while within the hypolimnion, where stratification was weaker and eddy diffusivities larger, fluxes between strata were more substantial (12% of total fluxes). For this lake and other small lakes with low wind speeds and Lake numbers near 10, mixing due to turbulence should be included in computations of metabolism within the hypolimnion. However, single-station measurements from within the epilimnion provide a reasonable estimate of seasonal metabolism, especially in the autumn when the lake is mixing on a diel basis.

Ecosystem metabolism characterizes the dynamic balance between primary production and community respiration. When gross primary production (GPP) exceeds community respiration (CR) the system is autotrophic, fixing more organic matter than it respires. However, with enough subsidy of organic matter, aquatic systems respire more organic carbon than they produce and are heterotrophic. Aquatic ecosystem metabolism has a long history of study using both free-water and bottle incubation techniques (Odum 1956; Talling 1957). Although free-water measurements are generally considered to characterize spatially integrated rates better than bottles, there are few studies that have used free-water methods to characterize variability in volumetric metabolic rates with depth, or to estimate whole-lake rates integrated through depth (Melack 1982; Gelda and Effler 2002; Coloso et al. 2008). Moreover, to our knowledge no such studies have focused on high-elevation lakes, which are characterized by extreme oligotrophy and low inputs of organic matter from their catchments. Either because of the methodological challenges that come with making free-water, depth-weighted measurements or because metabolic processes were assumed to occur primarily within the surface waters, the majority of recent studies using free-water measurements have focused on the upper mixed layer alone (Cole et al. 2000; Hanson et al. 2003; Staehr and Sand-Jensen 2007).

Characterizing variability in ecosystem metabolism with depth is important, especially in clear-water lakes where light penetration is sufficient to support GPP within and below the metalimnion. The presence of deep-water chlorophyll maxima (Kiefer et al. 1972; Fee 1976) and measurable primary productivity (Huovinen et al. 1999) within and below the metalimnion suggests that a significant fraction of ecosystem metabolism may be missed by focusing solely on surface waters. The sinking and subsequent accumulation of particulate matter and generally higher nutrient concentrations found at depth may similarly lead to increased rates of CR below the upper mixed layer. Although metabolism measurements within the upper mixed layer may characterize some portion of littoral benthic metabolism (Van de Bogert et al. 2007), the majority of the benthos may not be characterized, especially during periods of stratification. In contrast, depth-weighted metabolism estimates should incorporate more of the benthic signal than would be otherwise captured using single measurements from the upper mixed layer, yielding more accurate whole-lake estimates of ecosystem metabolism.

Although there are clear advantages to using a free-water, depth-weighted approach in estimating ecosystem metabolism, methodological challenges remain. Typically, discrete or continuous measurements of dissolved oxygen (DO) are made from multiple depths throughout the water column. Volumetric concentrations are either integrated through depth yielding a single areal measure of water column DO (Melack 1982) or by use of a volumetric mass balance to account for fluxes between strata (Bella 1970; Hornberger and Kelly 1974). Flux of DO within the water column and at the air–water interface is affected by a number of physical processes, such as wind (Imberger 1985), penetrative convection (MacIntyre et al. 2002), and upwelling and/or internal wave breaking, particularly near lateral boundaries (Saggio and Imberger 1998; MacIntyre et al. 1999). Such processes may result in episodic
deeper mixing of the upper mixed layer or cause mixing to occur within the seasonal thermocline. Further complicating interpretations are apparent fluxes within the water column that may result from fixed instruments sampling different masses of water (Coloso et al. 2008), as when internal waves pass through the metalimnion.

Accounting for the effects of turbulence within the water column is one of the largest methodological challenges in estimating free-water metabolism. Because of the complexity associated with directly measuring turbulence, its effects are more often estimated using coefficients of mass exchange. The coefficient of eddy diffusivity \( K_z \) is used to estimate vertical mass flux and is often computed using a heat-flux approach (Jassby and Powell 1975). The magnitude of \( K_z \) and the likelihood of fluxes from upwelling or internal wave-induced mixing can be predicted by computing Lake or Wedderburn numbers, which are based on density structure, wind regime, and basin morphometry (Imberger and Patterson 1989; Yeates and Imberger 2004; MacIntyre et al. 2009). For example, small sheltered lakes and larger lakes that are strongly stratified should have similarly high Lake number values (> 10). In these cases, values of \( K_z \) within the thermocline will be near molecular and vertical fluxes into the epilimnion should be negligible. However, within the hypolimnion where stratification is weaker, \( K_z \) may be substantially higher and should be considered when estimating metabolism. Gas exchange between the lake and overlying atmosphere is dependent on the gas exchange coefficient and the gradient in DO between the lake and overlying atmosphere is dependent on wind speed (Wanninkhof 1992; Cole and Caraco 1998) and rate of dissipation of turbulent kinetic energy (Banerjee et al. 1968; Zappa et al. 2007), with new models including turbulence based on heat gain and loss (MacIntyre et al. 2010). The effect of modeling fluxes rather than measuring them directly introduces uncertainty in metabolism estimates. However, the general extent of this uncertainty may be assessed when fluxes are placed in the context of the stratification within the lake, surface meteorology, relevant indices such as Lake number, and relative strength of biological signal.

This study uses vertical profiles of DO collected over the course of two consecutive ice-free seasons in an oligotrophic high-elevation lake to investigate patterns in volumetric metabolic rates with depth. We do so in relation to physical and chemical conditions in the lake, characterizing environmental drivers and illustrating mechanisms of control. For each depth strata, we characterize the relative contributions of \( K_z \), atmospheric gas exchange, and ecosystem metabolism to total mass flux estimates. Additionally, we explore seasonal variability in depth-weighted, whole-lake metabolism over 2 consecutive years using three approaches and evaluate the degree to which measurements made in the upper mixed layer alone characterize whole-lake metabolism. Finally, we evaluate the effect on metabolic rates of basing atmospheric gas flux estimates on measurements of DO made within the upper mixed layer rather than directly below the air–water interface. Few studies of ecosystem metabolism include variability with depth, and results are rarely placed in the context of physical processes; our results help clarify how such processes influence the ecological conclusions drawn from metabolism studies.

Methods

Site description—Emerald Lake is an oligotrophic high-elevation, headwater lake located on the western slope of the south-central Sierra Nevada (California, \( 36^\circ35'49'' \text{N}, 118^\circ40'29'' \text{W}; 2800 \text{ m above sea level} \)). This remote lake sits in a glaciated scoured cirque, where high surrounding ridges limit the amount of direct sun exposure on the lake surface. The lake has a surface area of 0.027 km\(^2\) and a maximum depth of 10 m; it is representative of the more than 4000 high-elevation lakes throughout the range (Melack and Stoddard 1991). With snowmelt-dominated hydrology and a catchment comprised primarily of granite or granodioritic rock, Emerald Lake has minor groundwater inputs and weakly buffered waters with little acid neutralizing capacity (10–45 \( \text{mg L}^{-1} \); Melack and Stoddard 1991). With a sparsely vegetated catchment, it receives little terrestrial input of dissolved organic matter (DOM; Nelson 2009). The hydrology, biogeochemistry, and ecology of Emerald Lake have been characterized for over three decades (Sickman et al. 2003).

Measurement of environmental data and calculations of physical properties—The following meteorological data were collected at 10-s intervals and recorded as 5-min averages at a station maintained \( \sim 30 \text{ m from and } \sim 8 \text{ m above the southeastern shore of Emerald Lake} \): air temperature and relative humidity (Vaisala ES 120), wind speed (R.M. Young propeller anemometer; \( 1.0 \text{ m s}^{-1} \) threshold \( \pm 0.3 \text{ m s}^{-1} \)), downwelling shortwave radiation (285–2800 nm; Eppley Precision Spectral Pyranometer), and downwelling longwave radiation (3.5 to 50 \( \mu \text{m} \); Eppley Precision Infrared Pyrgeometer). Wind speed in 2007 was collected as hourly averages and interpolated to 5-min intervals, resulting in lower overall values than measured in 2008. Surface albedo was assumed to be 5%, and upwelling longwave radiation was computed according to MacIntyre et al. (2002). Thermal structure was characterized at 6-min intervals over the deepest part of the lake using temperature loggers (Onset TidBit v2; \( \pm 0.2^\circ \text{C} \)) deployed at \( \sim 0.5-\text{m} \) depth intervals from 0.05 m to 10 m. Discharge was measured at the outlet at 10-s intervals and recorded as hourly averages using a calibrated weir and pressure transducer corrected for fluctuations in atmospheric pressure. Residence time was computed as the number of preceding discharge days required to equal lake volume. The vertical attenuation coefficient for photosynthetically active radiation (\( k_d \text{PAR} \)) was measured three times in 2007 and seven times in 2008. It was calculated as the slope of the linear regression model of the natural logarithm of irradiance with depth from measurements of \( \text{PAR} \) made at 0.5-m intervals throughout the water column (LiCor LI-250A with a LI-192 quantum sensor).

Thermal stability was calculated from temperature profiles according to Schmidt (1928) following the modi-
fications of Idso (1973). Buoyancy flux and Lake number were computed from surface meteorology and time-series temperature measurements (Imberger 1985; Imberger and Patterson 1989; MacIntyre et al. 2002). The computation of buoyancy flux requires an estimate of the depth of the actively mixing layer, that is, the region within the upper mixed layer that is turbulent. In general, turbulence in the upper mixed layer is constrained to be above or is enhanced above the diurnal thermocline in the day and descends to the base of the mixed layer at night. If diurnal stratification extends to the surface of the lake, turbulence may be damped and an actively mixing layer may not be present or may be only a few centimeters thick (MacIntyre 1996). Despite efforts to define the mixing layer depth (MLD) based on temperature or density alone, fixed criteria do not exist (Shay and Gregg 1986; Brainerd and Gregg 1995). We selected a density criterion of 0.05 kg m\(^{-3}\) after evaluating the fits of MLD computed using a range of values (0.1–0.005 kg m\(^{-3}\)) against high-resolution, temperature–depth contour plots (0.5°C contour intervals) in which diel fluctuations in thermal stratification were evident. We interpolated water density (Millero and Poisson 1981) to 0.1-m intervals and identified the depth > 0.1 m at which density was 0.05 kg m\(^{-3}\) greater than surface density. K\(z\) was estimated below the epilimnion using the heat flux method (Jassby and Powell 1975) averaged over 2 d (MacIntyre et al. 2009). In both years, K\(z\) was computed to a depth of 9 m.

**Water sample collection**—Water samples were collected at approximately biweekly intervals between July (1–3 weeks after ice-off) and early November of 2007 and 2008. Samples were collected from four depths throughout the water column (usually 1, 4, 7, and 9 m) using a hand-operated peristaltic pump and stored in low-density polyethylene cubitainers for < 4 h before being filtered or decanted into sample bottles. In both years we analyzed for the following parameters: dissolved inorganic nitrate + nitrite (NO\(_3\)); total dissolved nitrogen (TDN); soluble reactive phosphorus (SRP); total dissolved phosphorus (TDP); chlorophyll \(a\) (Chl \(a\)); dissolved organic carbon (DOC); and fluorescence index (FI), a relative measure of allochthonous and autochthonous fulvic acids in the bulk DOM pool (McKnight et al. 2001). Particulate carbon (PC), nitrogen (PN), and phosphorus (PP) were collected only in 2008. All dissolved nutrient samples were filtered through 1.0-μm polycarbonate membrane filters (Nuclepore), all particulate samples were filtered through glass fiber filters (Gelman A/E, 1.0-μm nominal pore size), and Chl \(a\) samples were collected on 0.45-μm nitrocellulose filters (Millipore). DOC and FI samples were filtered through Whatman GF/F filters (0.7-μm nominal pore size) into amber borosilicate vials with Teflon-coated septa and acidified with HCl to pH < 2. We precombusted all glass fiber filters (2 h at 450°C) and glass vials (12 h at 450°C) prior to use.

**Water sample analysis**—Cadmium reduction and phosphomolybate methods (Strickland and Parsons 1972) were used to measure NO\(_3\) and SRP, with oxidative reduction (Valderrama 1981) done for TDN, TDP, and PP. Nutrient samples were analyzed on a Lachat autoanalyzer (Lachat Instruments Quickchem 8000), and PC and PN were determined by combustion in an elemental analyzer (Control Equipment Corporation). Chl \(a\) samples were extracted for 24 h in 90% acetone prior to analysis on a Turner AU-10 fluorometer. FI samples were analyzed on a Shimadzu Total Organic Carbon analyzer using high-precision methods adapted for low concentrations (Carlson et al. 2010). Dissolved organic nitrogen (DON) and phosphorus (DOP) were computed as the difference between the inorganic and total dissolved fractions, while total phosphorus (TP) was the sum of all dissolved and particulate phosphorus species. Because ammonium concentrations in Sierran waters are typically near detection limits (Sickman et al. 2001) and are a very small fraction of dissolved inorganic nitrogen (DIN), they were not measured.

**Metabolism measurements**—Starting at dawn each sampling day, profiles of DO were collected manually approximately every 2 h during daylight and at least once between sunset and sunrise the following morning. Measurements were made using high-precision optical oxygen sensors (D-opto, Zebra-Tech) calibrated in 0% and 100% saturation solutions prior to deployment. Average accuracy and precision of instruments after calibration were 250 ± 30 μg L\(^{-1}\) and 8 ± 1 μg L\(^{-1}\), respectively; drift was evaluated and found to be negligible over the 24-h duration of our profiles. Measurements were made at the surface (0.05 m) and at 1-m intervals from 1–10-m depth. DO loggers were kept saturated in lake water between profiles and allowed to equilibrate in surface water for ~ 10 min prior to starting a new profile. When profiling, we lowered a logger between depth intervals and allowed it to equilibrate at each depth for 1 min prior to 3 consecutive minutes of data collection. A range of longer equilibrium and averaging times was tested and found to be no different from those we used.

We used a modified mass balance approach (Odum 1956; Bella 1970) in computing volumetric metabolic rates over each time step; this involved dividing the water column into ten 1-m strata and, for each stratum, computing net ecosystem production as: NEP = ΔDO + F\(_{ge}\)/MLD + F\(_{ed}\)/h\(^{2}\), where, for any given time step, NEP (g m\(^{-3}\)) is the net change in DO concentration attributed to biological metabolism; ADO (g m\(^{-3}\)) is the measured change in DO; F\(_{ge}\) (g m\(^{-3}\) h\(^{-1}\)) is flux due to atmospheric gas exchange: MLD (m) is the mixing layer depth, that is, the depth over which the gas is initially exchanged; F\(_{ed}\) (g m\(^{-3}\) h\(^{-1}\)) is flux due to K\(z\); and h (m) is the height of each depth stratum, that is, the assumed length scale of mixing.

Atmospheric gas exchange can be into or out of the lake (i.e., positive or negative) and is a function of the gradient between lake water and atmosphere: F\(_{ge}\) = k\(_{DO}\)(DO\(_{water}\) – DO\(_{Sat}\)), where k\(_{DO}\) (m h\(^{-1}\)) is the gas exchange coefficient for DO at ambient temperature, DO\(_{water}\) (g m\(^{-3}\)) is the concentration of DO in the surface water, and DO\(_{Sat}\)
(g m$^{-3}$) is the saturation concentration of DO at ambient atmospheric temperature and pressure. Because gas exchange is governed by the concentration gradient between the very surface layer of water and the atmosphere, we used DO measurements from 0.05-m depth when computing exchange; for comparative purposes, we also computed gas exchange based on measurements of DO from the more commonly used depth of 1 m. The gas exchange coefficient ($k_{600}$) was modeled based on wind speed (Cole and Caraco 1998; MacIntyre et al. 2010) and computed for DO at ambient temperatures ($k_{DO_{2}}$) using the relationship between Schmidt numbers described by Jahne et al. (1987). In 2007 gas flux was estimated from wind speed measured at the meteorological tower adjacent to the lake (see above), but in 2008 measurements made directly at the lake shore were used (Onset cup anemometer; 1.0 m s$^{-1}$ threshold ± 0.4 m s$^{-1}$). In both years, wind speed was converted for model inputs from the height of measurement to a standardized height of 10 m accounting for air column stability (Hicks 1975; Smith 1988). We compared estimates of $k_{600}$ from Cole and Caraco (1998) and MacIntyre et al. (2010) and found them to be similar in this small lake with its low wind speeds. Estimates of $k_{600}$ from MacIntyre et al. (2010) were occasionally lower but more often higher over windy periods during the day and higher at night than those from Cole and Caraco (1998); on an average daily basis they were 11% higher, resulting in estimates of gas exchange that were 13% higher than those from Cole and Caraco (1998). Such differences, however, had little effect on metabolism estimates because surface DO concentrations in Emerald Lake did not deviate much from saturation, and the results we report are based on estimates of $k_{600}$ using the Cole and Caraco (1998) model.

Atmospheric gas flux into the lake was assumed to be evenly distributed among those depth strata within the upper mixing layer and was divided by the mixing layer depth. At times when the lake was heating and diurnal stratification caused the upper mixing layer to become shallower than 1 m, we assumed, based on observations in MacIntyre et al. (2010), that gas exchange functionally ceased and we set $F_{ed}$ to zero. The accuracy of this approach stems from the depth resolution of the DO and thermistor data used to compute the mixing layer depth and to estimate metabolism. The effect of gas exchange on metabolism estimates will largely depend on the relative magnitude of biological signal to gas exchange (Coloso et al. 2011).

Mass flux between depth strata below the upper mixed layer was computed using $K_{s}$ and the DO gradient between layers: $F_{ed(i)} = K_{s(i)} (DO_{i} - DO_{i+1}) + K_{s(i+1)} (DO_{i+1} - DO_{i-1})$, where $K_{s(i)}$ and $K_{s(i+1)}$ (m$^2$ h$^{-1}$) are $K_{s}$ bounding depth $i$, and DO$_{i-1}$ and DO$_{i+1}$ (g m$^{-3}$) are DO for the depth strata bounding depth $i$; negative values are fluxes into and positive values fluxes out of a given depth stratum. Because the epilimnion mixed every night, mass flux across the thermocline into or out of the upper mixed layer was assumed to be evenly distributed among all the depth strata therein. Entrainment of gases from within the metalimnion due to deepening of the seasonal thermocline was not included in our budget because we did not find a measurable change in maximum daily MLD between successive dawns on any of our sample days. Because our profiles were made at one location in the center of the lake, we have no basis to account for advection and assume it to be zero in our computations.

We summed NEP from all the time steps over individual dawn-to-dawn 24-h periods to derive daily rates. CR was computed by summing nighttime NEP and dividing by the time interval over which it was summed to derive an average hourly nighttime rate, which was then applied over an entire 24-h period. Daily GPP was computed as the sum of NEP and CR: $GPP = NEP + CR$, where respiration is treated as a positive value. Our methods for estimating metabolic rates produce results identical to those produced by the methods recommended by Staehr et al. (2010). Although our approach to computing CR assumes no diel variability, there is evidence that daytime rates in Emerald Lake may be higher than nighttime rates (Sadro et al. 2011). Not accounting for such diel variability causes us to underestimate CR and GPP but does not affect our direct measurements of NEP.

We estimated whole-lake metabolism using volume-weighted and depth-integrated approaches. In the whole-lake, volume-weighted (WLWV) approach we multiplied the daily mass balance corrected metabolic rate associated with a given depth stratum by the volume of that stratum; summing the resulting mass through all depth strata and dividing by the surface area of the lake yielded volume-weighted areal estimates. The whole-lake, upper mixed layer (WLUML) approach, representative of single-station epilimnion measurements, was computed in the same way as the WLWV approach, except that we used only the metabolism measurements from the 2.0-m depth interval scaled to the volume of the entire lake. The whole-lake, depth-integrated (WLDI) approach was based on integration of DO concentrations through all depth strata and did not require the volumetric mass balance accounting of the volumetric methods. For WLDI we used hypsographic curves to compute the areal proportion of each of the 10 depth strata ($P_{AZ}$). That proportion was then multiplied by the DO (g m$^{-3}$) concentration of each strata ($z$) at each time step. Integrating through all the depths for each time step yielded a single time series of whole-lake areal values for mass of DO (DO$_{t}$): $DO_{t} = \int_{0}^{z} (P_{AZ} \times DO_{z})$, where DO$_{t}$ is WLDI DO concentration (g m$^{-2}$). WLDI NEP ($NEP_{1}$) was then computed using DO$_{t}$ as: $NEP_{1} = \Delta DO_{1} + F_{ge}$, where $\Delta DO_{1}$ is change in areal-weighted, depth-integrated DO (g m$^{-2}$) over each time step and $F_{ge}$ (g m$^{-2}$) is exchange with the atmosphere. We summed NEP$_{1}$ for all time steps within a dawn-to-dawn 24-h period to compute daily NEP$_{1}$ and computed CR$_{1}$ and GPP$_{1}$ as described above. NEP$_{1}$, GPP$_{1}$, and CR$_{1}$ were all computed using the areal-weighted WLDI approach.

**Data analysis**—We used correlation analysis with Pearson correlation coefficients to explore relationships between metabolic rates and seasonal drivers. We tested for the effect of depth on volumetric metabolic rates using one-way ANOVA. The relative proportion of each of the fluxes in the mass balance equation (e.g., NEP, $F_{ed}$, and $F_{ge}$) was...
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determined for each depth strata by summing the absolute value of a given flux over the course of the day and dividing by the total for all fluxes. To test for difference in metabolism estimates among the three different treatments, we used a mixed-effects model that included treatment and day, treating day as a random effect; significant differences among methods were investigated using paired t-tests. We log10- or power-transformed data as necessary to meet assumptions of homoscedasticity of variance and normality of residuals. All statistical analyses were done using JMP (version 9; SAS Institute).

Results

Physical and chemical conditions—Below average snowpack in 2007 resulted in peak outflow discharge (~250 L s−1) below what was measured in the average snowpack year of 2008 (~450 L s−1). By the start of sampling after ice-off in 2007 (Fig. 1), discharge was below 20 L s−1, residence time was ~30 d, and the temperature gradient through the water column was 9 °C. At the start of sampling in 2008 (Fig. 2), discharge was above 100 L s−1, residence time was ~10 d, and the temperature gradient through the water column was 6 °C. Differences in timing of the onset of stratification are reflected in lake stability, which at the start of July in 2007 had already peaked at ~56 J m−2, while in 2008 the peak of ~66 J m−2 was not reached until early August. Lake temperatures increased through late August before declining steadily with decreasing average daily irradiance and air temperature in the autumn.

Wind speeds in both years were low. Diel maxima were typically 3 m s−1 with occasional events larger than 6 m s−1. Although hourly average values in 2007 were lower than 5-min average values in 2008, there was no statistical difference between seasonal means (~1.4 m s−1), suggesting that wind speeds were generally comparable between years. Diel heating with resulting formation of diurnal stratification occurred throughout the period with higher lake stability. In both years, the lake mixed to the bottom starting in mid-September, beginning a period of diel overturn when lake stability was <1–10 J m−2. Diurnal thermoclines were still prevalent during the period of fall overturn, except on cloudy days when buoyancy flux remained < 0. Lake number was always above 10 during the period of stratification in 2007. Values were comparable in 2008, except early in the season when they decreased to near 1 and midsummer when they occasionally dropped to ~10. The small vertical fluctuations in isotherm depth within the metalimnion (Figs. 1A, 2A) were due to a combination of solar heating (kθ was 0.27–0.32 m−1) and high frequency waves with amplitudes 0.2 to 0.5 m. During periods when lake stability and Lake numbers were highest, Kz’s within the thermocline equaled molecular values. However, early in 2008, and below the thermocline in all years, Kz equalled or exceeded 10−6 m2 s−1. Once the lake fully mixed, the low Lake numbers reflect low stability and are not necessarily indicative of wind-induced internal wave activity. Kz’s in the mixed layer are not shown; however, parameterizing the turbulence as in Imberger (1985) and Kz as in MacIntyre et al. (2009) results in Kz ranging from 0.01 to 0.04 m2 s−1 within the mixed layer. Given that the timescale for mixing is l/2Kz, the surface mixing layer (l) would mix in less than 0.5 h.

There were seasonal and spatial patterns in many of the water chemistry parameters we measured (Fig. 3). NO3 declined from an early season peak of ~4 μmol L−1 to late seasonal lows of <0.3 μmol L−1. Although concentrations in the epilimnion were higher than at depth (sixfold higher, on average, during periods of stratification), NO3 throughout the water column decreased seasonally. SRP remained low, ranging from 0.05–0.07 μmol L−1, with concentrations in the hypolimnion occasionally exceeding those in the epilimnion. Average water column Chl a showed a positive seasonal trend, increasing from an early season low of <0.5 μg L−1 to an autumn-overturn seasonal peak of 2.8 μg L−1. Subsurface (>4 m) concentrations of Chl a were 1.3–6.8 times higher than epilimnetic concentrations during stratification. Water column DOC averaged ~65–75 μmol L−1 after snowmelt and fluctuated by ~15–20 μmol L−1 throughout the ice-free season without a trend. In contrast, FI values increased steadily. Within the upper mixed layer this increase mirrored the pattern seen in Chl a (including both years: n = 15, r = 0.61, p = 0.015), indicating an overall shift from allochthonous to autochthonous DOM in conjunction with increasing phytoplankton biomass. During stratification, the particulate fraction for N, P, and C was higher in the hypolimnion than in the epilimnion, reflecting the higher Chl a concentrations found at depth.

Volumetric metabolic rates by depth—DO saturation in the surface stratum ranged between 93–109% and 101–110% in 2007 and 2008, respectively. The vertical gradient in DO throughout the water column was ~6% early in the season before stratification had fully developed, and it increased during stratification to a peak of 28–39% before disappearing after the onset of autumn overturn. Satura-

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Fig. 1. Seasonal changes in environmental and lake physical properties for Emerald Lake in 2007. (A) Time–depth contour plot of lake temperature (temp); isotherms were made at 1 °C intervals using a kriging function (Surfer 8.0). (B) Mixing layer depth showing diel variability. (C) Time–depth contour plot of the coefficient of eddy diffusivity (Kz). (D) Lake discharge (solid line, left y-axis) and residence time (RT; dotted line, right y-axis). (E) Air (solid line, left y-axis) and water (dotted line, right y-axis) temperatures. (F) Wind speed. (G) Downwelling shortwave (SW) radiation. (H) Buoyancy flux (BF), reflecting periods when the lake is heating (positive) and cooling (negative). (I) Lake number, a dimensionless index of stability incorporating density structure, wind regime, and basin morphometry. (J) Schmidt stability, reflecting the energy necessary to overcome resistance to mixing throughout the water column. Darker shades represent higher values in contour plots. DOY is day of the year.
tion maxima occurred within the metalimnion, where concentrations reached $>130\%$ in both years. A diel pattern in DO was evident in most depth strata early in the season when the upper mixed layer was shallow (Fig. 4A). Although all the strata within the upper mixed layer showed similar diel patterns during stratification (Fig. 4B), the magnitude of diel DO evolution ($\sim10\ \text{mol L}^{-1}$) was small relative to the vertical gradient in DO found throughout the water column ($50–80\ \text{mol L}^{-1}$). By the time the lake was mixing completely in the autumn, the magnitude of diel change in DO was the same throughout the water column (Fig. 4C). Regardless of degree of stratification or vertical gradient in DO, depth-integrated DO concentrations showed a clear diel pattern (Fig. 4).

Seasonally averaged volumetric metabolic rates (Fig. 5) varied by a factor of up to $\sim7$ with depth. Average rates of CR were 1.90 to 15.2 $\mu$mol L$^{-1}$ d$^{-1}$, and GPP varied between 2.16 and 17.6 $\mu$mol L$^{-1}$ d$^{-1}$. Average water column NEP was positive in both years, and individual values between 2.16 and 17.6 $\mu$mol L$^{-1}$ d$^{-1}$. Volumetric metabolic rates varied with depth during periods of stratification but were relatively consistent when the lake was mixing (Fig. 6). During stratification both CR and GPP, which were positively correlated with depth (Table 1A), had subsurface maxima below $6\ $m. NEP among depths within the upper mixed layer was occasionally negative, especially early in the season, but was positive on average during both years. Periods of heterotrophy occurring below the thermocline during both years (Fig. 6) caused NEP to be negatively correlated with depth during stratification (Table 1A) and were correlated with increased concentrations of Chl $a$, PC, and PN (Table 1B). Since primary production occurred throughout the entire water column, the proportion of metabolism occurring exclusively within the epilimnion was largely a function of the mixed layer depth (Fig. 7; CR: $R^2 = 0.80$, $F_{1,26} = 103.3$, $p < 0.001$; GPP: $R^2 = 0.78$, $F_{1,26} = 93.6$, $p < 0.001$) rather than of variability in rates at depth.

**Estimates of whole-lake metabolism**—For the three methods of estimating whole-lake metabolism between the 2 yr (Fig. 8), whole-lake estimates of GPP were 9.51 to 95.9 mmol m$^{-2}$ d$^{-1}$, estimates of CR were 3.26 to 89.5 mmol m$^{-2}$ d$^{-1}$, and NEP ranged from autotrophy of $-22.9$ mmol m$^{-2}$ d$^{-1}$ to heterotrophy of $-32.9$ mmol m$^{-2}$ d$^{-1}$. CR and GPP were both significantly higher in 2008 than 2007 by all three estimates (CR pooled data: $F_{1,82} = 20.19$, $p < 0.001$; GPP pooled data: $F_{1,82} = 28.99$, $p < 0.001$); however, there was no difference in NEP between the 2 yr. The lake was autotrophic on average during the ice-free season of both years according to all three methods of estimating whole-lake NEP (Fig. 9).

At the seasonal scale there was no statistical difference among the three methods of computing metabolism. At the daily timescale, however, there were significant differences in estimates of CR and GPP among the three methods (CR: $F_{2,54} = 6.76$, $p = 0.002$; GPP: $F_{2,54} = 9.57$, $p < 0.001$) but no differences among estimates of NEP (NEP: $F_{2,54} = 1.903$, $p = 0.159$). Although there was some variability associated with whether the lake was stratified or mixed, in general the WLVW method produced the lowest and the WLUML method the highest estimates of CR and GPP, with WLDI estimates intermediate. Pairwise comparisons among the three methods (Table 2) illustrate the significance and average magnitude of differences among them. On average, metabolism estimates using the WLVW method were 1% to 42% lower than estimates using the WLDI method or 12% to 70% lower than estimates using the WLUML method. Similarly, estimates using WLDI were 10% to 35% lower than estimates using WLUML. Pairwise differences were greater during periods of stratification than overturn; after the onset of autumn mixing, differences, although in some cases still statistically significant, were small, having dropped by 9–50%.

**Mass flux through the water column**—Estimates of gas flux averaged $6.0 \pm 2.6$ mmol m$^{-2}$ d$^{-1}$, an amount that when distributed throughout the volume of the surface mixing layer resulted in volumetric fluxes averaging $\sim5\ \text{mol L}^{-1}$ d$^{-1}$ during periods of stratification and $\sim1\ \text{mol L}^{-1}$ d$^{-1}$ during periods of overturn. Mass flux into the mixed layer due to turbulence within the thermocline and the higher DO concentrations within it averaged 1.10 $\pm 0.53$ mmol m$^{-2}$ d$^{-1}$. These values are low because $K_z$ was rarely above molecular conductivity. At the end of the season when concentrations were higher in the epilimnion than below, mass flux out of the mixed layer averaged 0.88 $\pm 0.30$ mmol m$^{-2}$ d$^{-1}$. $F_{\text{ed}}$ into the epilimnion, if evenly distributed throughout the volume of the upper mixed layer, resulted in an average increase in volumetric concentration of $\sim0.5\ \text{mol L}^{-1}$ d$^{-1}$. In contrast, the flux between individual depth strata due to $F_{\text{ed}}$ was higher within and below the metalimnion, where it averaged 2.09 $\pm 0.86$ mmol m$^{-2}$ d$^{-1}$.

Metabolism accounted for the majority of the combined factors in the mass balance equation on a seasonally averaged basis (89%), followed by water column turbulence (8%) and atmospheric gas exchange (6%). The relative proportion of fluxes due to physical processes varied with depth and degree of stratification, while the proportion attributed to metabolism remained relatively constant (Table 3). $F_{\text{ge}}$ was substantial early in the season when the epilimnion depth was shallow and increased to $\sim1$–3% of total fluxes with seasonal deepening of the thermocline as it was distributed over an increasing MLD volume. Turbulent fluxes, $F_{\text{ed}}$, were computed for strata below the upper mixed layer and across the thermocline, into or out of the epilimnion depending on the DO gradient. Turbulent fluxes within and below the metalimnion comprised 12% of the total mass balance on average. Fluxes across the thermocline, however, were lower, averaging only 4% of the total mass balance because of the lower $K_z$ values found within the thermocline.

Daily estimates of atmospheric gas flux were higher on average when DO measurements from subsurface rather than surface depths were used in the computation. $F_{\text{ge}}$ based on wind estimates of the gas exchange coefficient (Fig. 10A) and measurements of DO from the 1.0-m depth stratum were 9.1% higher on average than estimates based on DO measured at 0.05-m depth (i.e., surface; paired $t$-test).
Fig. 2. Seasonal changes in environmental and lake physical properties for Emerald Lake in 2008. See Fig. 1 for panel descriptions.
Temperatures heated and cooled more at 0.05 m than at 1 m, causing DO saturation to be alternately higher during the day and lower at night at the surface (Fig. 10B). Gas flux is a function of the DO gradient between the lake and the atmosphere. During the day, flux estimates based on 1-m DO measurements were lower (seasonal mean 3.2 ± 21.9%) and at night higher (seasonal mean 17.3 ± 32.6%) than surface-based estimates (Fig. 10C), resulting in a diel pattern in the magnitude and direction of the divergence (Fig. 10D). Measurements of CR and GPP using the 1-m gas flux estimates ranged from underestimates of 5% to overestimates of 2%. The effect on NEP was greater; measurement using the 1-m measurements of DO to estimate gas flux.

Discussion

Patterns in ecosystem metabolism with depth and their implications—Our study demonstrates a consistent pattern with depth in metabolic rates over two consecutive ice-free seasons in a high-elevation lake. In both years, the interplay between physical and biogeochemical dynamics affected patterns, with the strength and duration of stratification being an important factor. During periods of stratification, GPP and CR tended to increase with depth and NEP decrease with depth, patterns that weakened with the onset of autumn mixing. The epilimnion remained autotrophic on average during both years despite periodic heterotrophy at some depths within the upper mixed layer. Periods of stronger and more persistent
heterotrophy tended to occur below the thermocline during stratification, often in conjunction with elevated Chl a, PC, and PN concentrations. Despite these periods of heterotrophy at depth, the water column remained autotrophic on average over the entire ice-free season.

The increase of GPP with depth was probably caused by the presence of a deep Chl a maximum, a well-known condition (Fee 1976) broadly observed in clear-water mountain lakes (Priscu and Goldman 1983; Sickman and Melack 1992; Sawatzky et al. 2006). Based on the attenuation coefficient of PAR in Emerald Lake, the euphotic zone and compensation depths are estimated to be ~15 m, placing the entire water column within the euphotic zone, and midday PAR measurements down to ~9 m are approximately equal to the 129 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) average saturation irradiance levels measured by Sickman and Melack (1992). In deeper lakes, in which a substantial part of the water column lies below the euphotic zone, and in more productive lakes or lakes with higher concentrations of colored DOM, in which Chl a maxima tend to be shallower, GPP would be expected to decrease with depth (Coloso et al. 2008) as phytoplankton became light limited or primary producer biomass decreased.

The balance in time and space between primary production and CR determined the distribution of periods of heterotrophy in Emerald Lake. Heterotrophy in lakes is thought to occur largely because of terrestrial subsidies of organic matter (Cole et al. 2000; Prairie et al. 2002; Hanson et al. 2003). Despite net autotrophy of the water column in Emerald Lake, terrestrial inputs might explain the higher frequency of weakly heterotrophic episodes we observed at some depths within the epilimnion. Although DOC was generally low and did not show a seasonal trend (Fig. 3C,D), there was a strong seasonal shift in the

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Fig. 4. Examples of diel patterns in DO concentration measured over 2 consecutive days during the ice-free season of 2008 from (A) early season, (B) during summer stratification, and (C) after the onset of complete diel mixing. Thin lines correspond to individual depth strata (left y-axis; dotted are within the upper mixed layer and solid are within and below the metalimnion), and bold line corresponds to depth-integrated concentrations (right y-axis).
composition of DOM reflecting autochthonous replacement of allochthonous material (Fig. 3E,F). Episodes of heterotrophy within the epilimnion were more frequent early in the season when snowmelt runoff was still declining (Figs. 1D, 2D). Chl _a_ concentrations were at a seasonal minimum (Fig. 3A,B), GPP was just beginning to increase (Fig. 5C,D), and DOM was largely terrestrially derived. As the composition of DOM shifted toward autochthonous material later in the season, episodes of heterotrophy at depths within the epilimnion became less frequent. These results suggest that the composition of the DOM pool may be more important than bulk concentrations in affecting metabolic balance in lakes with low DOC.

Conditions under which heterotrophy occurred within the water column during stratification, however, were different, and were likely driven more by autochthonous processes than terrigenous DOM inputs. The magnitude of rates of GPP were exceeded by higher rates of CR when Chl _a_, PC, and PN concentrations were elevated. Although sinking and subsequent accumulation at depth may in part explain the higher concentrations of particulate organic matter found there (Steele and Yentsch 1960), higher GPP at depth, a deep Chl _a_ maxima, and lower concentration of nitrate within the hypolimnion than in the epilimnion all suggest increased rates of localized primary productivity (Figs. 3, 6). The pattern in 2008 of alternating periods of autotrophy and heterotrophy within and below the metalimnion during stratification (Fig. 6) suggests that periods of comparatively higher primary productivity were followed by periods of increased ecosystem respiration, most likely as bacterioplankton responded to the increase in available organic matter. The coarser temporal sampling in 2007 may have missed the intervening periods of higher productivity evident in 2008.

Bacterial abundance has been shown to be a seasonal driver of NEP within the epilimnion of Emerald Lake (Sadro 2011) and is likely a driver of variation in NEP with depth as well. Although not measured in this study, bacterioplankton abundance is known to increase with increasing depth and Chl _a_ concentration in Emerald Lake (Nelson 2008), a pattern of covariation that is also found in other lakes (Pace and Cole 1994), sometimes in response to the higher phytoplankton biomass of deep chlorophyll maxima (Cole et al. 1988). Particulate matter aggregates, as sometimes found in association with these deep Chl _a_ maxima, are known to be hot spots of microbial metabolic activity (Simon et al. 2002), capable of supporting higher bacterial production than extracellularly released organic matter alone (Cole et al. 1984). This suggests that episodes of heterotrophy during stratification in Emerald Lake, unlike the early-season heterotrophy resulting from allochthonous organic matter, stem from increases in bacterial abundance and metabolism that follow periods of increased primary production. Pace and Cole (1994)
similarly suggested a lag between episodes of increased primary and bacterial production to explain a weak contemporaneous correlation between the two. Our conclusion is consistent with the notion that bacterial production is primarily dependent on phytoplankton production in clear-water oligotrophic lakes (Jones 1992).

Table 1. Pearson correlation coefficients for relationships with A) depth and B) NEP for metabolic rates and other water chemistry variables during periods of stratification and mixing of the water column. GPP and CR data were power-transformed ($x^{0.25}$) to meet assumptions of normality of residuals and homoscedasticity of variance. Significant relationships ($p < 0.05$) are shown in bold; *, $p < 0.001$.

<table>
<thead>
<tr>
<th>Correlate 1</th>
<th>Correlate 2</th>
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<th>Stratified</th>
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</thead>
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Fig. 6. Time–depth contour plots characterizing seasonal changes in metabolism. (A, B) Community respiration (CR). (C, D) Gross primary production (GPP). (E, F) Net ecosystem production (NEP). Darker shades represent higher values for CR and GPP. For NEP two grayscales are used: gray to white illustrating decreasing autotrophy with depth (i.e., decreasingly positive NEP) and black to white illustrating increasing heterotrophy with depth below the thermocline during periods of stratification (i.e., increasingly negative NEP). Arrows indicate the onset of autumn mixing. Note that the apparent persistence in 2007 of negative NEP beyond the start of autumn overturn is an artifact of interpolation between sampling points straddling the date overturn began.

Fig. 7. The proportion of water column community respiration (CR; gray figures) and gross primary production (GPP; black figures) occurring within the epilimnion in 2007 (squares) and 2008 (circles).
Jansson et al. 2000) and that increased primary productivity is capable of fueling heterotrophy (Prairie et al. 2002). Indeed, a pattern of alternating autotrophy and heterotrophy (coupled with infrequent sampling that misses intervening periods of autotrophy) has been suggested to explain annual estimates of net heterotrophy in oligotrophic oceans (Karl 1999).

There are numerous ecological implications of spatial heterogeneity in rates of primary production throughout the water column. In addition to a greater abundance of phytoplankton biomass at depth, autochthonous organic matter is generally considered to be more labile than allochthonous organic matter and should result in higher bacterial growth efficiencies (del Giorgio and Cole 1998). Higher growth efficiencies and larger standing stocks of bacterial biomass should increase the amount of organic matter cycling through the microbial loop and possibly act as a positive feedback promoting the next relative increase in primary production. In addition, there is some evidence that bacterial community composition may be affected by pulses of hypolimnetic production (Crump et al. 1999). In a study of bacterioplankton community dynamics in Emerald Lake, community structure covaried with seasonal changes in organic matter source; and, during stratification, epilimnetic communities grew increasingly dissimilar from hypolimnetic communities (Nelson 2009). It is possible that in addition to differences in temperature, UV irradiance, and nutrient concentrations, gradients in GPP with depth indirectly contribute to differentiation among bacterial communities.

**Effects of physical processes on depth-differential lake metabolism**—When estimating atmospheric gas exchange, the gradient in DO between lake and atmosphere is often measured from depths ranging from 0.5–1.0 m (Staehr et al. 2010) rather than in near-surface water (e.g., 0.05 m), although concentrations within the surface layer may differ, especially during periods of diurnal stratification. Deviation from saturation in surface waters was small in this study, and we found that estimates of atmospheric exchange based on measurements of DO made at 1.0-m depth resulted in overestimates of gas exchange of ~ 9% relative to estimates based on measurements made just below the air–water interface (e.g., 0.05 m). Because there was a diel pattern to the error (i.e., underestimation during the day and overestimation at night), overall effects on daily or seasonally averaged estimates of metabolism were low. However, the magnitude of the gas flux error and...
Mixed WLDI–WLUML
Mixed WLVW–WLUML
Mixed WLVW–WLDI
Stratified WLDI–WLUML
Stratified WLVW–WLUML
Stratified WLVW–WLDI

Entire lake volume.

of metabolic rates; and whole-lake, upper mixed layer (WLUML) applies metabolic rates measured only in the upper mixed layer to

individual depth strata due to eddy diffusivity; whole-lake, depth-integrated (WLDI) integrates through all depths prior to computation

water column. Whole-lake, volume-weighted (WLVW) measures metabolic rates for each depth and explicitly accounts for flux between

Kz in the thermocline, similar to those from Gelda and Effler (2002), we found that the flux of DO across the thermocline into or out of the epilimnion was a small fraction of the total fluxes taking place within the upper mixed layer. That such fluxes were distributed throughout the entire volume of the upper mixed layer further reduced their relative contribution. Consequently, the effect of turbulent fluxes across the thermocline on metabolism within the epilimnion depended on epilimnetic volume,

overall effect on estimates of metabolism would be expected to be larger in lakes with a higher abundance of phytoplankton in near-surface waters such that gas saturation gradients with the atmosphere are larger, or in lakes with more pronounced diurnal stratification, where measurements at 0.5 or 1.0 m may not represent the actual gas concentration gradient with the atmosphere.

The effects of turbulence on oxygen fluxes depended on location within the water column. Due to the low values of Kz in the thermocline, similar to those from Gelda and Effler (2002), we found that the flux of DO across the thermocline into or out of the epilimnion was a small fraction of the total fluxes taking place within the upper mixed layer. That such fluxes were distributed throughout the entire volume of the upper mixed layer further reduced their relative contribution. Consequently, the effect of turbulent fluxes across the thermocline on metabolism within the epilimnion depended on epilimnetic volume,

which changed seasonally. Estimates of epilimnetic metabolism that did not include Fed in the mass balance were both higher and lower than estimates that did include it (ranging from < 1% to > 100%). Although individual variability between estimates that did and did not include Fed could be high, on average the difference was ~10%. In contrast, turbulent fluxes had a larger effect on metabolism estimates below the upper mixed layer, where they comprised a larger proportion of total fluxes. Although Kz was often at or near molecular rates in the thermocline, it was one to three orders of magnitude higher within the hypolimnion. On average, failure to include Fed when computing metabolism for depths below the thermocline caused NEP to be underestimated by ~50% and CR and GPP to be overestimated by ~35% and ~5%, respectively. For lakes such as Emerald Lake, with low wind speeds and Lake numbers near 10, mixing due to turbulence should be included in computations of metabolism within the hypolimnion. Furthermore, turbulence within the metalimnion may be important early in the season when stratification is still weak, when Lake numbers

Table 3. Relative proportions of different fluxes in the mass balance equation. Flux proportions (seasonal mean ± standard deviation [SD]) are given for individual depth strata and as averages for flux across the thermocline into the epilimnion (Epilim) and within the hypolimnion (Hypolim). Fge, flux due to atmospheric gas exchange; Fed, flux between strata due to eddy diffusivity; and MET, metabolism, the biological component of change.

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<th>Fed</th>
<th>SD</th>
<th>MET</th>
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which changed seasonally. Estimates of epilimnetic metabolism that did not include Fed in the mass balance were both higher and lower than estimates that did include it (ranging from < 1% to > 100%). Although individual variability between estimates that did and did not include Fed could be high, on average the difference was ~10%. In contrast, turbulent fluxes had a larger effect on metabolism estimates below the upper mixed layer, where they comprised a larger proportion of total fluxes. Although Kz was often at or near molecular rates in the thermocline, it was one to three orders of magnitude higher within the hypolimnion. On average, failure to include Fed when computing metabolism for depths below the thermocline caused NEP to be underestimated by ~50% and CR and GPP to be overestimated by ~35% and ~5%, respectively. For lakes such as Emerald Lake, with low wind speeds and Lake numbers near 10, mixing due to turbulence should be included in computations of metabolism within the hypolimnion. Furthermore, turbulence within the metalimnion may be important early in the season when stratification is still weak, when Lake numbers

Table 2. Comparison of three methods used to estimate whole-lake metabolism during periods of stratification and mixing of the water column. Whole-lake, volume-weighted (WLVW) measures metabolic rates for each depth and explicitly accounts for flux between individual depth strata due to eddy diffusivity; whole-lake, depth-integrated (WLDI) integrates through all depths prior to computation of metabolic rates; and whole-lake, upper mixed layer (WLUML) applies metabolic rates measured only in the upper mixed layer to the entire lake volume. Δ% is the percentage difference between pairs of methods.

<table>
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internal waves such as are found in Emerald Lake introduce uncertainty into our volumetric metabolism estimates, but their effect is minimized when metabolism is estimated for the whole lake.

**Estimates of whole-lake metabolism**—Theoretically, the volume-weighted and depth-integrated approaches of estimating whole-lake metabolism should have agreed. While there were significant differences among the methods at the daily scale, there was no difference in seasonal estimates, in large part because seasonal variability in metabolism was higher than variability among methods. Differences among daily whole-lake estimates were greatest during the period of stratification when gradients in water column temperature and DO were highest, but were substantially lower after the onset of diel mixing in the autumn. This suggests that during stratification the depth intervals at which we sampled were too wide for integration to sufficiently capture oxygen dynamics; in such cases, the volume-weighted approach may be more accurate.

Estimates of ecosystem metabolism are often made based on measurements of DO made at one depth within the epilimnion of a lake. The degree to which a single location from within the upper mixed layer may be used to infer whole-lake metabolism will depend on a number of factors, including lake morphometry, strength of vertical mixing (Figs. 1, 2), depth of the active mixing layer (Figs. 1, 2), the relative proportion of the water column contained therein (Fig. 7), and variability in the abundance of phytoplankton and bacterioplankton throughout the water column (Figs. 3, 6). In the case of Emerald Lake, and likely for the majority of similar Sierra Nevada lakes with their glacially scoured morphometries and small size, whole-lake estimates based on a single depth in the upper mixed layer are sufficient to characterize seasonal variability in metabolism. However, as this study has demonstrated, measurements from the upper mixed layer alone fail to capture the true degree of spatial variability in metabolism found throughout the water column (Fig. 6), especially during periods of stratification. Beyond seasonal estimates of net metabolic balance, much remains to be learned regarding the ecological implications of patterns of production and respiration occurring throughout the water column at shorter timescales. While discrete sampling methods such as we used are sufficient to characterize variability at less than seasonal timescales, the combination of continuous, high-frequency in situ measurements of DO and Chl a fluorescence, especially when made at similar timescales and over multiple depths, may better illustrate the dynamics between patterns of production and consumption of organic matter. Such data, when coupled to frequent sampling of physical, biogeochemical, and biological variables, may illustrate mechanistic relationships at timescales that are infrequently explored.

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