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Key Points:

- Under-ice DO metabolism at a diel scale is challenging because DO patterns do not always follow those dictated by biological processes
- Cluster analysis provided a way to choose appropriate days for metabolic calculations
- Under-ice DO depletion at a seasonal scale depends on snow cover, probably influencing photosynthesis

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Dissolved oxygen dynamics under ice: Three winters of high-frequency data from Lake Tovel, Italy

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Abstract Under-ice dissolved oxygen (DO) metabolism and DO depletion are poorly understood, limiting our ability to predict how changing winter conditions will affect lake ecosystems. We analyzed under-ice DO dynamics based on high-frequency (HF) data at two depths (5 and 25 m) for three winters (January–March 2014, 2015, and 2016) in oligotrophic Lake Tovel (1178 m above sea level; maximum depth 39 m). Specifically, we assessed diel metabolic rates based on HF data of DO, temperature, and light for winter 2016 and seasonal DO depletion rates based on HF data of DO for all three winters. For 2016, calculations of metabolic rates were possible only for 34% and 3% of days at 5 and 25 m, respectively; these metabolic rates generally indicated net heterotrophy at both depths. Low success in modeling metabolic rates was attributed to low diel DO variability and anomalous diel DO patterns, probably linked to under-ice physical processes. Seasonal DO patterns for the three winters showed increasing, decreasing, or stable DO trends at 5 m while at 25 m patterns always showed decreasing DO trends but with different rates. Our multiyear study permitted us to hypothesize that the observed intraannual and interannual differences in DO depletion can be attributed to variable snow cover determining the penetration of radiation and thus photosynthesis. This study brings new insights to DO dynamics in ice-covered systems, highlights the challenges linked to under-ice lake metabolism, and advocates for a modeling approach that includes physical processes.

Plain Language Summary More than half of the world's lakes freeze in winter, but scientists still know little about what happens under ice. A major challenge in dealing with winter conditions is the difficulty of sampling when snow and ice often restrict site accessibility. The use of underwater sensors that continuously measure temperature, oxygen, and light has partly overcome this obstacle. However in most lakes, sensors are removed during winter because ice breakup can damage this expensive equipment; Lake Tovel is one of the few lakes where sensors are deployed all year round. Oxygen is needed by organisms for respiration, and how much oxygen is still available in the lake when ice melts will have important implications for the rest of the year. We analyzed 3 years of under-ice oxygen data and show that oxygen can increase at 5 m depth but always decreased at 25 m depth. Climate change predictions indicate less snow in the Alps and earlier ice breakup. We show how water movement and snow influence under-ice oxygen. Our study brings new insights to oxygen dynamics in ice-covered systems and highlights the challenges in understanding the biological and physical factors that influence oxygen in ice-covered lakes.

1. Introduction

Ecosystem metabolism is a fundamental process related to biological carbon fixation by photosynthesis and oxidation of organic carbon by respiration, and its study will contribute to a better understanding of habitat conditions, food-web dynamics, carbon circulation, and energy turnover in freshwater systems [*Cole et al.*, 2007; *Tranvik et al.*, 2009; *Hanson et al.*, 2015; *Peeters et al.*, 2016]. Lake metabolism can be quantified by diel variations in dissolved oxygen (DO) [*Odum*, 1956; *Staehr et al.*, 2010], and the production and consumption of DO can be quantified by the free-water DO (FWDO) method [*Staehr et al.*, 2010; *McNair et al.*, 2015]. Different versions of the FWDO method estimate gross primary production (GPP), total respiration (R), and net ecosystem production (NEP) [*McNair et al.*, 2015]. When GPP $>$ R, then NEP indicates autotrophy, while when GPP $<$ R, then NEP indicates heterotrophy.

In dimictic lakes, the temporal and spatial variability of DO dynamics differ markedly between ice-free and ice-covered periods. Under ice, thermal stratification is inversed, water temperature is low, air-water gas exchange, wind mixing, and atmospheric inputs are essentially halted, and depending on ice and snow cover, light penetration can be blocked [*Kirillin et al*., 2012; *Leppäranta*, 2015]. These conditions make the under-ice habitat a peculiar system, where only in-lake processes alter DO concentrations. Generally, the main biological and chemical processes determining DO variability under ice are light-dependent production through photosynthesis and light-independent consumption through chemical reactions and respiration of organisms [*Hanson et al*., 2006; *Bertilsson et al*., 2013].

Winter DO concentrations have long-lasting impacts on the subsequent season, and this legacy effect has led to a renewed interest in understanding the ecological processes occurring under ice [*Hampton et al*., 2015]. Despite half of the world's lakes periodically freezing [*Hampton et al*., 2017], understanding DO dynamics under ice is hampered by the scarcity of limnological studies in winter [*Salonen et al*., 2009; *Hampton et al*., 2015; *Kalinowska and Grabowska*, 2016], when snow and ice often restrict site accessibility, sampling, and measurements. Therefore, the relatively few studies of gas evolution (drivers of CO_2 variability or DO depletion rates) under ice often rely on occasional probe profiles or measurements based on headspace analysis or calculations [e.g., *Welch and Bergmann*, 1985; *Catalan*, 1992; *Terzhevik et al*., 2009; *Karlsson et al*., 2008; *Denfeld et al*., 2015]. In contrast to seasonal depletion rates based on discrete sampling events, the fairly recent advent of high-frequency (HF) measurements in lakes offer the opportunity to study lake metabolism based on diel variations in DO [*Staehr et al*., 2010; *Marcé et al*., 2016]. In ice-free lakes, calculations of lake metabolism can be straightforward in eutrophic lakes that show substantial diel DO variations [e.g., *Cole et al*., 2000; *Hanson et al*., 2003, 2008; *Staehr et al*., 2010; *Laas et al*., 2012; *Solomon et al*., 2013; *Obrador et al*., 2014] or more demanding in oligotrophic lakes where the low diel DO variation hinders the application of standard methods [*Richardson et al*., 2016]. While HF measurements represent a unique opportunity to study under-ice DO patterns without the usual constraints tied to winter sampling, under-ice HF measurements are still quite few [*Baehr and DeGrandpre*, 2004; *Terzhevik et al*., 2009; *Couture et al*., 2015] because buoys are generally removed to prevent ice damage [*Richardson et al*., 2016]. Under ice, a further complicating factor is water movement caused by river runoff, oscillations of the ice cover caused by wind and differences in atmospheric pressure, and radiatively driven convective mixing caused by solar radiation penetrating the ice and heat release from bottom sediments [*Bengtsson*, 1996; *Petrov et al*., 2007; *Bouffard et al*., 2016]. These water movements can lead to horizontal and vertical circulation by standing waves and currents under ice [*Warwick et al*., 2008; *Zyryanov*, 2011; *Bouffard et al*., 2016] that can influence DO patterns. In fact, DO in ice-covered lakes is not only a crucial ecological parameter but also a sensitive indicator of physical transport processes [*Kirillin et al*., 2012]. Thus, assessment of lake metabolism in ice-covered, oligotrophic lakes is a challenge.

Lake Tovel (Italy) is a deep, oligotrophic lake that is frozen from the end of December to the beginning of April. The lake is a long-term ecological research (LTER) site with a permanent central platform, equipped with *in situ* HF sensors. Here we characterize under-ice DO dynamics of Lake Tovel by means of HF measurements of temperature, DO, and light at two different depths (5 and 25 m) during three winters and focus on the following aspects: (1) challenges related to the calculations of lake metabolism for an ice-covered, oligotrophic lake, (2) sign of net ecosystem production, and (3) differences between metabolic rates and seasonal depletion rates. Our results will contribute to a better understanding of winter limnology, including DO variability in ice-covered, oligotrophic lakes.

2. Materials and Methods

2.1. Site Description

Lake Tovel (LTER site IT09–005-A; 46.26137°N, 10.94934°E; 1178 m above sea level) is a small (area: 0.4 km^2; maximum depth: 39 m; mean depth: 19 m; volume: 7.4×10^6 m^3), glacial lake located in the Adamello Brenta Natural Park (Trentino, Italy). Geological substrate is dolomite and limestone, and the catchment is pseudokarst in nature leading to marked changes in water level [*Obertegger et al*., 2007]. The lake has a deep (39 m) NE basin and a shallow (4 m) SW basin with over 80% of the inflow entering the lake through underwater springs situated in the shallow basin. The lake is oligotrophic with long-term annual mean values of total phosphorus < 10 $\mu g\ L^{-1}$, chlorophyll $a < 3$ $\mu g\ L^{-1}$, DOC < 1 $mg\ L^{-1}$, coefficient of light extinction $< 0.18\ m^{-1}$, and water transparency > 10 m [*Cellamare et al*., 2016]. Mean annual precipitation is ~1200 mm [*Eccel and Toller*, 2006]. A lake platform over the deep basin is equipped with HF sensors deployed all year round for water level, temperature, DO (since 2013), and light (since autumn 2015). The platform was constructed to follow water level fluctuations [see *de Eyto et al*., 2016]. An on-site meteorological station provides air temperature and pressure, precipitation, relative humidity, wind velocity and direction, and global solar radiation at 15 min intervals.

2.2. Data Acquisition

Optical DO sensors (HOBO DO Logger model U26–001; Onset Computer Corporation, Bourne, MA) were deployed at 5 and 25 m depths and provided measurements every 30 min. The positioning of the two sensors was based on long-term monthly DO profiles that generally showed an extended zone of higher DO concentrations between 5–10 and 20–25 m with respect to other layers. Sensor accuracy was $\pm 0.2\ mg\ L^{-1}$ with DO concentrations up to $8\ mg\ L^{-1}$ and $\pm 0.5\ mg\ L^{-1}$ with DO concentrations from 8 to $20\ mg\ L^{-1}$; resolution was $0.02\ mg\ L^{-1}$. The sensors were calibrated according to the manufacturer's instructions. In the following text, we refer to DO values at 5 m as DO_{5m} and DO values at 25 m as DO_{25m}. Light meters (HOBO Pendant Temperature/Light Data Logger Model UA-002-08) were deployed at 0.1, 1, 2, 5, 10, and 25 m depths and provided measurements of light intensity (lux) every 30 min. Temperature sensors (HOBO Water Temp Pro v2: accuracy $\pm$ 0.2°C, resolution $\pm$ 0.02°C) were deployed at 0.1, 0.25, 0.5, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 20, 25, 30, and 35 m and bottom and provided measurements every hour.

2.3. Ice-Covered Period

Lake Tovel is surrounded by mountains that greatly limit exposure to sunlight in winter, with no direct sunlight on most of the lake from approximately 20 November to 20 January [*Carli et al*., 1981]. Thus, the lake is usually frozen from the last week of December to the first two weeks of April. Nevertheless, ice-on and ice-off dates are not always easily defined with possible recurring thawing and freezing, especially at the beginning and the end of winter [*Kirillin et al*., 2012]. Here we focused on the period from 1 January to 31 March of 2014, 2015, and 2016, which guaranteed that the lake was completely ice covered. Once ice-on occurs, ice thickness continues to increase as long as the released latent heat can be conducted through the ice to the atmosphere [*Leppäranta*, 2015]; snow cover instead can decrease ice growth due to the low heat conductivity of snow [*Kirillin et al*., 2012]. To further characterize winter climatic conditions, we calculated freezing degree days (FDDs; sum of mean diel air temperature < 0°C) from 15 November to 31 March. Mid-November (air temperature < 2°C) was chosen as the FDD starting date because it ensured capturing the onset of cooling air temperatures. Mean diel air temperature was taken from the on-site meteorological station.

2.4. Metabolic Calculations at a Diel Scale

We assessed under-ice lake metabolism by two FWDO methods with different methodological assumptions, the book keeping (BK) [*Cole et al*., 2000] and the inverse modeling approach (IM) [*Hanson et al*., 2008]. Both approaches provide diel estimates of GPP, R, and NEP. The BK and the IM approaches have their strengths and weaknesses: for example, in contrast to IM, the BK approach has no error term, daytime respiration is assumed to be the same as nighttime respiration, and it incorporates the error in the estimates of metabolic rates; IM relies on temperature and light dependence of respiration and photosynthesis and often requires noise reduction techniques such as smoothing with noisy data [*Batt and Carpenter*, 2012; *Obrador et al*., 2014]. In any case, both methods rely on light data; while for IM continuous light data are necessary as direct input data [*Hanson et al*., 2008], for BK the timing of sunrise and sunset is needed [*Cole et al*., 2000]. Because ice thickness and snow cover reduce under-ice light, the timing of sunrise and sunset are shifted, resulting in a shorter day length under ice; furthermore under ice, days with no light penetration can occur. Therefore, under-ice metabolic calculations based on surface solar radiation would give falsified results. Considering the peculiarities of the under-ice light regime, we performed metabolic calculations only for winter 2016 for which under-ice light measurements were available.

High-frequency DO, light, and temperature data were smoothed by a running average of 4 h. We then calculated the diel DO range as the difference between the maximum DO daytime value and the minimum nighttime DO value and excluded a priori from metabolic calculations those days (i.e., 32 days at 5 m and 48 days at 25 m) with a day/night range smaller than sensor resolution ($<0.02\ mg\ L^{-1}$). The remaining days were grouped according to the presence/absence of under-ice light (59 days at 5 m and 24 days at 25 m with under-ice light and 19 days at 25 m without under-ice light), and we expected different DO patterns for the two categories. For each depth, the days within each category were grouped according to their observed DO temporal pattern by cluster analysis. To apply cluster analysis to diel DO time series, we normalized data, used dynamic time warping as a proximity index, and used average clustering as implemented in package TSclust [*Montero and Vilar*, 2014]. For the "light" category, only clusters of days with an expected DO pattern with respect to light (i.e., a DO maximum during daytime and a DO decrease during nighttime, roughly following the diel under-ice radiation pattern) were considered for metabolic calculations. For the "no-light" category, only clusters of days with an expected steady DO decrease for the 24 h period were considered, assuming $GPP = 0$ in metabolic calculations.

In both BK and IM calculations of metabolism, the fundamental equation governing the change of lake DO concentration at each time step (ΔDO) is based on the balance of NEP and air-water gas flux (F): $\Delta DO = NEP + F$. In this study, F was set to zero because ice cover blocks gas exchange with the atmosphere [*Leppäranta*, 2015]. GPP and R are positive rates, and NEP can be a negative, zero, or positive rate. We excluded days with $GPP < 0$ from data analysis despite these results being algebraically possible in BK.

BK calculations followed procedures in *Cole et al*. [2000] that basically consist of a mass balance of DO separating nighttime and daytime periods. During nighttime, changes in DO ($\Delta DO_{darkness}$) reflect R, whereas during daytime changes in DO reflect the balance between GPP and R [*Cole et al*., 2000]. We calculated $\Delta DO_{darkness}$ for each 30 min interval from midnight to 1 h before sunrise and from 1 h after sunset until midnight [*Hanson et al*., 2003; *Batt and Carpenter*, 2012], and considered only negative $\Delta DO_{darkness}$ to avoid considering DO increases not linked to respiration. Night respiration ($R_{darkness}$) was set as the mean of $\Delta DO_{darkness}$ and was multiplied by the length of daylight to give $R_{daylight}$ (i.e., respiration during the light hours of the day). During daylight, the change of the DO concentration for each time interval ($\Delta DO_{daylight}$) was attributed to respiration and photosynthesis. We calculated $\Delta DO_{daylight}$ for each 30 min interval from 1 h after sunrise to 1 h before sunset [*Hanson et al*., 2003]. We assessed GPP_{day} (mmol DO m^{-3} d^{-1}) as the mean $\Delta DO_{daylight}$ multiplied by daylight duration plus $R_{daylight}$. NEP_{day} (mmol DO m^{-3} d^{-1}) was calculated as GPP_{day} minus R_{day}, where $R_{day} = R_{darkness} \times 24$ (mmol DO m^{-3} d^{-1}).

In IM, NEP was modeled as a function of photosynthesis dependent on light and respiration dependent on temperature (T; °C) [*Hanson et al*., 2008]. Specifically, we modeled photosynthesis as a linear function of light, assuming no light inhibition of photosynthesis under ice. Light data (lux) were transformed into photosynthetically active radiation (PAR; μmol photons m^{-2} s^{-1}) by regressing (type II linear regression) lux against PAR data ($n = 91$; $R^2 = 0.91$; $p < 0.001$) from the meteorological station. The governing equation in IM was: $NEP = \alpha \times PAR - R_4 \times k^{(T-4)}$ where α is photosynthetic efficiency at 4°C, R_4 is the respiration rate at 4°C, and k is the Arrhenius constant of thermal dependence of respiration (set to 1.07) [*Jorgensen and Bendericchio*, 2001]. We assessed respiration at 4°C because this was close to the mean water temperature under ice. We estimated the parameters α and R_4 for every day by linear regression, and inserted these parameters in the above equation to get hourly metabolic rates ($GPP = \alpha \times PAR$; $R = R_4 \times k^{(T-4)}$) for the day considered. Finally, we calculated the mean of these hourly values and multiplied it by 24 to get diel metabolic rates (GPP_{day}, NEP_{day}, R_{day}; mmol DO m^{-3} d^{-1}). We considered diel metabolic rates only when the parameters α and R_4 were statistically significant ($p < 0.05$).

2.5. Depletion Rates at a Seasonal Scale

We estimated the diel under-ice gain or loss of DO by assessing the trend in diel mean DO values. Trends often show critical change points, and neglecting a change point biases time series analysis [*Zeileis et al*., 2003]. Therefore, we first tested for a change point in the variance of the time series and split the time series if any change point was found. We used package changepoint [*Killick et al*., 2016], function cpt.var to get 95% confidence intervals in the change point estimation. We estimated any change point in the raw or detrended data; detrending was done by first order differencing if a trend could be visually suspected. Finally, trend estimation was done by modeling DO data (for each winter there was one or two time series depending on the absence or presence of a change point) as an autoregressive integrated moving average (ARIMA(p,d,q)); p is the number of autoregressive terms, d the degree of differencing, and q is the number of lagged forecast errors. When data are not stationary ($d = 1$), then there is a trend that is also an estimate of the mean of the differenced data [*Hyndman and Athanasopoulos*, 2014]. Stationarity of time series was tested with the Kwiatkowski-Phillips-Schmidt-Shin test. The residuals of the ARIMA model were checked for white noise by plotting autocorrelation functions and performing the Ljung-Box test. In case of heterogeneity of residuals, a higher order of q and p in ARIMA was applied. For ARIMA, we used package forecast [*Hyndman*, 2016], function Arima.

2.6. Water Level Decrease

Water level was measured with a HOBO U20 Water Level Logger U20-001-03 every hour (sensor accuracy was ±0.5–1 cm and resolution was 0.2 cm). Water movement [see *Kirillin et al*., 2012] may influence metabolic rates. Thus for 2016, we assessed (1) if daytime and nighttime mean rates of water level decrease were different by a *t* test and (2) if daytime and nighttime mean rates of water level decrease, respectively, were related to the successful assessment of metabolic rates (i.e., days were coded as "yes" if metabolic rates were obtained and as "no" if no rates were obtained) by a *t* test. The mean rate of water level decrease for daytime and nighttime was calculated at the same intervals as metabolic rates.

All calculations and analyses from 2.4 to 2.6 were done in R 3.3.1 [*R Core Team*, 2016].

3. Results

Freezing degree days (FDDs), air temperature, and precipitation are useful indices to characterize the duration and intensity of cold weather and compare weather patterns among years. FDDs from 15 November to 1 January were lowest in 2015 (50°C days) and almost equal in 2014 (88°C days) and 2016 (78°C days); after the first week of March, FDDs no longer increased (Figure 1). Generally, air temperature decreased from January to February and then increased in March (Figure 1). Total precipitation (rain and snow) from January to March was more than double in 2014 than in 2015 and in 2016 (Figure 1).

Water temperature is a main factor influencing biological and chemical reactions. Water temperature at 5 m increased during all three winters: +0.3°C in 2014, +0.4°C in 2015, and +0.5°C in 2016. While in 2014 and 2015 the increase was gradual, 2016 was characterized by a marked increase from mid-January to the first week of February followed by a decrease and again an increase in the last two weeks of March (Figures 2 and 3). As shown by webcam images, these 2016 increases corresponded to little snow cover and to snow and ice thawing, respectively. Water temperature at 25 m was almost stable in 2014 (increase of 0.02°C in 91 days), but increased in 2015 and 2016 (+0.3 and +0.4°C, respectively; Figures 2 and 3).

Under-ice water movements are an important factor for understanding DO variability. In Lake Tovel, the decline in water level for the period 1 January to 31 March was 1.5 m in 2014, 2.6 m in 2015, and 2.8 m in 2016; water level continuously declined in 2015 and 2016 but increased in 2014 after mid-March (Figure 4).

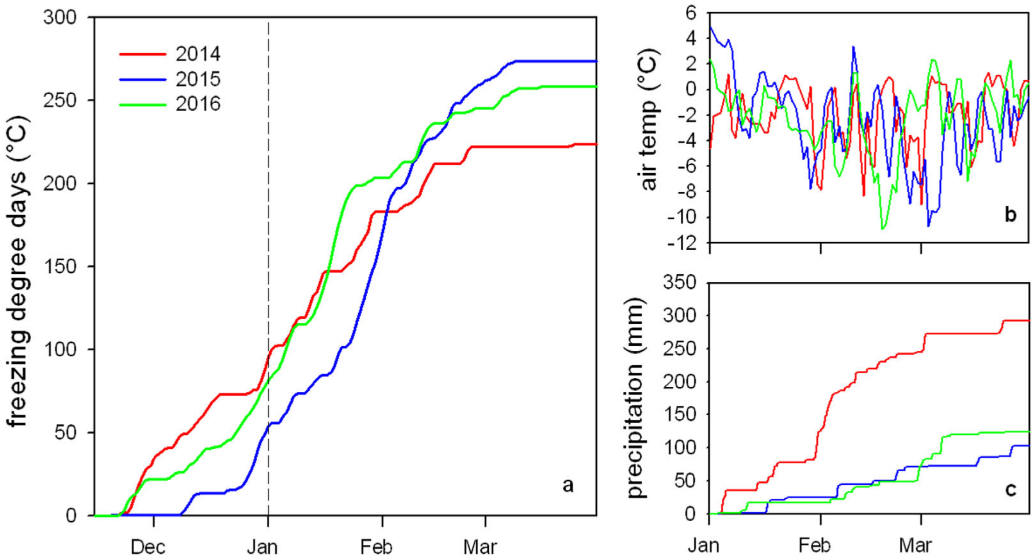

Figure 1. Meteorological parameters: (a) freezing degree days from 15 November of the preceding year to 31 March for under-ice periods 2014, 2015, and 2016; the vertical line indicates 1 January; (b) diel mean air temperature (air temp) and (c) cumulative precipitation (mm) for three winters (1 January to 31 March).

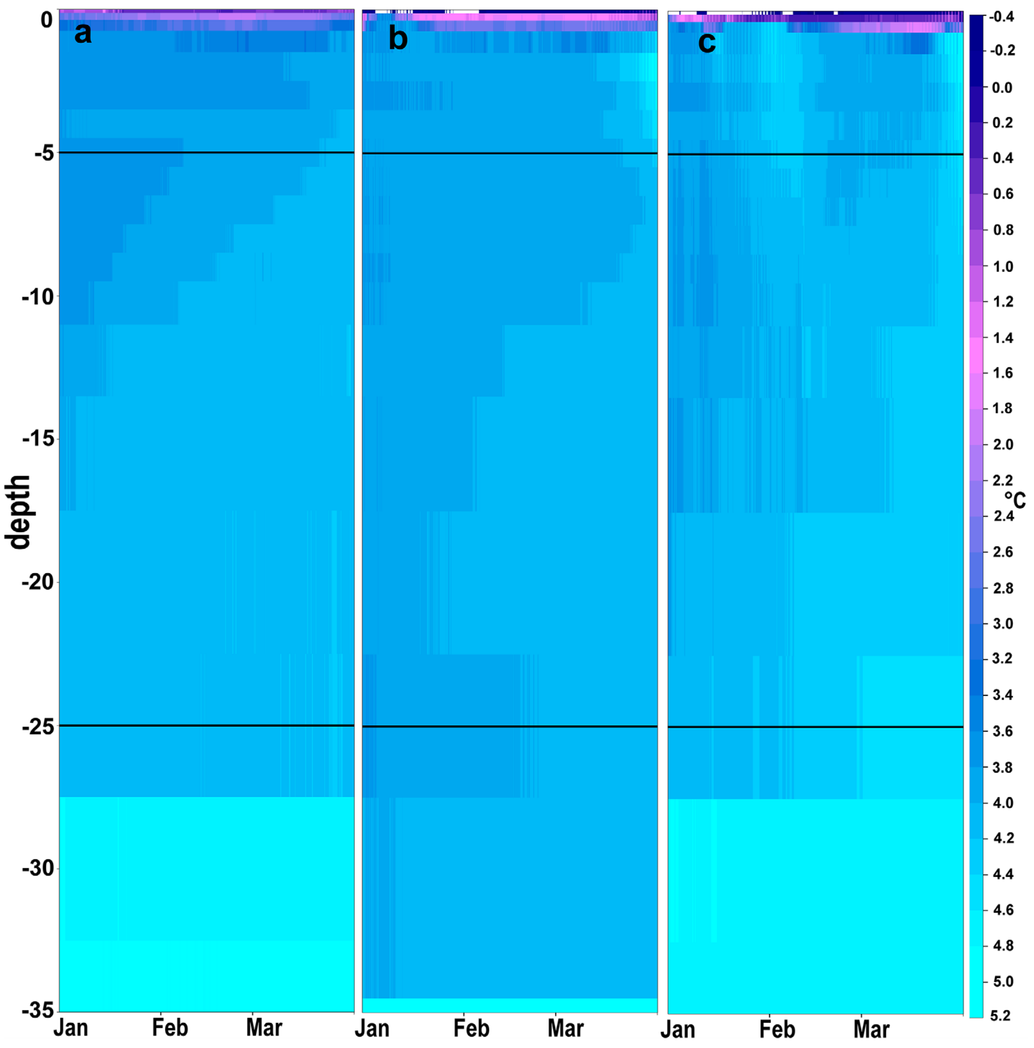

Figure 2. Depth-time contour plots of under-ice water temperature for winters (a) 2014, (b) 2015, and (c) 2016; the black lines indicate the position of the DO sensors at 5 and 25 m depths.

In 2016, the rate of daytime water level decrease (0.15 ± 0.11 cm h^{-1}, mean ± standard deviation) was larger (*t* test; $p < 0.01$) than nighttime decrease (0.11 ± 0.09 cm h^{-1}).

Under-ice light sustains photosynthesis and can be a proxy for penetrating heat radiation, and both light and temperature are important drivers of DO variability. Light data were available only for winter 2016 (Figure 3), and we linked the under-ice light regime to human influence and weather conditions. Specifically, during the first 2 days in January 2016, low PAR at 5 m was likely linked to a heavily scratched ice by ice-skating as shown by webcam images. On 3 January, 2 cm of snow led to almost zero PAR values at 5 m and further access to the lake was blocked by a rockslide on 9 January. After 11 January, PAR at 5 m increased (12 mm rain melted the snow leading to a smooth ice cover) and remained high until the first week of February (Figure 3) when snowfall essentially blocked any light. PAR at 5 m increased again with the second week of March when thawing set in and large water patches appeared on the snow cover as shown by webcam images. PAR at 25 m was approximately 0.1% that of PAR at 5 m and was essentially zero from the first week of February to the second week of March (Figure 3).

DO data must meet certain criteria regarding timing of light and DO variation before applying calculations of lake metabolism. After excluding days with low DO_{5m} variability (i.e., diel variability < sensor resolution; see section 2.4), cluster analysis based on the remaining 59 days with under-ice light allowed discriminating 14 patterns of DO_{5m} diel variations (Figure 5). Only days belonging to clusters 1, 3, 5, 8, 9, and 14 (12 days in January, 5 days in February, and 14 days in March) were considered as having the expected or close-to-

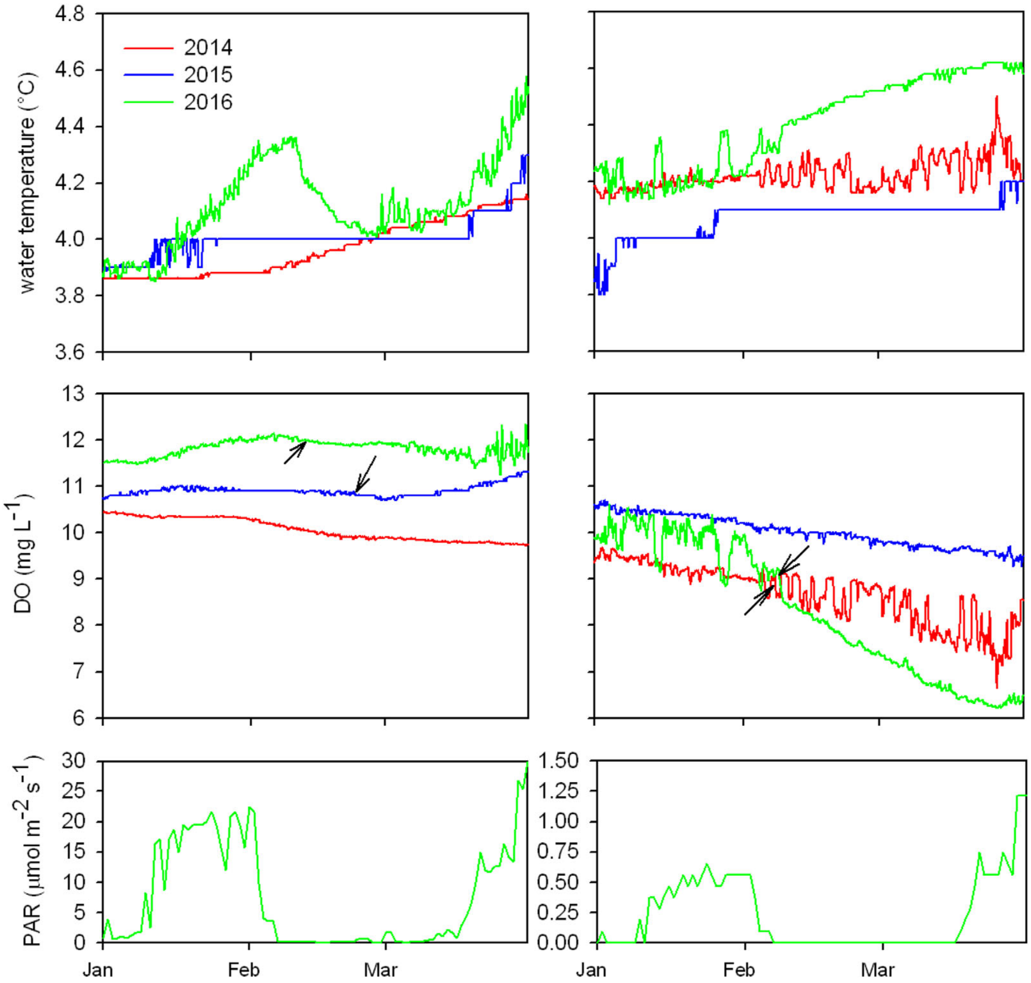

Figure 3. (first row) Under-ice water temperature, (second row) DO concentration, and (third row) maximum diel light intensity at (left column) 5 m and (right column) 25 m; temperature and DO data were available for 2014, 2015, and 2016 while light intensity was available only for 2016 (note different axis scales for 5 and 25 m). Arrows indicate change points in DO variance.

expected patterns overlapping with under-ice light patterns (Figure 5) and were therefore used for metabolic calculations. With the BK estimate of metabolism at 5 m for the 31 days with an expected DO pattern, R was always larger than GPP resulting in a negative NEP (Figure 6). Daytime and nighttime water level decreases were not significantly different (*t* test; $p > 0.05$) between those days with a BK estimate of metabolic rates at 5 m with respect to those without.

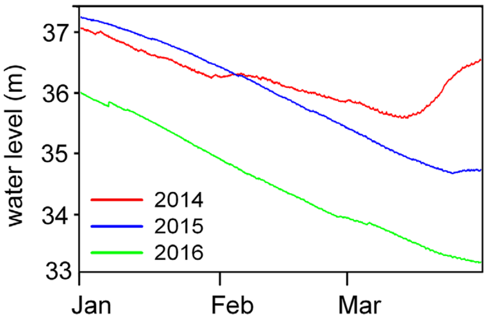

Figure 4. Under-ice water level from 1 January to 31 March for the 3 years considered.

Of the IM estimates of metabolism at 5 m, only 12 of the 31 days had significant parameters for both α and R_4, 8 of which had a negative NEP. When comparing metabolic rates ($n = 12$) estimated by BK and IM, GPP_{BK} was not significantly different from GPP_{IM} (*t* test; $p = 0.14$) while R_{BK} and R_{IM} were different (*t* test; $p = 0.03$), and thus also NEP_{BK} and NEP_{IM} (*t* test; $p = 0.02$). Generally, R_{BK} was greater than R_{IM} and NEP_{BK} was more negative than NEP_{IM}. Both methods gave a negative NEP, except for two cases in January in which IM provided slightly positive NEP values.

More days were excluded at 25 m (48 days) because of their low DO signal than at 5 m (32 days). At 25 m,

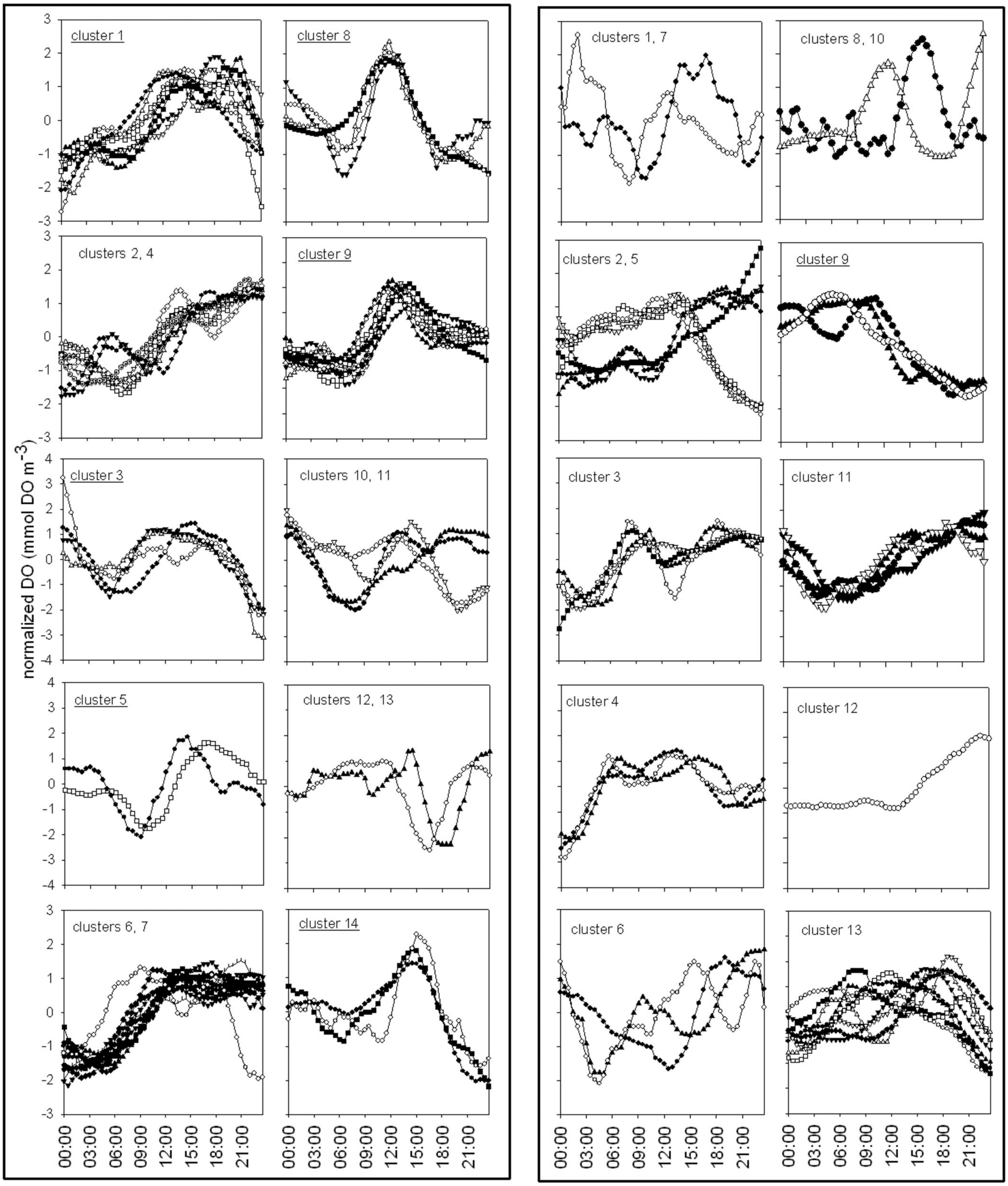

Figure 5. Clusters of diel DO patterns (normalized to zero mean and unit variance) at (left panel) 5 m and (right panel) 25 m; at 5 m all days, excluding those with diel DO variability < sensor resolution, had under-ice light; at 25 m, days in clusters 1–7 belonged to the "light" category, while days in clusters 8–13 belonged to the "no-light" category. With more than one cluster per graph, clusters are separated by filled and empty symbols; clusters considered for metabolic calculations are underlined.

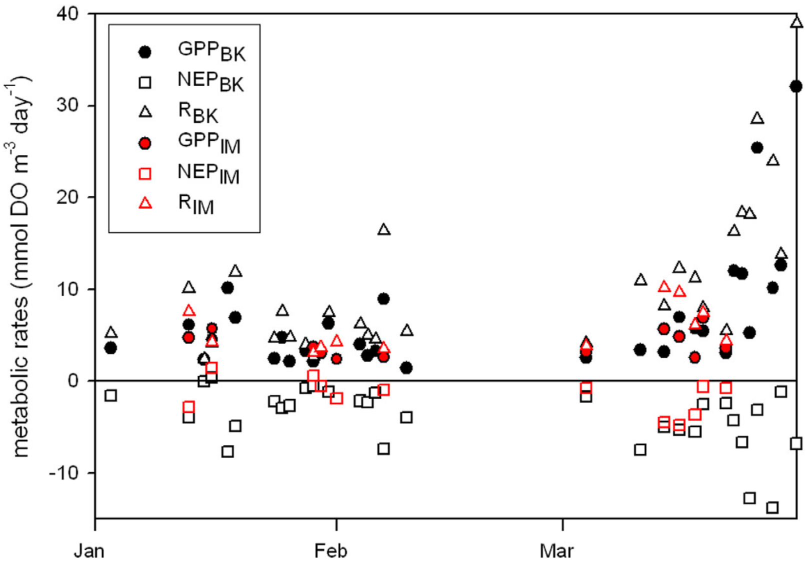

Figure 6. Under-ice metabolic rates at 5 m assessed by BK and IM for the period 1 January to 31 March 2016. Only 31 (BK) and 12 (IM) diel rates are shown (see section 2).

none of the 24 days with under-ice light (i.e., "light" category) showed the expected or close-to-expected DO patterns (Figure 5), and thus no metabolic calculations were applied at this depth. Of the 19 days with zero light under ice (i.e., "no-light" category), only 3 days (5 January, 9 January, and 18 February) showed the expected DO pattern and were used to calculate respiration rates. In BK, by not considering short-lived DO increases, respiration rates were 26.1, 7.8, and 8.9 mmol DO m^{-3} d^{-1}. With IM only two (9 January and 18 February) of the 3 days gave statistically significant respiration rates ($R_{IM} = 0.36$ and 0.77 mmol DO m^{-3} d^{-1}, respectively).

At a seasonal scale, long-term DO patterns characterize net DO concentrations irrespective of diel changes and cannot be linked directly to biological, chemical, and/or physical processes. Diel mean DO_{5m} during 2014 showed a continuous decreasing trend without any change point (–0.22 mmol DO m^{-3} d^{-1}; Figure 3 and Table 1). During 2015, DO_{5m} showed a change in variance on 22 February; DO_{5m} did not change significantly before the change but afterward increased by 0.47 mmol DO m^{-3} d^{-1}. During 2016, DO_{5m} showed a change in variance on 13 February; before the change, DO_{5m} increased by 0.34 mmol DO m^{-3} d^{-1} but afterward did not change significantly. DO_{25m} for 2014 showed a change in variance on 7 February; before the change DO_{25m} decreased by 0.56 mmol DO m^{-3} d^{-1}, and afterward decreased by 0.47 mmol DO m^{-3}

Table 1. Change Point (CP) Test on the Variance of Time Series, Significance of the Kwiatkowski-Phillips-Schmidt-Shin Test (P_{KPSS}) Assessing Stationarity of a Time Series and Slope Estimates of ARIMA Models (See Section 2) for Diel Mean DO Data[a]

DO	Year	CP and Stationarity Test	ARIMA Model	Slope	SE
DO_{5m}	2014	No CP	$ARIMA(1,1,2)_{1Jan\text{-}31Mar}$	−0.22	0.06
		$P_{KPSS} < 0.01$			
	2015	CP on 22 Feb			
		P_{KPSS} 1 Jan to 22 Feb = 0.04	$ARIMA(1,1,2)_{1Jan\text{-}22Feb}$	n.s.	n.s.
		P_{KPSS} 23 Feb to 31 March < 0.01	$ARIMA(0,1,2)_{23Feb\text{-}31March}$	0.47	0.16
	2016	CP on 13 Feb			
		P_{KPSS} 1 Jan to 13 Feb = 0.01	$ARIMA(0,1,1)_{1Jan\text{-}13Feb}$	0.34	0.12
		P_{KPSS} 14 Feb to 31 Mar < 0.01	$ARIMA(0,1,1)_{14Feb\text{-}31March}$	n.s.	n.s.
DO_{25m}	2014	CP on 7 Feb			
		P_{KPSS} 1 Jan to 7 Feb < 0.01	$ARIMA(0,1,1)_{1Jan\text{-}7Feb}$	−0.56	0.12
		P_{KPSS} 8 Feb to 31 Mar < 0.01	$ARIMA(0,1,1)_{8Feb\text{-}31March}$	−0.47	0.62
	2015	No CP	$ARIMA(0,1,1)_{1Jan\text{-}31Mar}$	−0.41	0.06
		$P_{KPSS} < 0.01$			
	2016	CP on 8 Feb			
		P_{KPSS} 1 Jan to 8 Feb < 0.01	$ARIMA(0,1,2)_{1Jan\text{-}8Feb}$	n.s.	n.s.
		P_{KPSS} 9 Feb to 31 Mar < 0.01	$ARIMA(0,1,1)_{9Feb\text{-}31Mar}$	−1.28	0.28

[a] When significant, the slope (mmol DO m^{-3} d^{-1}) and standard error (SE) are shown; non significant estimates of the slope (n.s.).

d^{-1}. During 2015, DO_{25m} did not show a change in variance and continuously decreased by 0.41 mmol DO m^{-3} d^{-1}. During 2016, DO_{25m} showed a change in variance on 8 February; from 1 January to 8 February 2016, DO_{25m} decreased by 0.78 mmol DO m^{-3} d^{-1} and afterward by 1.28 mmol DO m^{-3} d^{-1} (Figure 3 and Table 1).

4. Discussion and Conclusions

The availability of HF data for both DO and light permitted calculating under-ice lake metabolism for winter 2016. To the best of our knowledge, under-ice metabolic rates based on HF data have only been calculated by *Baehr and DeGrandpre* [2004] for a brief period before ice-off in mesotrophic Lake Placid. Here we attempted to provide under-ice metabolic rates at two different depths in an oligotrophic lake for a whole winter period. We applied strict criteria for data management before calculating lake metabolism by excluding days with low DO variability (less than sensor resolution) and days that showed anomalous diel DO patterns that could not be directly linked to biological processes. After excluding these days, where we reasoned that the observed DO pattern was not related to photosynthesis or respiration, some days remained with short-lived episodes of nighttime DO increases. For metabolic calculations, only by excluding these episodes did BK give sensible results, while in IM, days with such a pattern gave model parameters that were not statistically significant. By using two common methods of lake metabolism, we were able to get reliable estimates of lake metabolism only for a few days at either depth, and the number of valid estimates was much higher at 5 m than at 25 m (34% and 3% of days, respectively). Recently, more sophisticated methods have been incorporated into lake metabolism calculations such as Kalman filtering [*Batt and Carpenter*, 2012], Bayesian modeling [*Cremona et al*., 2014; *Staehr et al*., 2016], or methods including chlorophyll *a* and temperature dependency of photosynthesis as model parameters [*McNair et al*., 2015]. However, we strongly doubt that with our data the use of a more sophisticated method would have given better results regarding model fit and applicability. In fact, *McNair et al*. [2015] show that when the basic model fails, more sophisticated approaches also fail to correctly model the observed DO pattern. We suggest that under-ice metabolic calculations require stringent data filtering before applying methods and a prescreening of days with patterns reflecting biological processes to get reliable results.

In Lake Tovel, processes other than biology might have influenced under-ice DO patterns. *Richardson et al*. [2016] point out that in oligotrophic lakes with low metabolic activity (diel DO fluctuations < 1 mg L^{-1}) the greatest challenge in modeling lake metabolism is the difficulty in separating physical from biological processes. Here many clusters of observed DO patterns showed a daytime increase with no under-ice light or a nighttime increase. Considering such DO patterns would have given biased metabolic rates. We excluded changes in sensor position as a contributing factor in these anomalous diel DO dynamics, because the Lake Tovel platform follows water level changes with DO sensors always positioned at 5 and 25 m from the surface. Instead, we suggest that a nighttime DO increase at 5 m might be linked to water movements. Physical mechanisms such as internal waves and density currents can cause mixing in ice-covered lakes [*Bengtsson*, 1996; *Petrov et al*., 2007; *Bouffard et al*., 2016], and thus influence DO patterns. While we do not have direct information on these mechanisms in Lake Tovel, they together with different day/night water level decreases might have influenced DO patterns. We can only speculate about the details of these physical processes that would merit an in-depth analysis. In fact, there is a growing awareness among limnologists that to accurately model metabolic rates, physical processes must be considered [*Hanson et al*., 2008], especially in oligotrophic lakes [*Sadro et al*., 2011; *McNair et al*., 2015; *Richardson et al*., 2016]. Given the data at hand, we suggest that in Lake Tovel physical processes affecting water movements were overwhelming and probably overlapped with lake metabolism at both depths. This reasoning did not nullify our modeling results because we took the necessary steps to prune noisy days and to filter out unsuitable days in our calculations but it implied a cautionary interpretation of our metabolic rates.

BK and IM gave similar GPP_{5m} values, and this congruence indicated that the biological signal was accurately captured by the two methods. However, the different respiration rates estimated by BK and IM indicated that nighttime estimates of respiration were sensitive to methodological approaches. Estimates of NEP_{5m} generally indicated net heterotrophy under ice. The GPP_{5m} and NEP_{5m} values obtained were in the range of those for Lake Placid with late season under-ice DO data at 2 and 20 m [*Baehr and DeGrandpre*, 2004]. Based on NEP_{5m}, a general DO decrease was expected; however, this was not indicated by the seasonal DO pattern (i.e., initial increase in DO followed by a steady state). Under-ice metabolism can fluctuate between net autotrophy and heterotrophy [*Baehr and DeGrandpre*, 2004]. In Lake Tovel, respiration and primary production rates might have changed from day to day, and thus single metabolic rates could hardly be compared to seasonal patterns if no continuous metabolic rates were available. We suggest that in 2016 seasonal DO consumption at 5 m was compensated by photosynthetic activity and/or physical processes leading to the observed DO increase. Algal photosynthetic activity compensates for respiration, but under-ice conditions are considered harsh, and phytoplankton abundances tend to be low with respect to ice-free periods [*Hampton et al.*, 2015, 2017], even though algae adapted to low light conditions and cold temperature can thrive [*Bertilsson et al.*, 2013; *Twiss et al.*, 2012; *Kalinowska and Grabowska*, 2016]. In Lake Tovel, algal biomass is low [*Cellamare et al.*, 2016], and most of the phytoplankton community is composed of mixotrophs (chrysophytes, cryptomonads, and dinoflagellates) and osmotrophs (diatoms) that are adapted to low light and cold temperatures [*Flaim et al.*, 2014; *Cellamare et al.*, 2016]. While under-ice PAR intensity at 5 m was low (mean = 7.4 μmol photons m^{-2} s^{-1}; median = 1.8), these observed low light intensities were within the range that enables photosynthetic activity in algae adapted to deep waters [see *Leukart and Lüning*, 1994; *Gomez et al.*, 1997]. Thus, assuming photosynthetic activity under ice seemed reasonable and probably occurred at a higher rate above a depth of 5 m.

At 25 m, only 3 days were useful for metabolic calculations; all these days had no under-ice light. Thus, only respiration rates were calculated that directly translated into negative NEP_{25m}. Respiration rates estimated by BK were higher than those of IM. In comparison to the 2016 seasonal depletion rate, respiration according to BK was 6–7 times higher while respiration according to IM was very similar. Both FWDO methods and the seasonal method all indicated net heterotrophy and a DO decrease.

In contrast to metabolic rates, seasonal DO depletion rates based on HF data were representative for the whole under-ice period. The observed DO depletion rates were higher at 25 m than at 5 m. Similar results have already been noted [*Puklakov et al.*, 2002; *Terzhevik et al.*, 2009; *Kirillin et al.*, 2012; *Pulkkanen and Salonen*, 2013; *Couture et al.*, 2015; *Deshpande et al.*, 2015] indicating that this is a general pattern. While DO usually shows a rapid decrease after ice-on [*Bertilsson et al.*, 2013], in Lake Tovel DO_{5m} actually increased or remained stable except in 2014 when DO_{5m} showed a small but steady decline. We suggest that in 2014 the continuous DO_{5m} decline was related to no under-ice light caused by ice cover and snow as indicated by webcam images and climatological indices such as FDD and precipitation data. Instead in 2015, less snow cover, possibly enabling photosynthetic activity, might be linked to an almost stable DO_{5m}. However during March 2015, the increase in DO_{5m} could be related to increased light penetration as indicated by webcam images showing the first patches of melting snow on the ice on 9 March. Contrarily to 2014 and 2015, in 2016 DO_{5m} increased and then remained stable. We suggest that also during this first period light penetrated into the water column and possibly led to increased photosynthesis.

The seasonal pattern of DO_{25m} showed a decline during all 3 years, but with different rates: the DO_{25m} depletion rates in 2014 and 2015 were similar, while the DO_{25m} depletion rate in the second part of 2016 was the largest and overlapped with zero light reaching 25 m. We suggest that the different interannual patterns were related to an interaction between DO consumption and physical processes such as water level decline and snow cover and ice thickness influencing the amount of radiation penetrating into the water column. In Lake Tovel, depletion rates both at 5 and 25 m were in the lower range of values reported by several authors (0.01–1 mg DO L^{-1} d^{-1}) [*Kirillin et al.* 2012; *Pulkkanen and Salonen*, 2013; *Deshpande et al.*, 2015]. DOC concentrations have been positively linked to DO depletion rates [*Clilverd et al.*, 2009; *Bertilsson et al.*, 2013; *Couture et al.*, 2015], and the low DOC values in oligotrophic Lake Tovel could be related to the lake's very low DO depletion rates. Concomitantly to these low depletion rates, the seasonal DO pattern under ice showed no anoxia in agreement with monthly profiles showing DO concentrations rarely $<15\%$ saturation, at least until 35 m.

Climate models predict marked decreases in snow cover at mid-altitudes in the Alps [*Gobiet et al.*, 2014]. In the future, dimictic lakes within this altitudinal range could show a higher under-ice transparency with far-reaching effects on DO consumption and production. Here we show that under-ice DO depletion was higher with snow cover than with no snow. Even though ice-cover duration is also decreasing [*Leppäranta*, 2015], earlier ice-out does not necessarily foster longer spring mixing because warming air temperatures generally induce earlier stratification [*Adrian et al.*, 2009], thereby limiting DO repletion in the lower layers.

An understanding of the effects of snow-dependent DO depletion rates requires long-term studies to assess all possible scenarios, and our three winters of under-ice HF data provided a first approximation of interannual variability of under-ice DO depletion rates.

In summary, our study of under-ice DO variability at two different depths outlined problems associated with modeling methods. Lake metabolism calculations, made possible with HF data for DO and light for 2016, underlined the difficulties in modeling biological phenomena in oligotrophic systems with low DO signals without accounting for physical processes. The DO pattern at a seasonal scale, especially using HF data as opposed to discrete sampling events, was complementary to metabolism calculations. Whole-lake metabolism estimates require the deployment of DO sensors at several depths [*Staehr et al*., 2012; *Obrador et al*., 2014; *Giling et al*., 2017]. Our results are representative for the depths investigated and might not apply to the whole water column. However, while more sensors would give a better spatial resolution of DO patterns in Lake Tovel, we are sceptical that more sensors would have given a better estimate of metabolic rates for single days at different depths. A more holistic modeling approach coupled with HF measurements will undoubtedly bring new insights to crucial DO dynamics in ice-covered aquatic systems.

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