

# Differing Winter Oxygen Regimes in Clear and Turbid Shallow Lakes

Joseph S. Rabaey<sup>1</sup>, Kyle D. Zimmer<sup>2</sup>, Leah M. Domine<sup>2</sup>, James B. Cotner<sup>1</sup>

<sup>1</sup> Department of Ecology, Evolution and Behavior, University of Minnesota - Twin Cities, St. Paul, Minnesota <sup>2</sup> Department of Biology, University of St Thomas, St Paul, Minnesota

Corresponding author: Joseph Rabaey ([rabaec005@umn.edu](mailto:rabaec005@umn.edu))

## Key Points:

- Winter oxygen regimes differed between clear and turbid shallow lakes.
- Clear lakes had significantly higher oxygen depletion rates under ice cover.
- Oxygen depletion rates were highly correlated with summer macrophyte biomass.

## Abstract

Dissolved oxygen controls important processes in lakes, from chemical reactions to organism community structure and metabolism. In shallow lakes, small volumes allow for large fluctuations in dissolved oxygen concentrations, and the oxygen regime can greatly affect ecosystem-scale processes. We used high frequency dissolved oxygen measurements to examine differences in oxygen regimes between two alternative stable states that occur in shallow lakes. We compared annual oxygen regimes in four macrophyte-dominated, clear state lakes to four phytoplankton-dominated, turbid state lakes by quantifying oxygen concentrations, anoxia frequency, and measures of whole-lake metabolism. Oxygen regimes were not significantly different between lake states throughout the year except for during the winter under-ice period. During winter, clear lakes had less oxygen, higher frequency of anoxic periods, and higher oxygen depletion rates. Oxygen depletion rates correlated positively with peak summer macrophyte biomass. Due to lower levels of oxygen, clear shallow lakes may experience anoxia more often and for longer duration during the winter, increasing the likelihood of experiencing fish winterkill. These observations have important implications for shallow lake management, which typically focuses efforts on maintaining the clearwater state.

## Plain Language Summary

In lakes, the amount of oxygen dissolved in the water has a profound impact on lake processes, from chemical reactions to the kinds and quantities organisms present. In shallow lakes, the amount of dissolved oxygen can vary greatly due to the differences in the rates of production, mostly through photosynthesis, and consumption, mostly through respiration. In this study, we compared patterns of dissolved oxygen availability seasonally between two common states found in shallow lakes; a turbid, low clarity state dominated by phytoplankton, and a clear state dominated by submersed aquatic plants. We used dissolved oxygen measurements to compare oxygen patterns between shallow lakes in these two states throughout the year. Patterns of oxygen were similar between the two lake states in all seasons except winter. During the winter under-ice period, clear lakes had significantly less oxygen compared to turbid lakes, and lost oxygen at a faster rate through the winter. The lower levels of oxygen in clear lakes during the winter could affect many lake processes, such as the winterkill of fish. Management of shallow lakes often tries to maintain lakes in the clear state because of better water quality and wildlife diversity, and these results can help inform management strategies.

## 1 Introduction

Dissolved oxygen in lake waters controls multiple physical and biological processes. Anoxia, or the absence of oxygen, can affect organism habitat as well as chemical and biological processes in lakes. Low oxygen concentrations can lead to fish kills (Greenbank, 1945), with effects on fish community composition (Tonn & Magnuson, 1982) and trophic levels and the food web structure of lakes (Carpenter et al., 2001). Anoxia also influences rates of chemical and biological processes such as decomposition rates and nutrient cycling (Burdige, 2007), due in part to the inhibition of aerobic metabolism and a shift to anaerobic metabolism (such as sulfate reduction, denitrification, and methanogenesis). Anaerobic metabolism can also release toxic compounds, such as methane and hydrogen sulfide, into the water column, further affecting aquatic organisms. Oxygen depletion can occur due to nutrient enrichment coupled with increased primary production, limited mixing, and degraded water quality (Gelda & Auer, 1996), as is commonly observed in hypoxic/anoxic marine waters near river plumes (Li et al., 2002;

Turner & Rabalais, 1994; Van Der Zwaan & Jorissen, 1991). While physical drivers such as mixing, atmospheric exposure, and temperature can drive oxygen concentrations in lakes, biological drivers such as oxygenic photosynthesis and aerobic respiration become particularly important in the most productive ecosystems. Hence, understanding oxygen regimes in lakes is important to predict ecosystem health and biological processes.

Oxygen regimes in large deep lakes have been well studied, and models of oxygen consumption as a function of physical characteristics, nutrients, and productivity have accurately predicted oxygen depletion in large lakes (Charlton, 1980; Jackson & Lasenby, 1982; Stefan & Fang, 1994). Shallow lakes have been more difficult to accurately predict oxygen depletion, possibly due to the dynamic nature of shallow lakes, which are sensitive to environmental change (Stefan & Fang, 1994). With small volumes, shallow lakes respond quickly to nutrient inputs, as well as temperature and precipitation change (Gerten & Adrian, 2000; Schindler et al., 1996). Many shallow lakes experience occasional or frequent anoxia during the summer when stratification and production are high (Papst et al. 1980), and during the winter when oxygen is depleted under ice cover (Baird et al., 1987; Meding & Jackson 2003). Small, shallow lakes have a large global surface area with an estimated 1.8 million km<sup>2</sup> total area for lakes smaller than 1 km<sup>2</sup>, compared to 2.4 million km<sup>2</sup> for lakes larger than 1 km<sup>2</sup> (Downing et al., 2006), though the number of shallow lakes could be even greater than previously estimated (Cael et al., 2017). This high global abundance combined with their high rates of primary production (Laas et al., 2012) and potential for high rates of carbon burial (Cole et al., 2007; Tranvik et al., 2009), makes shallow lakes important in freshwater carbon cycling. Dissolved oxygen can affect both production and carbon burial rates in shallow lakes (Hobbs et al., 2013; Sobek et al., 2009), and thus understanding and predicting oxygen dynamics in shallow lakes is important for global carbon cycling.

Shallow lake community structure can exhibit two distinct alternative stable states, dominated by two different primary producers. The clear-water state is characterized by high abundance of submersed macrophytes, with low turbidity and low phytoplankton abundance. The turbid-water state is phytoplankton dominated with high turbidity and a low abundance of or absent macrophytes (Scheffer et al., 1993; Scheffer & Jeppesen 2007). Lake state can be influenced by various drivers, including nutrient load, temperature, and morphological features (Scheffer & Van Nes 2007). Lake states can have large community-scale differences, including food web components and wildlife use (Hanson & Butler, 1990, 1994). Despite differences in community structure, ecosystem-scale processes have not been differentiated between clear and turbid lake states, including ecosystem metabolism rates and carbon burial (Zimmer et al., 2016). Distinguishing differences, if any, in ecosystem-scale processes is important, as future impacts of climate change and eutrophication are expected to drive more shallow lakes to the turbid state (Hargeby et al., 2004), while many shallow lakes are actively managed for the clear state (Hanson & Butler, 1994).

With oxygen levels driving many ecosystem-scale processes, differences in the oxygen regimes of clear and turbid shallow lakes could result in fundamental differences between lake states. Several studies have examined oxygen depletion in shallow lakes (Barica & Mathias, 1979; Malve et al., 2005; Mathias & Barica, 1980; Papst et al., 1980), but few have compared differences between clear and turbid-state lakes (Meding & Jackson, 2003), with none comparing responses over multiple years. Algal blooms, turbidity, and stratification can all affect oxygen depletion and anoxia, and may lead to differing oxygen dynamics between clear and turbid lake

states. With shallow lakes shifting between clear and turbid states often (Zimmer et al., 2009), differences in oxygen depletion could have profound effects on carbon fluxes and production.

In the present study, we used high frequency oxygen measurements to compared oxygen regimes throughout the year in clear and turbid shallow lakes in the Prairie Pothole Region of central North America. We quantified oxygen regimes using measurements of oxygen concentration, frequency of anoxia, and oxygen depletion rate under ice cover. We then compared oxygen regimes with potential drivers, including nutrient loads, morphological features, and ecosystem metabolism. We hypothesized that turbid lakes would experience lower oxygen and more anoxia in the summer months, while clear lakes would experience more anoxia in the winter, due to more biomass degradation.

**Table 1.**

*Watershed Characteristics and Water Chemistry of Individual Study Lakes*

| Lake       | State<br>(C / T) | Area<br>(ha) | Volume<br>(m <sup>3</sup> ) | Max Depth<br>(m) | Mean TP<br>(µg/l) | Mean Chl<br>a (µg/l) | Mean DOC<br>(mg/l) |
|------------|------------------|--------------|-----------------------------|------------------|-------------------|----------------------|--------------------|
| Pisa       | C                | 11.3         | 111540                      | 1.6              | 51.88             | 10.3                 | 15.9               |
| Org        | C                | 3.61         | 73530.3                     | 3.8              | 75.12             | 29.6                 | 14.6               |
| Blakesly   | C                | 4.99         | 49027.1                     | 1.8              | 56.04             | 15.9                 | 14.3               |
| Skunk      | C                | 11.2         | 91200.9                     | 1.4              | 27.69             | 6.00                 | 14.7               |
| Bellevue   | T                | 9.18         | 236524                      | 3.0              | 108.03            | 56.7                 | 14.7               |
| Morrison   | T                | 15.1         | 344359                      | 3.2              | 142.52            | 67.6                 | 15.1               |
| Murk       | T                | 15.2         | 295509                      | 2.4              | 120.76            | 70.9                 | 17.6               |
| Mavis west | T                | 15.5         | 430951                      | 4.4              | 126.66            | 48.4                 | 12.8               |

Note. Phosphorus, chlorophyll, and dissolved organic carbon measurements represent an average of measurements taken throughout the year.

## 2 Materials and Methods

### 2.1 Site Description

The eight study lakes are all located in west-central Minnesota, in the southeastern portion of the Prairie Pothole Region, a 715,000 km<sup>2</sup> area of central North America characterized by thousands of shallow lakes (Euliss Jr. et al., 1999; Waiser & Robarts, 2004; Zimmer et al., 2009). The lakes were dispersed across a 3570 km<sup>2</sup> area centered at 45.859°N and 95.858°W. Lakes were categorized as “clear lakes” that were in a clear-water state for all years of data collection, and “turbid lakes” that were in a turbid-water state for all years of data collection (Table 1). Lakes were classified as turbid or clear using the approach of Zimmer et al. (2009), with k-means cluster analysis of chlorophyll a and macrophyte biomass used to categorize each lake in one state or the other. There were no significant differences among the lake groups for either lake surface area or maximum depth, however, mean depth and lake volume were greater in turbid lakes (Table 2).

## 2.2 Field Measurements

Water chemistry (total phosphorus, total nitrogen, dissolved organic and inorganic carbon, chl *a*) was sampled throughout the year for each lake from February 2010 to April 2013. Estimates for each lake were obtained by averaging all values (Table 1). Macrophytes were sampled in the summer of 2010 and 2011. Macrophyte abundance was determined by sampling plants at 15 stations in each lake by dragging a rake across 3 m of lake bottom and weighing plant biomass collected on the rake. Plant biomass was averaged across the 15 stations and used as a CPUE (catch per unit effort) index of macrophyte abundance.

**Table 2.**

*Summary of Watershed Characteristics and Water Chemistry Measurements for Clear and Turbid Lakes*

| Variable  | Clear Lakes Mean (sd) | Turbid Lakes Mean (sd) | P-Value (significance at $\alpha = 0.05$ ) |
|---|-----------------------|------------------------|--|
| Winter O <sub>2</sub> Exponential Decay Rate (g m <sup>-3</sup> d <sup>-1</sup> ) | 0.117 (0.0402)        | 0.0147 (0.00695)       | 0.0133*                                    |
| Winter O <sub>2</sub> Level (mg/l)  | 3.09 (1.77)           | 6.83 (2.63)            | 0.0624                                     |
| Winter Anoxia Frequency (%)   | 61.8 (22.7)           | 21.5 (18.1)            | 0.0340*                                    |
| Surface Area (ha)   | 7.76 (4.03)           | 13.8 (3.05)            | 0.0584                                     |
| Volume (m <sup>3</sup> )  | 81,300 (26,500)       | 327,000 (82,000)       | 0.00637*                                   |
| Mean Depth (m)  | 1.21 (0.559)          | 2.19 (0.450)           | 0.0354*                                    |
| Max Depth (m)   | 2.15 (1.11)           | 3.25 (0.839)           | 0.169                                      |
| TP (µg/l)   | 52.7 (19.5)           | 124 (14.3)             | 0.00138*                                   |
| Chl <i>a</i> (µg/l)   | 15.5 (10.2)           | 60.9 (10.3)            | <0.001*                                    |
| DOC (mg/l)  | 14.9 (0.704)          | 15.1 (1.97)            | 0.876                                      |
| TN (mg/l)   | 1.52 (0.267)          | 2.46 (0.500)           | 0.0239*                                    |
| Macrophyte Biomass (CPUE)   | 0.994 (0.834)         | 0 (0)                  | 0.0344*                                    |

Note. Means were calculated from individual lake averages. Winter oxygen measurements were averaged for individual lakes across all winters with available data, and then averaged between lake states.

Dissolved oxygen (DO) measurements were taken in each lake over the course of four winters from 2009-2010 to 2012-2013. DO and water temperature were sampled at 1 – 4 h intervals with a multiprobe sonde (Hydrolab Datasonde or Minisonde). The sondes were deployed at the center of each lake within the mixed layer (0.5m depth). There were not enough sondes to continuously monitor every lake simultaneously, so they were serviced (cleaned and re-calibrated) and rotated among lakes approximately every 3 weeks, though field conditions led to some longer or shorter periods. This rotation, as well periods of failure by DO sensors, led to an average of two winters of reliable oxygen data for each lake, on average. The DO sensors were calibrated using air saturated water, and site-specific atmospheric pressure prior to deployment.

## 2.3 Oxygen Level and Anoxia Frequency Calculations

For both clear and turbid lakes ( $n = 4$  for each state), oxygen concentrations ( $\text{mg O}_2 \text{ L}^{-1}$ ), saturation levels, and anoxia frequencies were averaged for each season across the three years of data collection. Seasons were defined in three-month periods; December – February defined as winter, March – May as spring, June – August as summer, and September – November as fall. Average oxygen levels were estimated with near- continuous measurement of water column DO throughout the year. Conditions were considered anoxic when oxygen levels fell below  $1 \text{ mg O}_2 \text{ L}^{-1}$ . Though the geochemical definition of anoxia is  $0 \text{ mg O}_2 \text{ L}^{-1}$ , many processes that require oxygen shift to anaerobic metabolism below approximately  $1 \text{ mg O}_2 \text{ L}^{-1}$  (Greenbank, 1945; Nürnberg, 1995). In addition, the threshold for many fish species tolerance can be as high as  $4 \text{ mg O}_2 \text{ L}^{-1}$  (Greenbank, 1945). Frequencies of anoxia were calculated as the percentage of all measurements that fell below the  $1 \text{ mg O}_2 \text{ L}^{-1}$  threshold.

## 2.4 Ecosystem Metabolism

Ecosystem metabolism was calculated as in Zimmer (2016), and metabolism data for the summers of 2010 and 2011 were previously reported in that study. Changes in DO reflect changes in ER (ecosystem respiration), GPP (gross primary production), NAP (net aquatic production), and atmospheric exchange (Cole et al., 2000; Coloso et al., 2008; Odum, 1956; Van de Bogert et al., 2007). The net aquatic production (NAP) term is used instead of NEP to acknowledge that primary production by emergent macrophytes is not represented by changes in water column DO (Hagerthey et al., 2010). Metabolism equations described in Van de Bogert et al. (2007) and Coloso et al. (2008) were used to calculate NAP, GPP, and ER in the 8 study lakes. Changes in oxygen from 1 h past sunset to 1 h before sunrise qualified as nighttime ER, which was assumed equivalent to daytime ER (Cole et al., 2000; Coloso et al., 2008), therefore the mean hourly ER rate was multiplied by 24 to estimate daily ER ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). GPP was estimated by subtracting the mean hourly ER rate from the mean hourly rate of change in oxygen during the daylight hours, and that difference was multiplied by total daylight hours to quantify daily GPP ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). Daily NAP was calculated as  $\text{GPP} - \text{ER}$  ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ; Van de Bogert et al. 2007).

Changes in oxygen concentrations due to diffusion between the lake and atmosphere were calculated and removed as non-biologically mediated changes. The diffusion of oxygen either into or out of the lake was estimated as the gas piston velocity ( $K$ ) multiplied by the difference between the concentration of DO in the water at equilibrium with the atmosphere and the actual DO concentration in the water (Coloso et al., 2008).  $K$  was calculated based on equations presented in Cole and Caraco (1998), and took into account the Schmidt number for oxygen (and therefore water temperature, [Wanninkhof 1992]) and the effect of wind speed using the wind power relationship (Jähne et al., 1987). Hourly wind speed data were obtained from a local weather station (Wahpeton ND, 43–104 km from the study sites; North Dakota Agricultural Weather Network database). Days with impossible metabolism values, such as negative GPP values and positive ER values, were deleted from the data set. Areal metabolism rates ( $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) were estimated by multiplying volumetric rates by the mixing depth. Mixing depths were estimated from temperature profiles taken at the beginning and end of each deployment, and were defined as the depth where less than a  $1^\circ\text{C}$  change occurred over 0.5 m (or for lakes less than 2 m deep a  $0.5^\circ\text{C}$  change over 0.25 m (Coloso et al., 2011)). Daily metabolism

values were averaged for each lake for a seasonal comparison between lake states.

## 2.5 Winter Oxygen Depletion

Winter oxygen decay rates were calculated with a single exponential decay model ( $O_2 = A^{-kt}$ ; where  $O_2$  is the dissolved oxygen concentration,  $A$  is the initial  $[O_2]$  at ice-on,  $e$  is the base of the natural logarithm,  $k$  is the decay rate, and  $t$  is time), which was deemed the most appropriate for shallow lakes (Meding & Jackson, 2001, 2003) (Figure 3). Model fits were evaluated and compared with simple linear models (Babin & Prepas, 1985) by visual examination of the residuals and by using Akaike's information criterion (AIC) (Akaike, 1981). For all but one lake, the exponential decay mode fit had a lower AIC than the simple linear model (Table 3), and in this case the exponential decay model was still chosen for analysis to maintain consistency. The models began with time-0 at the highest oxygen level subsequent to ice-on. To correct for atmospheric oxygen inputs during the initial period after freezing, as well as brief periods of freeze and thaw, data points were removed from this time point consecutively until a model was able to be fit. Once a model was fit data were no longer removed. The number of points removed using this method ranged from no points up to a week of data in some situations. Once a model was fit, the  $k$  value (decay rate,  $g\ m^{-3}\ d^{-1}$ ) was averaged and compared for each lake state. For all statistical tests and comparisons between lake states, lake means were used, giving eight total replicates and four per lake state.

## 3 Results

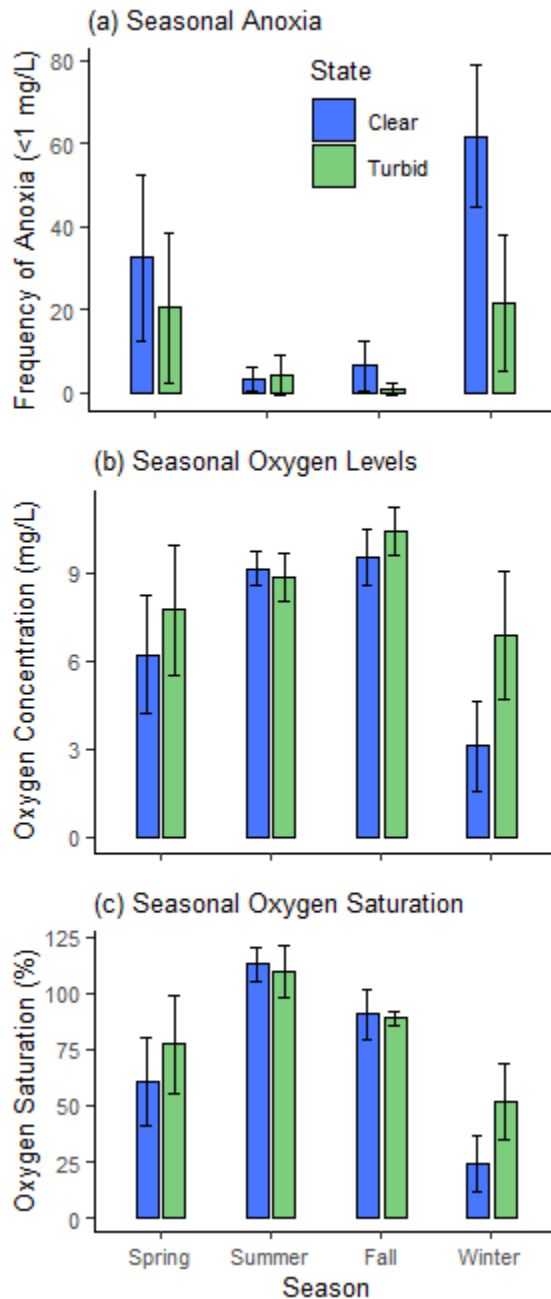
### 3.1 Oxygen Levels in Clear and Turbid Lakes

Both clear and turbid shallow lakes exhibited similar oxygen concentrations and saturation levels throughout the summer and fall (Figure 1). There were slight differences between clear and turbid lakes in the spring, but the largest differences occurred in the winter, with clear lakes having lower oxygen concentrations than turbid lakes (Figure 1), though not statistically significant at the  $\alpha = 0.05$  level ( $p = 0.0624$ , Table 2). Differences in oxygen saturation levels in the winter and spring mirrored the differences in oxygen concentrations between the two lake types, confirming that this was not a function of temperature differences between clear and turbid lakes.

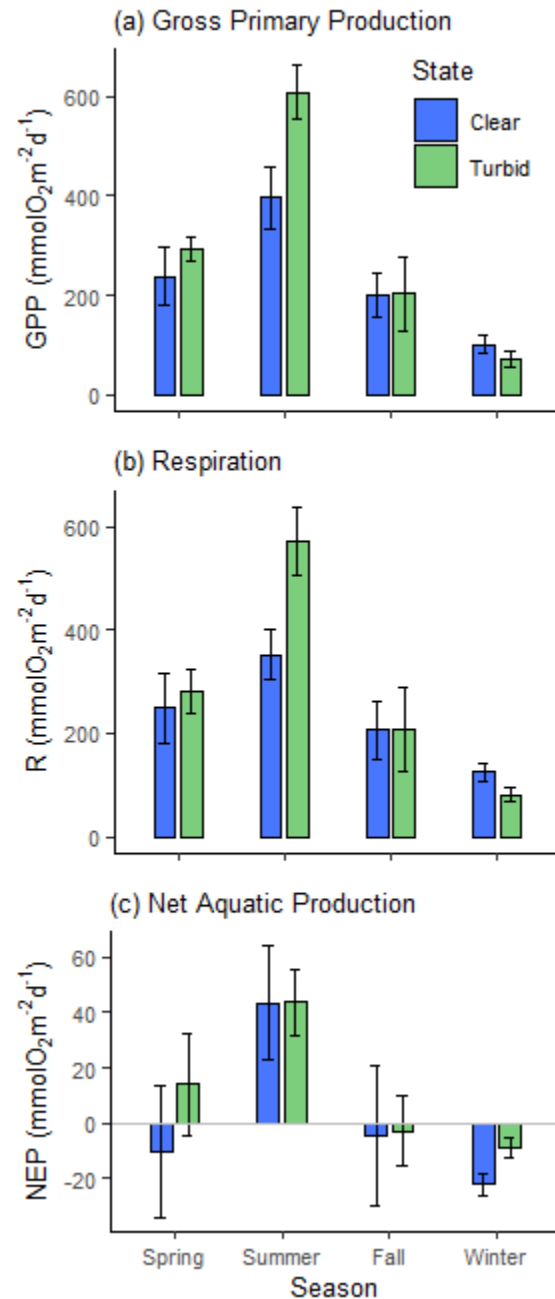
Both clear and turbid lakes showed very low frequencies of anoxia in the summer and fall (Figure 1). With all the lakes having depths less than 5 m, stratification was not strong enough to develop persistent anoxic conditions without ice present, though brief periods of stratification did occur in the summer months. In winter, clear lakes showed significantly higher frequency of anoxia compared to turbid lakes, experiencing anoxic conditions almost three times as often as turbid lakes (62% vs. 22%) ( $p = 0.0340$ , Table 2). In the spring, clear lakes also showed a higher frequency of anoxia, though the difference was not as pronounced (Figure 1) most likely due to the fact that ice out typically occurred in late March or early April.

### 3.2 Metabolism Rates

All lakes exhibited expected trends in metabolism throughout the year, with the highest rates of ER and GPP in the summer, and lowest in the winter (Figure 2). Clear and turbid lakes had similar rates of ER and GPP in the spring and fall, while turbid lakes had significantly higher rates of ER and GPP in the summer ( $p = 0.0396$ , and  $p = 0.0437$ , respectively). Clear lakes had slightly higher rates of ER and GPP in the winter. Despite the large differences of ER and GPP



**Figure 1.** Seasonal comparisons of anoxia frequency (a), oxygen levels (b), and oxygen saturation (c), for clear and turbid lakes. Error bars indicate  $\pm 1$  SE.



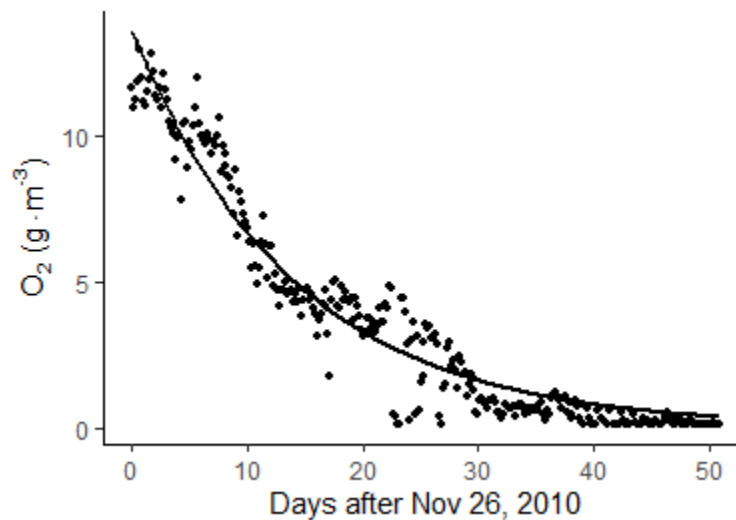
**Figure 2.** Seasonal comparisons of ecosystem respiration (a), gross primary production (b), and net ecosystem production (c), for clear and turbid lakes. Error bars indicate  $\pm 1$  SE.



between clear and turbid lakes in the summer months, NAP was almost identical between the two groups. NAP was only significantly different between clear and turbid lakes during the winter, where clear lakes had an average daily rate over twice as negative as turbid lakes ( $-22 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$  vs.  $-9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ,  $p = 0.0421$ ).

### 3.3 Winter Oxygen Depletion Rates

Exponential decay models were fit for all lakes, for every year of complete winter data (e.g. Figure 3). For most lakes most years, points were removed at the beginning of the ice cover period due to inconsistent freezing and inputs of oxygen from freeze out of gases (Meding & Jackson, 2001). Average rates for all lakes ranged from  $0.00134 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$  to  $0.196 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$  (Table 3). Overall, clear lakes ( $0.117 \text{ g m}^{-3} \text{ d}^{-1}$ ) showed significantly higher oxygen depletion



**Figure 3.** Oxygen depletion curve example from Pisa lake in the winter of 2010 – 2011. Solid line represents the exponential decay model predicted curve. November 26<sup>th</sup> was the start of oxygen decline in the lake.

rates compared to turbid lakes ( $0.0147 \text{ g m}^{-3} \text{ d}^{-1}$ ) ( $p = 0.0133$ , Table 2).

**Table 3.**

*Oxygen depletion rates and model AIC comparison for the eight study lakes.*

| Lake     | State (C/T) | Winter Year | $k$ (exponential decay rate $\text{g m}^{-3} \text{ d}^{-1}$ ) | Exponential Model AIC | Linear Model AIC |
|----------|-------------|-------------|--|-----------------------|------------------|
| Pisa     | C           | 2010 – 2011 | 0.167  | 930.3                 | 963.4            |
| Org      | C           | 2009 – 2010 | 0.196  | 453.8                 | 549.2            |
| Org      | C           | 2010 – 2011 | 0.0715   | 856.0                 | 1344.6           |
| Org      | C           | 2012 – 2013 | 0.0312   | 1193.9                | 1153.6           |
| Blakesly | C           | 2010 – 2011 | 0.0732   | 910.6                 | 1225.4           |
| Skunk    | C           | 2010 – 2011 | 0.164  | 645.6                 | 653.4            |
| Skunk    | C           | 2012 – 2013 | 0.0926   | 1200.2                | 1571.5           |
| Bellevue | T           | 2009 – 2010 | 0.00134  | 717.2                 | 719.8            |

|            |   |             |         |        |        |
|------------|---|-------------|---------|--------|--------|
| Bellevue   | T | 2010 – 2011 | 0.0333  | 1280.4 | 1984.7 |
| Morrison   | T | 2011 – 2012 | 0.0215  | 1005.7 | 1009.8 |
| Murk       | T | 2009 – 2010 | 0.0115  | 437.5  | 501.9  |
| Murk       | T | 2010 – 2011 | 0.0184  | 901.3  | 1151.8 |
| Mavis West | T | 2009 – 2010 | 0.0059  | 128.2  | 214.7  |
| Mavis West | T | 2012 – 2013 | 0.00427 | 1236.4 | 1241.8 |

### 3.4 Correlations Between Watershed Characteristics, Water Chemistry, and Winter Oxygen Dynamics

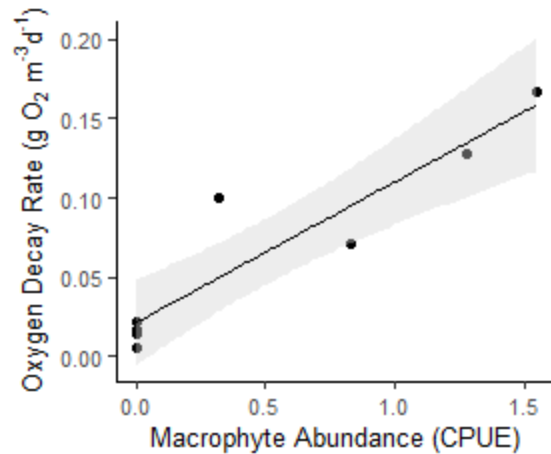
Turbid lakes had significantly higher concentrations of total phosphorus (TP) and chl *a* than clear lakes ( $p = <0.001$  for TP,  $p = 0.00138$  for chl *a*, Table 2). Turbid lakes also had significantly higher concentrations of total nitrogen (TN) ( $p = 0.0239$ , Table 2), likely due to higher rates of denitrification in clear lakes, as well as uptake of nitrogen by macrophytes (Ginger et al., 2017). Dissolved organic carbon (DOC) was not significantly different between clear and turbid lakes ( $p = 0.876$ , Table 2). Clear lakes had significantly higher macrophyte abundance ( $p = 0.0344$ , Table 2), with no macrophyte biomass observed in any of the turbid lakes.

Summer macrophyte abundance correlated highly with oxygen decay rates in winter (Table 4), and explained 87% of the variability in oxygen decay rate in a linear regression across all lakes (Figure 4). Total phosphorus and chl *a* were highly correlated, and both correlated negatively with summer macrophyte abundance. Total phosphorus and chl *a* both correlated negatively with oxygen decay rate, however neither related as strongly as decay rate did with macrophyte biomass. Among oxygen measures, decay rate correlated more highly with anoxia frequency than with winter oxygen concentration (Table 4).

**Table 4.**  
*Pearson Correlation Matrix for Lake Characteristics, Water Chemistry, and Winter Oxygen Dynamics*

|  | Area   | Volume  | Depth   | TP      | Chl <i>a</i> | DOC   | TN      | Macro   | Decay rate | Winter O2 | Anoxia |
|--|--------|---------|---------|---------|--------------|-------|---------|---------|------------|-----------|--------|
| Area (ha)  | 1      |         |         |         |              |       |         |         |            |           |        |
| Volume (m <sup>3</sup> )                               | 0.82*  | 1       |         |         |              |       |         |         |            |           |        |
| Max Depth (m)  | 0.135  | 0.629   | 1       |         |              |       |         |         |            |           |        |
| Mean TP (µg/l)   | 0.575  | 0.887*  | 0.704   | 1       |              |       |         |         |            |           |        |
| Mean Chl <i>a</i> (µg/l)                               | 0.542  | 0.798*  | 0.56    | 0.951*  | 1            |       |         |         |            |           |        |
| Mean DOC (mg/l)  | 0.208  | -0.106  | -0.476  | 0.032   | 0.253        | 1     |         |         |            |           |        |
| Mean TN (mg/l)   | 0.431  | 0.595   | 0.35    | 0.79*   | 0.938*       | 0.483 | 1       |         |            |           |        |
| Macrophyte Biomass (CPUE)                              | -0.28  | -0.718* | -0.776* | -0.896* | -0.906*      | 0.073 | -0.819* | 1       |            |           |        |
| Oxygen Decay Rate (g m <sup>-3</sup> d <sup>-1</sup> ) | -0.324 | -0.737* | -0.652  | -0.851* | -0.833*      | 0.14  | -0.713* | 0.921*  | 1          |           |        |
| Winter Oxygen Concentration (mg/l)                     | 0.397  | 0.689   | 0.607   | 0.802*  | 0.725*       | -0.25 | 0.575   | -0.768* | -0.696     | 1         |        |
| Winter Anoxia Frequency (%)                            | -0.283 | -0.705  | -0.769* | -0.839* | -0.773*      | 0.341 | -0.618  | 0.898*  | 0.814*     | -0.947*   | 1      |

Note. \* Indicates significance at the 0.05  $\alpha$  level.



**Figure 4.** Regression analysis of summer macrophyte abundance and the winter oxygen decay rate for all study lakes ( $p = 0.00078$ ,  $R^2 = 0.867$ )

## 4 Discussion

### 4.1 Differences in Oxygen Regime

Clear and turbid lakes had similar oxygen regimes throughout much of the summer. This was somewhat unexpected, as the turbid lakes had much higher nutrient concentrations and chlorophyll levels (Table 1) and the relationship between eutrophication, algal bloom collapse, and anoxia is well established (Anderson et al., 2002; Hutchinson, 1957; Nürnberg, 1995). However, in clear lakes, most of the nutrients are tied up in macrophyte biomass, and would not be represented by water column nutrient concentrations. In addition, it was expected that the turbid lakes may have stronger stratification due to higher light extinction coefficients (Heiskanen et al., 2015; Jones et al., 2005), which again could lead to longer periods of anoxia in the summer. While shallow eutrophic prairie lakes can often have periods of oxygen depletion during the summer (summerkill) (Papst et al., 1980), turbid lakes only experienced slightly more anoxia than clear lakes in the summer months (Figure 1). All of the study lakes experienced frequent surface mixing, likely due to the strong and frequent winds in this prairie study region (Coburn, 2019). This likely helped keep much of the water column oxygenated throughout the summer, even if short term stratification occurred.

The largest difference in oxygen regimes between clear and turbid lakes was evident during the winter under-ice period. It is well known that shallow lakes often experience oxygen depletion and anoxia during the winter (Babin & Prepas, 1985; Baird et al., 1987; Barica & Mathias, 1979; Nürnberg, 1995). Both clear and turbid lakes experienced significant drawdown of oxygen concentrations during the winter months, with clear lakes having lower overall concentrations.

## 4.2 Ecosystem Metabolism

Studies of summer lake metabolism of the same lakes used in this study found no significant difference in metabolism during June - August between clear and turbid states (Zimmer et al., 2016), while the present study found significantly higher GPP and ER during the summer in turbid lakes. These differing results are likely due to two more years of data added in this study (2010 -2013 in this study, 2010-2011 in the previous study), as well as a different analysis design (previous study used averages on a yearly basis and a two-way ANOVA). Though the turbid lakes had higher GPP and ER during the summer, NAP was not significantly different and almost identical during the summer and fall. NAP was only significantly different between clear and turbid lakes during the winter, where clear lakes had a larger negative NAP than turbid lakes. This corresponds to the lower winter oxygen levels and higher oxygen depletion rates in clear lakes, as higher rates of respiration compared to production (or a more negative NAP) would lead to more oxygen drawdown.

## 4.3 Oxygen Depletion Models

Winter oxygen depletion rates calculated using an exponential decay model (Meding & Jackson, 2001) were nearly eight times higher in clear lakes compared to turbid lakes (Table 2,  $p = 0.0133$ ). Oxygen depletion rate models have commonly been used for shallow lakes, though models for predicting oxygen depletion have largely relied on lake morphological characteristics, such as depth and volume (Babin & Prepas, 1985; Barica, 1984; Mathias & Barica, 1980). While oxygen depletion rate did correlate negatively with lake volume and mean depth in these study lakes, the highest correlation among predictors for oxygen depletion rate was macrophyte abundance in the summer (Table 4). This corresponded to a significantly higher average oxygen depletion rate in clear lakes compared to that of turbid lakes, which all had no recorded macrophyte biomass (Table 2). This finding is in agreement with a study by Meding and Jackson (2003), which to our knowledge is the only other study of this kind measuring macrophyte biomass as a predictor of oxygen depletion rates in shallow lakes. They did not find a significant difference between clear and turbid lakes, but the turbid lakes they measured had higher levels of macrophytes compared to the study lakes in our work, which had none. Macrophytes represent the primary source of organic matter in clear-state shallow lakes, which often have macrophyte growth throughout nearly the entire water column. Oxygen decay rates depend on organic matter available for degradation (Greenbank, 1945; Jackson & Lasenby, 1982; Lasenby, 1975; Mathias & Barica, 1980), therefore making total macrophyte biomass an important predictor of oxygen decay.

Macrophytes have slower decomposition rates compared to phytoplankton (Enríquez et al., 1993; Twilley et al., 1986; Wang et al., 2018), and decomposition extending further into the ice-on period of winter may result in the much larger oxygen decay rate observed in clear lakes. If large amounts of phytoplankton biomass in turbid lakes decomposed before the ice-on period, oxygen consumption may slow down during the winter compared to clear lakes. This agrees with the respiration rate differences between clear and turbid lakes, as turbid lakes had higher respiration rates in all seasons except winter, suggesting higher rates of decomposition under the ice in clear, macrophyte dominated lakes.

## 4.4 Consequences of anoxia and implications for management

Shallow lakes around the globe are often managed for the clear-water state (Hosper, 1997; Qin et al., 2007; Zimmer et al., 2009), due to many ecosystem services including wildlife and fish habitat, improved water quality, and greater appeal for recreational use (Moss et al., 1996). Flipping shallow lakes from a turbid to clear state can often prove more difficult than simply removing nutrients or inducing a trophic cascade. Internal loading of phosphorus can be high in shallow lakes, due to frequent resuspension of sediment and occasional periods of anoxia (Welch & Cooke, 1995). The relationship between anoxia and internal loading of phosphorus is well known (Welch & Perkins, 1979), and greater frequency of anoxia during the winter in clear-state shallow lakes could lead to higher rates of internal loading in these systems and may be an important driver that causes lakes to switch from the clear to the turbid state. Turbid lakes that are managed for a clear state can often flip back to the turbid state a few years after intervention (Theissen et al., 2012), even after nutrient inputs are reduced. Internal loading during winters in the clear-state could contribute to the difficulties of keeping shallow lakes in the clear-state long term.

Fish populations can also have profound effects on the state of shallow lakes. Planktivorous fish in shallow lakes can release phytoplankton from zooplankton consumption, and removal of these fish can lead to less phytoplankton and bring the lake to a clear state (Hanson & Butler, 1994). In addition, benthivorous fish can resuspend sediment and detritus, not only increasing the turbidity but also resuspending nutrients and increasing rates of internal loading, driving shallow lakes into the turbid state (Meijer et al., 1990). Historically, many shallow lakes were fishless, especially in the prairie pothole region containing the lakes in this study (McLean et al., 2016). Rising water levels, fish stocking, ditching, and accidental introductions have led to the presence of fish in many shallow lakes in the prairie pothole region (Herwig et al., 2010). One factor that may have played a role in maintaining fishless lakes is the higher frequency of anoxia in clear lakes during the winter. Many fish species cannot survive conditions with oxygen levels below 3-5 mg/l, and sustained periods of anoxia can result in fish kills (Greenbank, 1945), though some fish are more adapted to low oxygen conditions than others (Magnuson et al., 1985). Our data suggest that clear-state shallow lakes experience much higher frequencies of anoxia during the winter, with 60% of oxygen measurements below 1 mg/l O<sub>2</sub>, compared to 20% in turbid-state lakes (Figure 1), potentially leading to higher rates of winterkill in clear-state shallow lakes. This could contribute to a positive feedback loop where higher frequency of anoxia due to macrophytes decomposition in winter induces winterkill of fish, which stabilizes high macrophyte abundance and additional winterkill, as fish often induce shifts to turbid states (Zimmer et al., 2009).

#### 4.5 Conclusions

Our results indicate differing oxygen regimes during the winter in clear and turbid shallow lakes. Clear lakes showed lower winter oxygen concentrations, higher frequency of anoxia, and higher oxygen depletion rates. With the importance of oxygen in many ecological and physical processes, clear and turbid lake states may experience many differences in functioning during the winter under-ice period. This has important implications for shallow lake management. Land-use changes, rising water levels, and rising temperatures will impact shallow lake ecosystems in the future, and it is important to continue to understand how differences in biotic and geochemical feedbacks interact with lake state.

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Data availability statement: Data will be made available in the Data Repository for University of Minnesota (DRUM) repository.

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