

## Winter Oxygen Regimes in Clear and Turbid Shallow Lakes

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### Key Points:

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

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## 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. Winter 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 fish winterkills. 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 varieties and quantities of 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 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. Patterns of oxygen were similar between the two lakes 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. Lake managers typically try to maintain shallow lakes in the clear state because of better water quality and increased wildlife diversity. Winter fish kills could help maintain lakes in the clear state, but may also select for rough fish that can drive shifts to the turbid state.

## 1 Introduction

Dissolved oxygen levels in lake water control multiple physical and biological processes. Anoxia is defined as the absence of oxygen, though waters are often considered anoxic when oxygen concentrations fall below  $1 \text{ g m}^{-3}$  (Nürnberg, 1995). Anoxia can directly impact aquatic organisms as well as exert control over important chemical reactions. Low oxygen concentrations can lead to fish kills (Greenbank, 1945), with effects on fish community composition (Tonn & Magnuson, 1982) and the food web structure of lakes (Brothers et al., 2014; Carpenter et al., 2001). Anoxia also influences rates of decomposition 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 some aquatic organisms. Oxygen depletion can occur due to the decomposition of excess organic matter, such as that provided from nutrient enrichment coupled

with increased primary production (Gelda & Auer, 1996). This phenomenon is commonly observed in hypoxic/anoxic marine waters near river plumes (Li et al., 2002; Turner & Rabalais, 1994; Van Der Zwaan & Jorissen, 1991). Oxygen depletion is also common in the hypolimnion of stratified lakes, where oxygen exchange is cut off from the surface water and the atmosphere (Foley et. al., 2012; Steinsberger et. al., 2020). While physical drivers such as mixing, atmospheric exchange, 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, productivity, and the mineralization rates of organic matter have accurately predicted oxygen depletion in large lakes (Charlton, 1980; Knoll et al., 2018; Müller et. al., 2012; Steinsberger et al., 2020). 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). Shallow lakes often have a maximum depth of less than 5m, which contributes to rapid mixing events of the whole water column during high wind speed conditions or sharp temperature changes (Meerhoff & Jeppesen, 2009), as well as sediment respiration impacting the entire water column (Baxa et al., 2020). With small volumes, shallow lakes respond quickly to nutrient inputs, as well as temperature and precipitation change (Gerten & Adrian, 2000; Golosov et. al., 2012; Schindler et al., 1996). Many shallow lakes experience occasional or frequent anoxia during the summer when stratification is strong and production is high (Foley et al., 2012; 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 and respiration (Laas et al., 2012) and potential for high rates of carbon burial (Cole et. al., 2007; Tranvik et al., 2009; Zimmer et al., 2016), makes shallow lakes important in freshwater carbon cycling. Dissolved oxygen can affect the rate of both carbon respiration and carbon burial in shallow lakes, as hypoxic and anoxic conditions can lead to more efficient carbon burial (Hobbs et al., 2013; Sobek et al., 2009). Thus, oxygen dynamics in shallow lakes are important to our understanding of the global carbon cycle.

Oxygen regimes in shallow lakes may be influenced by alternative states. The alternative stable state theory in shallow lakes states that vegetation can stabilize water clarity up to relatively high nutrient loadings, but when nutrient inputs reach a certain threshold phytoplankton growth can shade out plants and abruptly reduce water clarity. It then take a larger reduction of nutrients to improve water clarity again and enable recolonization of vegetation (Scheffer et. al., 1993). Therefore, shallow lakes exist in two different stable states defined by water clarity. 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 or absent macrophyte abundance (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 been little differentiated between clear and turbid lake states, including ecosystem metabolism rates and rates of carbon burial in the sediments (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, dissolved nutrients, primary producer biomass, and stratification patterns can all affect oxygen depletion and subsequently anoxia frequency, 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 compare 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.

## 2 Materials and Methods

### 2.1 Site Description

The eight study lakes were 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 carbon, chl *a*) was sampled throughout the year for each lake from February 2010 to April 2013. Surface samples for water chemistry were taken monthly at two different locations on each lake. Yearly averages

for each lake were obtained by averaging across measurements (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 (kg) was averaged across the 15 stations and used as a CPUE (catch per unit effort) index of macrophyte abundance. Lakes typically froze over during the third week in November, and experienced ice-out during the third week of April. During the ice cover period, ice and snow characteristics were measured. Snow depth, ice thickness, and light penetration through the ice and snow were sampled at five sites on each lake, twice during most winters.

Dissolved oxygen (DO) measurements were taken in each lake over the course of four years from the winter of 2009-2010 through the winter of 2012-2013. DO and water temperature were sampled with a multiprobe sonde (Hydrolab Datasonde or Minisonde) at 1 hr intervals during April through mid-October, and at 4 hr intervals from mid-October through March. 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 (the specific number of days each lake was monitored in each season can be found in tables S1 and S2 in the supporting information). This rotation led to oxygen and metabolism data for each season in each lake over the entire sampling period. 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 ( $\text{g O}_2 \text{ m}^{-3}$ ), 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  $1 \text{ g O}_2 \text{ m}^{-3}$ . Though the geochemical definition of anoxia is  $0 \text{ g O}_2 \text{ m}^{-3}$ , many processes that require oxygen shift to anaerobic metabolism below approximately  $1 \text{ g O}_2 \text{ m}^{-3}$  (Greenbank, 1945; Nürnberg, 1995). In addition, the threshold for many fish species tolerance can be as high as  $4 \text{ g O}_2 \text{ m}^{-3}$  (Greenbank, 1945). Frequencies of anoxia were calculated as the percentage of all measurements that fell below the  $1 \text{ g O}_2 \text{ m}^{-3}$  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 R (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 R in the 8 study lakes. Changes in

oxygen ( $\Delta O_2$ ) from 1 h past sunset to 1 h before sunrise qualified as nighttime R (after accounting for non-biologically mediated changes in oxygen, which is discussed in the next paragraph), which was assumed equivalent to daytime R (Cole et al., 2000; Coloso et al., 2008), therefore the mean hourly R rate was multiplied by 24 to estimate daily R ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). Since daytime R can likely be greater than nighttime R due to higher temperatures (Pace and Prairie 2005), daily rates of R (and therefore GPP) may be underestimated. However, NAP rates would not be affected by this assumption (Cole et al. 2000). GPP was estimated by adding the mean hourly R rate (as a positive rate) to the mean hourly rate of change in oxygen during the daylight hours, and that rate 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  $\text{GPP} - \text{R}$  ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ; Van de Bogert et al. 2007).

$$\Delta O_{2(\text{night})} = \text{R} + \text{D} \quad (1)$$

$$\Delta O_{2(\text{day})} = \text{GPP} - \text{R} + \text{D} \quad (2)$$

$$\text{NAP} = \text{GPP} - \text{R} \quad (3)$$

$$\text{D} = k_{O_2}(\text{DO}_{\text{sat}} - \text{DO}) \quad (4)$$

$$k_{600} = 2.07 + 0.215 * U_{10}^{1.7} \quad (5)$$

$$k_{O_2} = k_{600} * (\text{Schmidt}/600)^{-0.5} \quad (6)$$

$$\text{Schmidt} = (1800.6 - 120.10 * t + 3.7818 * t^2 - 0.047608 * t^3) \quad (7)$$

$$U_{10\text{m}} = U_{1\text{m}} * (10/U_{1\text{m}})^{0.143} \quad (8)$$

Changes in oxygen concentrations due to diffusion between the lake and atmosphere (non-biologically mediated changes) were subtracted from the changes in hourly oxygen content used to estimate biological metabolism. This diffusive flux was only calculated for ice-free days, as ice prevents diffusive exchange with the atmosphere. The diffusion of oxygen either into or out of the lake (D) was estimated as the gas piston velocity for oxygen ( $k_{O_2}$ ) multiplied by the difference between the concentration of DO in the water at equilibrium with the atmosphere ( $\text{DO}_{\text{sat}}$ ) and the actual DO concentration in the water (DO) (Coloso et al., 2008).  $k_{O_2}$  was calculated based on  $k_{600}$  defined 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). Wind speed at a height of 10m ( $U_{10}$ ) was scaled using measurements of wind speed 1m above the water surface ( $U_{1\text{m}}$ ) (Arya, 1988). 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, <http://ndawn.ndsu.nodak.edu>). Since the wind readings were taken at a different elevation than the surface of the study lakes, we made a general correction to the weather station wind speed measurements by comparing to wind speed measurements 1 m above one study lake (Mavis West). Weather station wind readings were compared to midsummer lake readings for 216 consecutive hours, and the weather station readings were approximately 1.32 ( $\pm 0.02$  SE) times higher than the readings above the lake. The corrected wind speed measurements were used in estimating lake metabolism. Wind speed correction minimally affected summer metabolism estimates (-2 to 7%) from two lakes with different sheltering in a relatively open versus protected



area (Morrison and Blakesly).

Days with impossible metabolism values, such as negative GPP values and positive R values, were typically caused by noise in the diel oxygen pattern and were deleted from the data set. Impossible values comprised approximately 7% of the daily estimates for spring, summer and fall seasons, and 25% of the winter data.

To estimate areal metabolism rates ( $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), volumetric rates were multiplied by the mixing depth. Mixing depths were estimated from temperature profiles taken during the ice-free period of the year. Temperature profiles were taken every 2-3 weeks during the spring and summer, once during fall before ice-over occurred, and once before the lakes thawed in the spring. Profiles were taken at the center of the lake near where the sondes were deployed for high frequency oxygen measurements. A few times throughout the study profiles done were at five different locations on a single sampling date to assess the representativeness of center profiles for the whole lake, and profiles taken within each lake on the same date were nearly identical to each other. Mixing depth during the ice-free periods was calculated as the depth with a temperature gradient of  $2^\circ\text{C m}^{-1}$  (Coloso, et. al., 2011). Although profiles were taken during the ice-covered periods, the mixing depth in the winter was assumed to be the entire water column as most profiles revealed an inverse stratification pattern, with close to  $1^\circ\text{C}$  under the ice to approximately  $2$  to  $3^\circ\text{C}$  near the sediment. Mixing depths were assigned to metabolism data collected between mixing profiles by assuming a linear change in mixing depth between dates mixing profiles were measured. Areal daily metabolism values were averaged for each lake for a seasonal comparison between lake states.

## 2.5 Winter Oxygen Depletion

A single exponential decay model was fitted to the observed winter oxygen data to calculate winter oxygen depletion rates ( $\text{O}_2 = Ae^{-kt}$ ; where  $\text{O}_2$  is the dissolved oxygen concentration,  $A$  is the initial  $[\text{O}_2]$  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 model choice for shallow lakes (Meding & Jackson, 2001, 2003). Model fits were evaluated and compared with simple linear models (Babin & Prepas, 1985) by visual examination of the residuals and by using root mean square error (RMSE, the standard deviation of the residuals), with smaller RMSE values indicating a better fit. Model quality was also compared between the exponential decay and the simple linear models using Akaike's information criterion (AIC) (Akaike, 1981). For all but one winter on one lake, the exponential decay mode fit had a lower RMSE and AIC than the simple linear model (Org 2012 – 2013, Table 4), and in this case the exponential decay model was still chosen for analysis to maintain consistency. The models began with time-0 at the start of oxygen concentration decline 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 the time of ice-on until oxygen concentrations began to decline. 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 (depletion rate,  $\text{g m}^{-3} \text{ d}^{-1}$ ) 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. Unequal variance t-tests were used for all comparisons between lake states, including water chemistry and metabolism data.

### 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 3). 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 5m, 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 3). In the spring, clear lakes also showed a higher frequency of anoxia ( $p = 0.155$ ), though the difference was not as pronounced (Figure 1) most likely due to the fact that ice out typically occurred during the third week in April.

#### 3.2 Metabolism Rates

All lakes exhibited expected trends in metabolism throughout the year, with the highest rates of R and GPP in the summer, and lowest in the winter (Figure 2). Clear and turbid lakes had similar rates of R and GPP in the spring and fall, while turbid lakes had significantly higher rates of R and GPP in the summer ( $p = 0.0396$ , and  $p = 0.0437$ , respectively). Clear lakes had slightly higher rates of R and GPP in the winter. Despite the large differences of R and GPP 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, when rates in clear and turbid lakes were negative and clear lakes had an average daily rate over two times less than 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 (Figure 3). For all lakes, points were removed at the beginning of the ice cover period due to inconsistent freezing and inputs of oxygen from freeze out of gases, until oxygen concentrations began to decline (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 4). Overall, clear lakes ( $0.117 \text{ g m}^{-3} \text{ d}^{-1}$ ) showed significantly higher oxygen depletion rates compared to turbid lakes ( $0.0147 \text{ g m}^{-3} \text{ d}^{-1}$ ) ( $p = 0.0133$ , Table 3).



### 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 winter oxygen depletion rates, and explained 85% of the variability in oxygen depletion rate across all lakes ( $r^2$  of the correlation in Table 5). 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 winter oxygen depletion rate, however neither related as strongly as depletion rate did with macrophyte biomass (Table 5).

## 4 Discussion

Both clear and turbid lakes had similar oxygen regimes and metabolism trends throughout most of the year. While both lake states had similar rates of GPP, R, and NAP, the main difference between clear and turbid states was where the biomass was stored, in macrophytes in clear lakes and in algae in turbid lakes. This difference had the largest impact during the winter, as macrophyte biomass was not completely degraded at the onset of ice cover, which led to higher degradation rates under the ice. The results of this study highlight key differences in the winter oxygen regime between clear and turbid shallow lakes, with clear lakes having lower oxygen concentrations, more frequent anoxia, and higher oxygen depletion rates.

### 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, which would not be represented by water column nutrient concentrations. In addition, it was expected that the turbid lakes may have had stronger stratification due to higher light extinction coefficients (Heiskanen et al., 2015; Jones et al., 2005), which can cause increased heat absorption in the surface water layer and increase the stability of the water column, again leading to longer periods of anoxia in the summer (Foley et al., 2012). The turbid lakes were also on average deeper (Table 2), which could contribute to more prolonged stratification. While shallow eutrophic prairie lakes can often have periods of oxygen depletion during the summer (summerkill) (Papst et al., 1980), the turbid lakes in this study only experienced slightly more anoxia than clear lakes in the summer months, with no significant difference between clear and turbid lakes (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 in both clear and turbid lakes, 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), and both clear and turbid lakes experienced significant drawdown of oxygen concentrations during the winter months, with clear lakes having lower overall concentrations. While ice and snow characteristics can affect under-ice photosynthesis and subsequently winter oxygen levels (Song et al., 2019), ice and snow depth were not significantly different between lake states (Table 3). In addition, light penetration under the ice was almost identical between lake states and chlorophyll levels were not significantly different, even with turbid lakes having significantly higher chlorophyll levels the rest of the year (Table 3). GPP was also similar between lake states during the winter (Figure 2), supporting that the differences in winter oxygen levels between clear and turbid were not driven by elevated under-ice photosynthesis in turbid lakes.

#### 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 R 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 R during the summer, NAP was not significantly different and almost identical during the summer and fall (Figure 2). NAP was only significantly different between clear and turbid lakes during the winter, where clear lakes had a more negative NAP than turbid lakes. This corresponds with 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, volume, and sediment area:volume ratio. (Babin & Prepas, 1985; Barica, 1984; Mathias & Barica, 1980; Meding & Jackson, 2003). While oxygen depletion rate did correlate negatively with lake volume, mean depth, and sediment area:volume ratio in these study lakes, the highest correlation among predictors for oxygen depletion rate was macrophyte abundance in the summer (Table 5). This corresponded to a significantly higher average oxygen depletion rate in clear lakes compared to that of turbid lakes, none of which had any 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 our study lakes. Macrophytes represent the primary source of organic matter in clear-state shallow lakes, which have macrophyte growth throughout the entire water column in these systems. 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. In addition to organic matter decomposition, nitrification can be an important contributor to winter oxygen depletion (Powers et al., 2017). While we did not measure nitrate concentrations in this study, measures of ammonium were slightly higher in clear lakes during the winter compared to turbid lakes, though not significantly different (Table 3). If degrading macrophytes in clear lakes during the winter do contribute to elevated ammonium concentrations, higher nitrification rates could be one of the factors leading to increased oxygen depletion rates.

#### 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), though sediment characteristics and type and quantity of sediment phosphorus can also influence internal loading (Hupfer & Lewandowski, 2008). If oxygen is a major regulator of internal loading in these lakes, a 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 and in the clear-state, 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 g m<sup>-3</sup>, 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 g m<sup>-3</sup> 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 in clear lakes, where macrophyte decomposition in winter induces winterkill of fish due to more anoxic periods. Fish kill then stabilizes high water clarity, macrophyte abundance, and additional winterkill, as fish often decrease water clarity and 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 had 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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**Table 1.**

*Watershed Characteristics and Water Chemistry of Individual Study Lakes*

| Lake          | State<br>(C / T) | Surface<br>Area<br>(ha) | Volume<br>(m <sup>3</sup> ) | Max Depth<br>(m) | Mean TP (mg m <sup>-3</sup> ) | Mean Chl <i>a</i><br>(mg m <sup>-3</sup> ) | Mean<br>DOC (g<br>m <sup>-3</sup> ) |
|---------------|------------------|-------------------------|-----------------------------|------------------|-------------------------------|--|-------------------------------------|
| Pisa          | C                | 11.3                    | 111540                      | 1.6              | 51.9 (14.6 – 151)             | 10.3 (1.52 – 40.3)                         | 15.9 (9.15 – 27.5)                  |
| Org           | C                | 3.61                    | 73530.3                     | 3.8              | 75.1 (46.3 – 97.4)            | 29.6 (7.08 – 78.8)                         | 14.6 (11.1 – 18.2)                  |
| Blakesly      | C                | 4.99                    | 49027.1                     | 1.8              | 56.0 (22.1 – 160)             | 15.9 (1.01 – 58.4)                         | 14.3 (9.79 – 28.3)                  |
| Skunk         | C                | 11.2                    | 91200.9                     | 1.4              | 27.7 (11.0 – 86.1)            | 6.00 (0.640 – 30.0)                        | 14.9 (9.34 – 28.5)                  |
| Bellevue      | T                | 9.18                    | 236524                      | 3.0              | 108 (68.5 – 139)              | 56.7 (16.5 – 160)                          | 15.0 (11.1 – 19.6)                  |
| Morrison      | T                | 15.1                    | 344359                      | 3.2              | 143 (83.7 – 228)              | 67.6 (6.45 – 164)                          | 15.1 (12.2 – 19.7)                  |
| Murk          | T                | 15.2                    | 295509                      | 2.4              | 121 (77.4 – 229)              | 70.9 (13.4 – 202)                          | 17.6 (13.2 – 23.2)                  |
| Mavis<br>West | T                | 15.5                    | 430951                      | 4.4              | 127 (75.3 – 178)              | 48.4 (5.00 – 101)                          | 12.8 (9.35 – 20.1)                  |

Note. Total phosphorus (TP), chlorophyll *a* (Chl *a*), and dissolved organic carbon (DOC) are means of measurements measured monthly throughout the year, parentheses show range.

**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 $\alpha = 0.05$ ) |
|---|-----------------------|------------------------|--|
| 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*                                   |
| Sediment Area:Volume Ratio (m <sup>-1</sup> ) | 0.936 (0.312)         | 0.472 (0.0916)         | 0.0537                                     |
| 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 (mg m <sup>-3</sup> )                      | 52.7 (19.5)           | 124 (14.3)             | 0.00138*                                   |
| Chl <i>a</i> (mg m <sup>-3</sup> )            | 15.5 (10.2)           | 60.9 (10.3)            | <0.001*                                    |
| DOC (g m <sup>-3</sup> )                      | 14.9 (0.704)          | 15.1 (1.97)            | 0.876                                      |
| TN (g m <sup>-3</sup> )                       | 1.52 (0.267)          | 2.46 (0.500)           | 0.0239*                                    |
| Summer Macrophyte Biomass (CPUE)              | 0.994 (0.834)         | 0 (0)                  | 0.0344*                                    |

Note. Total phosphorus (TP), chlorophyll *a* (Chl *a*), dissolved organic carbon (DOC), and total nitrogen (TN) means are whole-year averages calculated from individual lake averages. Macrophyte biomass was measured as kg collected in a rake throw, or catch per unit effort (CPUE).

**Table 3.**

*Winter Characteristics and Winter Oxygen Regimes 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> Depletion 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> Concentration (g m <sup>-3</sup> )                  | 3.09 (1.77)           | 6.83 (2.63)            | 0.0624                                     |
| Winter Anoxia Frequency (%)   | 61.8 (22.7)           | 21.5 (18.1)            | 0.0340*                                    |
| Average Snow Depth (cm)   | 5.15 (1.08)           | 6.71 (0.743)           | 0.0610                                     |
| Average Ice Thickness (cm)  | 50.3 (1.76)           | 49.6 (2.00)            | 0.631                                      |
| Light Penetration Under Ice (%)   | 8.55 (1.85)           | 8.46 (0.816)           | 0.932                                      |
| Winter Chl <i>a</i> (mg m <sup>-3</sup> )                                 | 26.0 (15.2)           | 49.0 (13.5)            | 0.0649                                     |
| Winter NH <sub>4</sub> (g m <sup>-3</sup> )                               | 0.527 (0.235)         | 0.430 (0.156)          | 0.521                                      |



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.

**Table 4.**

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

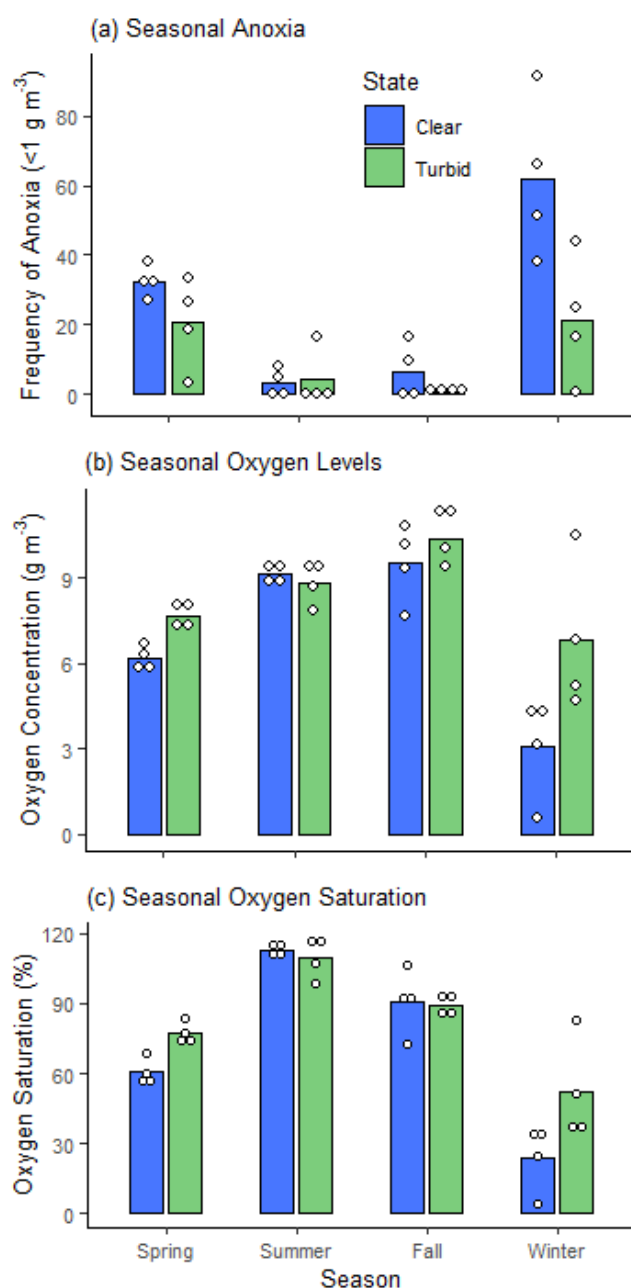
| Lake       | State (C/T) | Winter Year | $k$ (exponential decay rate $\text{g m}^{-3} \text{d}^{-1}$ ) | Exponential Model AIC | Linear Model AIC | Exponential Model RMSE | Linear Model RMSE |
|------------|-------------|-------------|---|-----------------------|------------------|------------------------|-------------------|
| Pisa       | C           | 2010 – 2011 | 0.167   | 930.3                 | 963.4            | 2.16                   | 2.69              |
| Org        | C           | 2009 – 2010 | 0.196   | 453.8                 | 549.2            | 1.32                   | 1.89              |
| Org        | C           | 2010 – 2011 | 0.0715  | 856.0                 | 1344.6           | 0.829                  | 1.68              |
| Org        | C           | 2012 – 2013 | 0.0312  | 1193.9                | 1153.6           | 1.74                   | 1.63              |
| Blakesly   | C           | 2010 – 2011 | 0.0732  | 910.6                 | 1225.4           | 1.24                   | 1.38              |
| Skunk      | C           | 2010 – 2011 | 0.164   | 645.6                 | 653.4            | 1.53                   | 1.82              |
| Skunk      | C           | 2012 – 2013 | 0.0926  | 1200.2                | 1571.5           | 1.70                   | 3.12              |
| Bellevue   | T           | 2009 – 2010 | 0.00134   | 717.2                 | 719.8            | 0.516                  | 0.527             |
| Bellevue   | T           | 2010 – 2011 | 0.0333  | 1280.4                | 1984.7           | 0.890                  | 1.21              |
| Morrison   | T           | 2011 – 2012 | 0.0215  | 1005.7                | 1009.8           | 1.75                   | 1.77              |
| Murk       | T           | 2009 – 2010 | 0.0115  | 437.5                 | 501.9            | 0.525                  | 0.592             |
| Murk       | T           | 2010 – 2011 | 0.0184  | 901.3                 | 1151.8           | 0.723                  | 0.985             |
| Mavis West | T           | 2009 – 2010 | 0.0059  | 128.2                 | 214.7            | 0.291                  | 0.334             |
| Mavis West | T           | 2012 – 2013 | 0.00427   | 1236.4                | 1241.8           | 0.901                  | 0.909             |

**Table 5.**

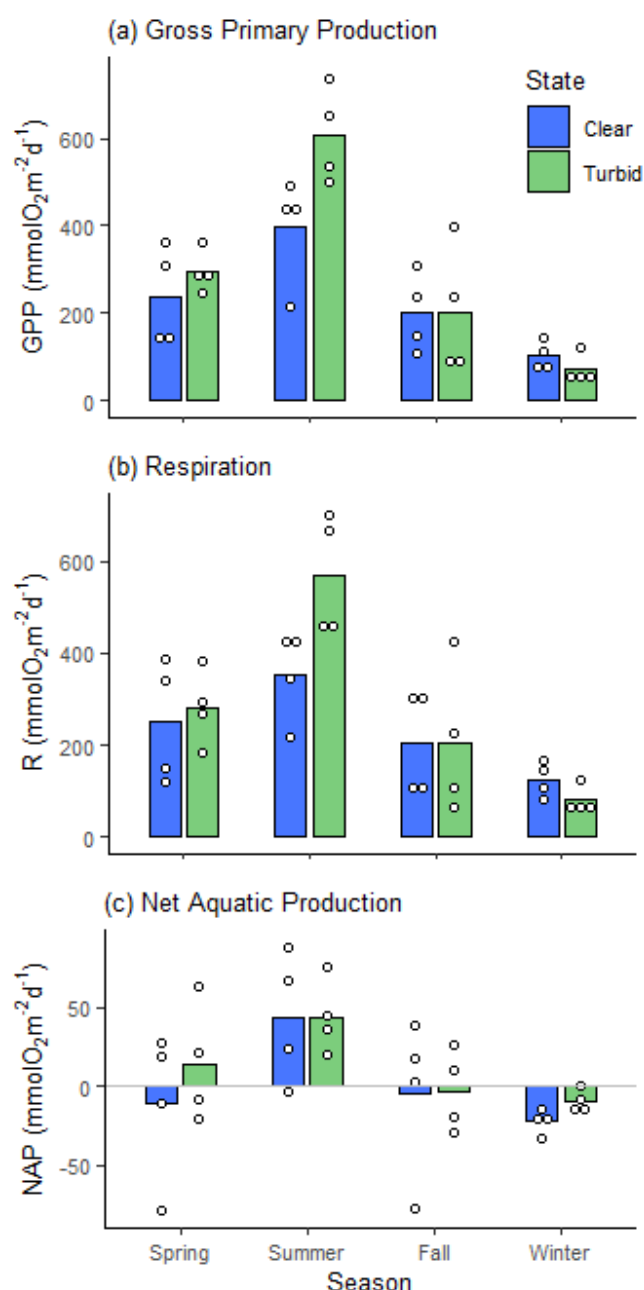
*Pearson Correlation Matrix for Lake Characteristics, Water Chemistry, and Winter Oxygen Dynamics*

|  | Area   | Volume  | Sediment: Volume Ratio | Depth   | TP      | Chl $\alpha$ | DOC   | TN      | Macro  | Depletion rate |
|--|--------|---------|------------------------|---------|---------|--------------|-------|---------|--------|----------------|
| Area (ha)  | 1      |         |                        |         |         |              |       |         |        |                |
| Volume (m <sup>3</sup> )   | 0.82*  | 1       |                        |         |         |              |       |         |        |                |
| Sediment Area:Volume Ratio                                       | -0.369 | -0.748* | 1                      |         |         |              |       |         |        |                |
| Max Depth (m)  | 0.135  | 0.629   | -0.896*                | 1       |         |              |       |         |        |                |
| Mean TP ( $\mu\text{g/l}$ )                                      | 0.575  | 0.887*  | -0.908*                | 0.704   | 1       |              |       |         |        |                |
| Mean Chl $\alpha$ ( $\mu\text{g/l}$ )                            | 0.542  | 0.798*  | -0.843*                | 0.56    | 0.951*  | 1            |       |         |        |                |
| Mean DOC (mg/l)  | 0.208  | -0.106  | 0.0820                 | -0.476  | 0.032   | 0.253        | 1     |         |        |                |
| Mean TN (mg/l)   | 0.431  | 0.595   | -0.691                 | 0.35    | 0.79*   | 0.938*       | 0.483 | 1       |        |                |
| Summer Macrophyte Biomass (CPUE)                                 | -0.28  | -0.718* | 0.912*                 | -0.776* | -0.896* | -0.906*      | 0.073 | -0.819* | 1      |                |
| Winter Oxygen Depletion Rate ( $\text{g m}^{-3} \text{d}^{-1}$ ) | -0.324 | -0.737* | 0.765*                 | -0.652  | -0.851* | -0.833*      | 0.14  | -0.713* | 0.921* | 1              |

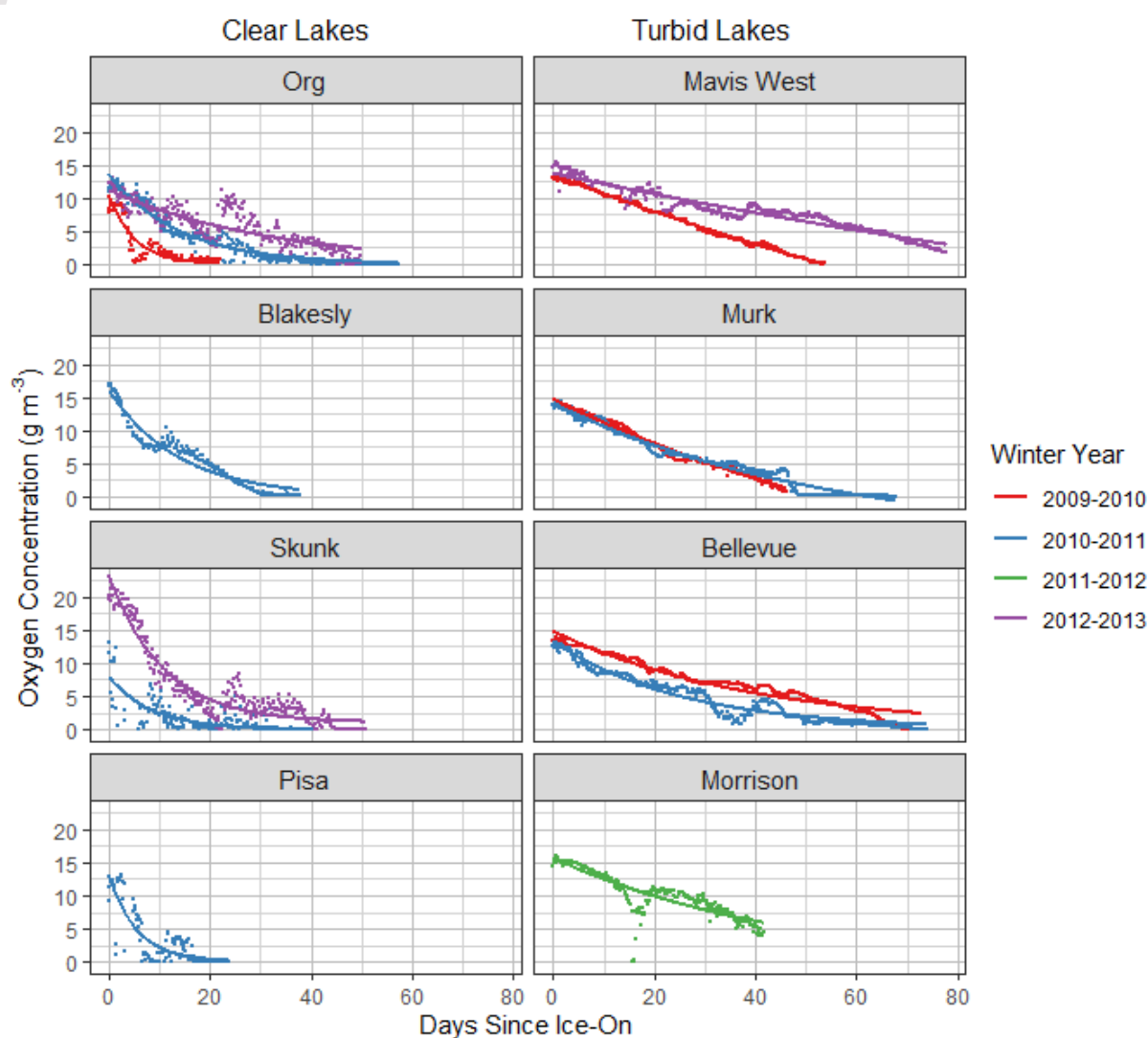
Note. \* Indicates significance at the 0.05  $\alpha$  level.



**Figure 1.** Seasonal comparisons of anoxia frequency (a), oxygen levels (b), and oxygen saturation (c), for clear and turbid lakes. Frequency of anoxia represents percentage of all oxygen measurements below  $1 \text{ g m}^{-3}$ . White points represent individual lake averages.



**Figure 2.** Seasonal comparisons of ecosystem respiration (a), gross primary production (b), and net ecosystem production (c), for clear and turbid lakes. White points represent individual lake averages.



**Figure 3.** Oxygen depletion curves for each lake in each year. Solid lines represent the exponential decay models predicted curves. Days since ice-on represents the start of oxygen decline after the lake had frozen.