Differing Winter Oxygen Regimes in Clear and Turbid Shallow Lakes

Joseph S. Rabaey¹, Kyle D. Zimmer,², Leah M. Domine², and James B. Cotner¹

¹University of Minnesota ²University of St. Thomas

November 24, 2022

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.

1 2	Differing Winter Oxygen Regimes in Clear and Turbid Shallow Lakes
3	Joseph S. Rabaey ¹ , Kyle D. Zimmer ² , Leah M. Domine ² , James B. Cotner ¹
4 5	¹ Department of Ecology, Evolution and Behavior, University of Minnesota - Twin Cities, St. Paul, Minnesota ² Department of Biology, University of St Thomas, St Paul, Minnesota
6	
7	Corresponding author: Joseph Rabaey (rabae005@umn.edu)
8	
9	Key Points:
10	• Winter oxygen regimes differed between clear and turbid shallow lakes.
11	• Clear lakes had significantly higher oxygen depletion rates under ice cover.
12 13	• Oxygen depletion rates were highly correlated with summer macrophyte biomass.

14 Abstract

15 Dissolved oxygen controls important processes in lakes, from chemical reactions to organism community structure and metabolism. In shallow lakes, small volumes allow for large 16 fluctuations in dissolved oxygen concentrations, and the oxygen regime can greatly affect 17 ecosystem-scale processes. We used high frequency dissolved oxygen measurements to examine 18 differences in oxygen regimes between two alternative stable states that occur in shallow lakes. 19 We compared annual oxygen regimes in four macrophyte-dominated, clear state lakes to four 20 21 phytoplankton-dominated, turbid state lakes by quantifying oxygen concentrations, anoxia frequency, and measures of whole-lake metabolism. Oxygen regimes were not significantly 22 different between lake states throughout the year except for during the winter under-ice period. 23 During winter, clear lakes had less oxygen, higher frequency of anoxic periods, and higher 24 oxygen depletion rates. Oxygen depletion rates correlated positively with peak summer 25 macrophyte biomass. Due to lower levels of oxygen, clear shallow lakes may experience anoxia 26 27 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, 28 which typically focuses efforts on maintaining the clearwater state. 29

30 Plain Language Summary

In lakes, the amount of oxygen dissolved in the water has a profound impact on lake 31 processes, from chemical reactions to the kinds and quantities organisms present. In shallow 32 lakes, the amount of dissolved oxygen can vary greatly due to the differences in the rates of 33 34 production, mostly through photosynthesis, and consumption, mostly through respiration. In this study, we compared patterns of dissolved oxygen availability seasonally between two common 35 states found in shallow lakes; a turbid, low clarity state dominated by phytoplankton, and a clear 36 state dominated by submersed aquatic plants. We used dissolved oxygen measurements to 37 compare oxygen patterns between shallow lakes in these two states throughout the year. Patterns 38 of oxygen were similar between the two lakes states in all seasons except winter. During the 39 winter under-ice period, clear lakes had significantly less oxygen compared to turbid lakes, and 40 lost oxygen at a faster rate through the winter. The lower levels of oxygen in clear lakes during 41 the winter could affect many lake processes, such as the winterkill of fish. Management of 42 shallow lakes often tries to maintain lakes in the clear state because of better water quality and 43 wildlife diversity, and these results can help inform management strategies. 44

45 **1 Introduction**

Dissolved oxygen in lake waters controls multiple physical and biological processes. Anoxia, 46 or the absence of oxygen, can affect organism habitat as well as chemical and biological 47 processes in lakes. Low oxygen concentrations can lead to fish kills (Greenbank, 1945), with 48 effects on fish community composition (Tonn & Magnuson, 1982) and trophic levels and the 49 food web structure of lakes (Carpenter et al., 2001). Anoxia also influences rates of chemical and 50 biological processes such as decomposition rates and nutrient cycling (Burdige, 2007), due in 51 part to the inhibition of aerobic metabolism and a shift to anaerobic metabolism (such as sulfate 52 reduction, denitrification, and methanogenesis). Anaerobic metabolism can also release toxic 53 compounds, such as methane and hydrogen sulfide, into the water column, further affecting 54 aquatic organisms. Oxygen depletion can occur due to nutrient enrichment coupled with 55 increased primary production, limited mixing, and degraded water quality (Gelda & Auer, 1996), 56 57 as is commonly observed in hypoxic/anoxic marine waters near river plumes (Li et al., 2002;

⁵⁸ Turner & Rabalais, 1994; Van Der Zwaan & Jorissen, 1991). While physical drivers such as

59 mixing, atmospheric exposure, and temperature can drive oxygen concentrations in lakes,

60 biological drivers such as oxygenic photosynthesis and aerobic respiration become particularly

61 important in the most productive ecosystems. Hence, understanding oxygen regimes in lakes is

62 important to predict ecosystem health and biological processes.

63 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 64 predicted oxygen depletion in large lakes (Charlton, 1980; Jackson & Lasenby, 1982; Stefan & 65 Fang, 1994). Shallow lakes have been more difficult to accurately predict oxygen depletion, 66 possibly due to the dynamic nature of shallow lakes, which are sensitive to environmental 67 change (Stefan & Fang, 1994). With small volumes, shallow lakes respond quickly to nutrient 68 inputs, as well as temperature and precipitation change (Gerten & Adrian, 2000; Schindler et al., 69 1996). Many shallow lakes experience occasional or frequent anoxia during the summer when 70 stratification and production are high (Papst et al. 1980), and during the winter when oxygen is 71 depleted under ice cover (Baird et al., 1987; Meding & Jackson 2003). Small, shallow lakes have 72 a large global surface area with an estimated 1.8 million km² total area for lakes smaller than 1 73 km², compared to 2.4 million km² for lakes larger than 1 km² (Downing et al., 2006), though the 74 number of shallow lakes could be even greater than previously estimated (Cael et al., 2017). This 75 76 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 77 shallow lakes important in freshwater carbon cycling. Dissolved oxygen can affect both 78 production and carbon burial rates in shallow lakes (Hobbs et al., 2013; Sobek et al., 2009), and 79 thus understanding and predicting oxygen dynamics in shallow lakes is important for global 80

81 carbon cycling.

82 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 83 84 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 85 or absent macrophytes (Scheffer et al., 1993; Scheffer & Jeppesen 2007). Lake state can be 86 87 influenced by various drivers, including nutrient load, temperature, and morphological features 88 (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 89 90 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). 91 Distinguishing differences, if any, in ecosystem-scale processes is important, as future impacts of 92 93 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 94 (Hanson & Butler, 1994). 95

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),

104 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
- 111 oxygen and more anoxia in the summer months, while clear lakes would experience more anoxia
- in the winter, due to more biomass degradation.
- 113

114 **Table 1.**

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

115 Watershed Characteristics and Water Chemistry of Individual Study Lakes

116

117 Note. Phosphorus, chlorophyll, and dissolved organic carbon measurements represent an average

- 118 of measurements taken throughout the year.
- 119

120 2 Materials and Methods

121 2.1 Site Description

The eight study lakes are all located in west-central Minnesota, in the southeastern 122 portion of the Prairie Pothole Region, a 715,000 km² area of central North America characterized 123 by thousands of shallow lakes (Euliss Jr. et al., 1999; Waiser & Robarts, 2004; Zimmer et al., 124 2009). The lakes were dispersed across a 3570 km² area centered at 45.859°N and 95.858°W. 125 Lakes were categorized as "clear lakes" that were in a clear-water state for all years of data 126 collection, and "turbid lakes" that were in a turbid-water state for all years of data collection 127 (Table 1). Lakes were classified as turbid or clear using the approach of Zimmer et al. (2009), 128 129 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 130 either lake surface area or maximum depth, however, mean depth and lake volume were greater 131

132 in turbid lakes (Table 2).

133 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.

141

142 **Table 2.**

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

Variable	Clear Lakes Mean	Turbid Lakes	P-Value	
	(sd)	Mean (sd)	(significance	
			at $\alpha = 0.05$)	
Winter O ₂ Exponential Decay Rate	0.117 (0.0402)	0.0147 (0.00695)	0.0133*	
$(g m^{-3} d^{-1})$				
Winter O ₂ 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 ³)	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 a (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*	

145

146 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 betweenlake states.

149 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 150 intervals with a multiprobe sonde (Hydrolab Datasonde or Minisonde). The sondes were 151 deployed at the center of each lake within the mixed layer (0.5m depth). There were not enough 152 sondes to continuously monitor every lake simultaneously, so they were serviced (cleaned and 153 re-calibrated) and rotated among lakes approximately every 3 weeks, though field conditions led 154 to some longer or shorter periods. This rotation, as well periods of failure by DO sensors, led to 155 an average of two winters of reliable oxygen data for each lake, on average. The DO sensors 156 157 were calibrated using air saturated water, and site-specific atmospheric pressure prior to deployment. 158

159 2.3 Oxygen Level and Anoxia Frequency Calculations

For both clear and turbid lakes (n = 4 for each state), oxygen concentrations (mg $O_2 L^{-1}$), 160 saturation levels, and anoxia frequencies were averaged for each season across the three years of 161 data collection. Seasons were defined in three-month periods; December –February defined as 162 winter, March – May as spring, June – August as summer, and September – November as fall. 163 Average oxygen levels were estimated with near- continuous measurement of water column DO 164 throughout the year. Conditions were considered anoxic when oxygen levels fell below 1 mg O₂ 165 1^{-1} . Though the geochemical definition of anoxia is 0 mg O₂ 1^{-1} , many processes that require 166 oxygen shift to anaerobic metabolism below approximately 1 mg $O_2 l^{-1}$ (Greenbank, 1945; 167 Nürnberg, 1995). In addition, the threshold for many fish species tolerance can be as high as 4 168 mg $O_2 l^{-1}$ (Greenbank, 1945). Frequencies of anoxia were calculated as the percentage of all 169 measurements that fell below the 1 mg $O_2 l^{-1}$ threshold. 170

171 2.4 Ecosystem Metabolism

Ecosystem metabolism was calculated as in Zimmer (2016), and metabolism data for the 172 summers of 2010 and 2011 were previously reported in that study. Changes in DO reflect 173 174 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 175 de Bogert et al., 2007). The net aquatic production (NAP) term is used instead of NEP to 176 acknowledge that primary production by emergent macrophytes is not represented by changes in 177 water column DO (Hagerthey et al., 2010). Metabolism equations described in Van de Bogert et 178 al. (2007) and Coloso et al. (2008) were used to calculate NAP, GPP, and ER in the 8 study 179 180 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 181 the mean hourly ER rate was multiplied by 24 to estimate daily ER (mmol $O_2 \text{ m}^{-3} \text{ d}^{-1}$). GPP was 182 estimated by subtracting the mean hourly ER rate from the mean hourly rate of change in oxygen 183 during the daylight hours, and that difference was multiplied by total daylight hours to quantify 184 daily GPP (mmol $O_2 \text{ m}^{-3} \text{ d}^{-1}$). Daily NAP was calculated as GPP - ER (mmol $O_2 \text{ m}^{-3} \text{ d}^{-1}$; Van de 185 Bogert et al. 2007). 186

187 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 188 either into or out of the lake was estimated as the gas piston velocity (K) multiplied by the 189 difference between the concentration of DO in the water at equilibrium with the atmosphere and 190 the actual DO concentration in the water (Coloso et al., 2008). K was calculated based on 191 192 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 193 using the wind power relationship (Jähne et al., 1987). Hourly wind speed data were obtained 194 from a local weather station (Wahpeton ND, 43–104 km from the study sites; North Dakota 195 196 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 197 rates (mmol $O_2 \text{ m}^{-2} \text{ d}^{-1}$) were estimated by multiplying volumetric rates by the mixing depth. 198 199 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°C change occurred over 0.5 m (or 200 for lakes less than 2 m deep a 0.5°C change over 0.25 m (Coloso et al., 2011)). Daily metabolism 201

- values were averaged for each lake for a seasonal comparison between lake states.
- 203 2.5 Winter Oxygen Depletion

Winter oxygen decay rates were calculated with a single exponential decay model ($O_2 =$ 204 A^{-kt} ; where O₂ is the dissolved oxygen concentration, A is the initial [O₂] at ice-on, e is the base 205 of the natural logarithm, k is the decay rate, and t is time), which was deemed the most 206 appropriate for shallow lakes (Meding & Jackson, 2001, 2003) (Figure 3). Model fits were 207 evaluated and compared with simple linear models (Babin & Prepas, 1985) by visual 208 examination of the residuals and by using Akaike's information criterion (AIC) (Akaike, 1981). 209 210 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 211 maintain consistency. The models began with time-0 at the highest oxygen level subsequent to 212 ice-on. To correct for atmospheric oxygen inputs during the initial period after freezing, as well 213 as brief periods of freeze and thaw, data points were removed from this time point consecutively 214 until a model was able to be fit. Once a model was fit data were no longer removed. The number 215 of points removed using this method ranged from no points up to a week of data in some 216 situations. Once a model was fit, the k value (decay rate, $g m^{-3} d^{-1}$) was averaged and compared 217 for each lake state. For all statistical tests and comparisons between lake states, lake means were 218 used, giving eight total replicates and four per lake state. 219

- 3 Results
- 221 3.1 Oxygen Levels in Clear and Turbid Lakes

222 Both clear and turbid shallow lakes exhibited similar oxygen concentrations and saturation levels throughout the summer and fall (Figure 1). There were slight differences 223 between clear and turbid lakes in the spring, but the largest differences occurred in the winter, 224 with clear lakes having lower oxygen concentrations than turbid lakes (Figure 1), though not 225 statistically significant at the $\alpha = 0.05$ level (p = 0.0624, Table 2). Differences in oxygen 226 saturation levels in the winter and spring mirrored the differences in oxygen concentrations 227 between the two lake types, confirming that this was not a function of temperature differences 228 between clear and turbid lakes. 229

Both clear and turbid lakes showed very low frequencies of anoxia in the summer and fall 230 (Figure 1). With all the lakes having depths less than 5 m, stratification was not strong enough to 231 232 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 233 anoxia compared to turbid lakes, experiencing anoxic conditions almost three times as often as 234 turbid lakes (62% vs. 22%) (p = 0.0340, Table 2). In the spring, clear lakes also showed a higher 235 frequency of anoxia, though the difference was not as pronounced (Figure 1) most likely due to 236 the fact that ice out typically occurred in late March or early April. 237

238 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 ± 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 ± 1 SE.

between clear and turbid lakes in the summer months, NAP was almost identical between the 244 two groups. NAP was only significantly different between clear and turbid lakes during the 245 winter, where clear lakes had an average daily rate over twice as negative as turbid lakes (-22 246 mmol $O_2 \text{ m}^{-2} \text{ d}^{-1} \text{ vs.} -9 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}, p = 0.0421$). 247

3.3 Winter Oxygen Depletion Rates 248

Exponential decay models were fit for all lakes, for every year of complete winter data 249

- (e.g. Figure 3). For most lakes most years, points were removed at the beginning of the ice cover 250 period due to inconsistent freezing and inputs of oxygen from freeze out of gases (Meding & 251
- Jackson, 2001). Average rates for all lakes ranged from 0.00134g $O_2 \text{ m}^{-3} \text{ d}^{-1}$ to 0.196g $O_2 \text{ m}^{-3} \text{ d}^{-1}$ 252

(Table 3). Overall, clear lakes $(0.117 \text{ g m}^{-3} \text{ d}^{-1})$ showed significantly higher oxygen depletion 253

10 0 10 0 20 30 40 50 Days after Nov 26, 2010

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 26th 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). 254

- 255
- 256 Table 3.

Oxygen depletion rates and model AIC comparison for the eight study lakes. 257

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



Bellevue	Т	2010 - 2011	0.0333	1280.4	1984.7
Morrison	Т	2011 - 2012	0.0215	1005.7	1009.8
Murk	Т	2009 - 2010	0.0115	437.5	501.9
Murk	Т	2010 - 2011	0.0184	901.3	1151.8
Mavis West	Т	2009 - 2010	0.0059	128.2	214.7
Mavis West	Т	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 260 than clear lakes ($p = \langle 0.001 \text{ for TP}, p = 0.00138 \text{ for chl } a$, Table 2). Turbid lakes also had 261 significantly higher concentrations of total nitrogen (TN) (p = 0.0239, Table 2), likely due to 262 higher rates of denitrification in clear lakes, as well as uptake of nitrogen by macrophytes 263 (Ginger et al., 2017). Dissolved organic carbon (DOC) was not significantly different between 264 clear and turbid lakes (p = 0.876, Table 2). Clear lakes had significantly higher macrophyte 265 abundance (p = 0.0344, Table 2), with no macrophyte biomass observed in any of the turbid 266 lakes. 267

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).

275 **Table 4.**

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

	Area	Volume	Depth	TP	Chl a	DOC	TN	Macro	Decay rate	Winter O2	Anoxia
Area (ha)	1										
Volume (m ³)	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 ⁻³ d ⁻¹)	-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

278 Note. * Indicates significance at the 0.05 α level.



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

279 **4 Discussion**

4.1 Differences in Oxygen Regime

Clear and turbid lakes had similar oxygen regimes throughout much of the summer. This 281 was somewhat unexpected, as the turbid lakes had much higher nutrient concentrations and 282 chlorophyll levels (Table 1) and the relationship between eutrophication, algal bloom collapse, 283 and anoxia is well established (Anderson et al., 2002; Hutchinson, 1957; Nürnberg, 1995). 284 However, in clear lakes, most of the nutrients are tied up in macrophyte biomass, and would not 285 be represented by water column nutrient concentrations. In addition, it was expected that the 286 turbid lakes may have stronger stratification due to higher light extinction coefficients 287 (Heiskanen et al., 2015; Jones et al., 2005), which again could lead to longer periods of anoxia in 288 the summer. While shallow eutrophic prairie lakes can often have periods of oxygen depletion 289 during the summer (summerkill) (Papst et al., 1980), turbid lakes only experienced slightly more 290 291 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 292 (Coburn, 2019). This likely helped keep much of the water column oxygenated throughout the 293 294 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.

301 4.2 Ecosystem Metabolism

Studies of summer lake metabolism of the same lakes used in this study found no 302 significant difference in metabolism during June - August between clear and turbid states 303 (Zimmer et al., 2016), while the present study found significantly higher GPP and ER during the 304 summer in turbid lakes. These differing results are likely due to two more years of data added in 305 this study (2010 - 2013 in this study, 2010-2011 in the previous study), as well as a different 306 analysis design (previous study used averages on a yearly basis and a two-way ANOVA). 307 308 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 309 between clear and turbid lakes during the winter, where clear lakes had a larger negative NAP 310 than turbid lakes. This corresponds to the lower winter oxygen levels and higher oxygen 311 depletion rates in clear lakes, as higher rates of respiration compared to production (or a more 312 negative NAP) would lead to more oxygen drawdown. 313

314 4.3 Oxygen Depletion Models

Winter oxygen depletion rates calculated using an exponential decay model (Meding & 315 Jackson, 2001) were nearly eight times higher in clear lakes compared to turbid lakes (Table 2, p 316 = 0.0133). Oxygen depletion rate models have commonly been used for shallow lakes, though 317 models for predicting oxygen depletion have largely relied on lake morphological characteristics, 318 such as depth and volume (Babin & Prepas, 1985; Barica, 1984; Mathias & Barica, 1980). While 319 oxygen depletion rate did correlate negatively with lake volume and mean depth in these study 320 lakes, the highest correlation among predictors for oxygen depletion rate was macrophyte 321 322 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 323 macrophyte biomass (Table 2). This finding is in agreement with a study by Meding and Jackson 324 325 (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 326 difference between clear and turbid lakes, but the turbid lakes they measured had higher levels of 327 macrophytes compared to the study lakes in our work, which had none. Macrophytes represent 328 the primary source of organic matter in clear-state shallow lakes, which often have macrophyte 329 growth throughout nearly the entire water column. Oxygen decay rates depend on organic matter 330 331 available for degradation (Greenbank, 1945; Jackson & Lasenby, 1982; Lasenby, 1975; Mathias & Barica, 1980), therefore making total macrophyte biomass an important predictor of oxygen 332 decay. 333

Macrophytes have slower decomposition rates compared to phytoplankton (Enríquez et 334 al., 1993; Twilley et al., 1986; Wang et al., 2018), and decomposition extending further into the 335 ice-on period of winter may result in the much larger oxygen decay rate observed in clear lakes. 336 If large amounts of phytoplankton biomass in turbid lakes decomposed before the ice-on period, 337 338 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 339 respiration rates in all seasons except winter, suggesting higher rates of decomposition under the 340 ice in clear, macrophyte dominated lakes. 341

342 4.4 Consequences of anoxia and implications for management

Shallow lakes around the globe are often managed for the clear-water state (Hosper, 343 1997; Qin et al., 2007; Zimmer et al., 2009), due to many ecosystem services including wildlife 344 and fish habitat, improved water quality, and greater appeal for recreational use (Moss et al., 345 1996). Flipping shallow lakes from a turbid to clear state can often prove more difficult than 346 simply removing nutrients or inducing a trophic cascade. Internal loading of phosphorus can be 347 high in shallow lakes, due to frequent resuspension of sediment and occasional periods of anoxia 348 (Welch & Cooke, 1995). The relationship between anoxia and internal loading of phosphorus is 349 well known (Welch & Perkins, 1979), and greater frequency of anoxia during the winter in clear-350 state shallow lakes could lead to higher rates of internal loading in these systems and may be an 351 important driver that causes lakes to switch from the clear to the turbid state. Turbid lakes that 352 are managed for a clear state can often flip back to the turbid state a few years after intervention 353 (Theissen et al., 2012), even after nutrient inputs are reduced. Internal loading during winters in 354 the clear-state could contribute to the difficulties of keeping shallow lakes in the clear-state long 355 356 term.

357 Fish populations can also have profound effects on the state of shallow lakes. Planktivorous fish in shallow lakes can release phytoplankton from zooplankton consumption, 358 and removal of these fish can lead to less phytoplankton and bring the lake to a clear state 359 (Hanson & Butler, 1994). In addition, benthivorous fish can resuspend sediment and detritus, not 360 only increasing the turbidity but also resuspending nutrients and increasing rates of internal 361 loading, driving shallow lakes into the turbid state (Meijer et al., 1990). Historically, many 362 shallow lakes were fishless, especially in the prairie pothole region containing the lakes in this 363 study (Mclean et al., 2016). Rising water levels, fish stocking, ditching, and accidental 364 introductions have led to the presence of fish in many shallow lakes in the prairie pothole region 365 (Herwig et al., 2010). One factor that may have played a role in maintaining fishless lakes is the 366 higher frequency of anoxia in clear lakes during the winter. Many fish species cannot survive 367 conditions with oxygen levels below 3-5 mg/l, and sustained periods of anoxia can result in fish 368 369 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 370 higher frequencies of anoxia during the winter, with 60% of oxygen measurements below 1 mg/l 371 O₂, compared to 20% in turbid-state lakes (Figure 1), potentially leading to higher rates of 372 373 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 374 375 fish, which stabilizes high macrophyte abundance and additional winterkill, as fish often induce shifts to turbid states (Zimmer et al., 2009). 376

377 4.5 Conclusions

Our results indicate differing oxygen regimes during the winter in clear and turbid 378 379 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 380 and physical processes, clear and turbid lake states may experience many differences in 381 functioning during the winter under-ice period. This has important implications for shallow lake 382 management. Land-use changes, rising water levels, and rising temperatures will impact shallow 383 lake ecosystems in the future, and it is important to continue to understand how differences in 384 biotic and geochemical feedbacks interact with lake state. 385

Acknowledgments, Samples, and Data 386

Brian Heriwg and Mark Hanson (MN DNR), and Will Hobbs assisted with data collection. 387

388 We thank all the undergraduate assistants for their help with this project. Also, Todd Call and

Nicky-Hansel Welch, Minnesota Department of Natural Resources, helped find study sites. 389

Funding was provided by the National Science Foundation (DEB-0919095; DEB-0919070; 390

DEB-0918753), the Minnesota Environment and Natural Resources Trust Fund (Award M.L. 391

2010, Chap. 362, Sec. 2, Subd. 5g), the University of St Thomas, and the University of 392 Minnesota.

- 393
- 394

Data availability statement: Data will be made available in the Data Repository for University of 395 396 Minnesota (DRUM) repository.

397

References 398

- Akaike, H. (1981). Likelihood of a model and information criteria. Journal of Econometrics, 399 16(1), 3-14. https://doi.org/10.1016/0304-4076(81)90071-3 400
- Anderson, D. M., Glibert, P. M., & Burkholder, J. M. (2002). Harmful Algal Blooms and 401 Eutrophication: Nutrient Sources, Composition, and Consequences. Estuaries, 25(4b), 704– 402 726. https://doi.org/10.5555/uri:pii:000399939190180Q 403
- Babin, J., & Prepas, E. E. (1985). Modelling Winter Oxygen Depletion Rates in Ice-Covered 404 Temperate Zone Lakes in Canada. Canadian Journal of Fisheries and Aquatic Sciences, 405 406 42(2), 239–249. https://doi.org/10.1139/f85-031
- Baird, D. J., Gates, T. E., & Davies, R. W. (1987). Oxygen Conditions in Two Prairie Pothole 407 408 Lakes During Winter Ice Cover. Canadian Journal of Fisheries and Aquatic Sciences, 44(5), 1092–1095. https://doi.org/10.1139/f87-131 409
- Barica, J. (1984). Empirical models for prediction of algal blooms and collapses, winter oxygen 410 depletion and a freeze-out effect in lakes: Summary and verification. SIL Proceedings, 411 1922-2010, 22(1), 309-319. https://doi.org/10.1080/03680770.1983.11897308 412
- Barica, J., & Mathias, J. A. (1979). Oxygen Depletion and Winterkill Risk in Small Prairie Lakes 413 Under Extended Ice Cover. Journal of the Fisheries Research Board of Canada, 36(8), 414 980-986. https://doi.org/10.1139/f79-136 415

Burdige, D. J. (2007). Preservation of organic matter in marine sediments: Controls, 416 mechanisms, and an imbalance in sediment organic carbon budgets? *Chemical Reviews*, 417 107(2), 467–485. https://doi.org/10.1021/cr050347a 418

- Cael, B. B., Heathcote, A. J., & Seekell, D. A. (2017). The volume and mean depth of Earth's 419 lakes. Geophysical Research Letters, 44(1), 209–218. 420 https://doi.org/10.1002/2016GL071378 421
- Carpenter, S. R., Cole, J. J., Hodgson, J. R., Kitchell, J. F., Pace, M. L., Bade, D., ... Schindler, 422
- 423 D. E. (2001). Trophic Cascades, Nutrients, and Lake Productivity: Whole-Lake
- Experiments Houser and Daniel E. Schindler Published by : Wiley on behalf of the 424

- Ecological Society of America Stable URL : https://www.jstor.org/stable/2657215 Wiley ,
 Ecological Society, 71(2), 163–186.
- Charlton, M. N. (1980). Hypolimnion Oxygen Consumption in Lakes: Discussion of
 Productivity and Morphometry Effects. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(10), 1531–1539. https://doi.org/10.1139/f80-198
- Coburn, J. J. (2019). Assessing wind data from reanalyses for the upper Midwest. *Journal of Applied Meteorology and Climatology*, 58(3), 429–446. https://doi.org/10.1175/JAMC-D 18-0164.1
- Cole, J. I., & Caraco, N. F. (1998). Atmospheric exchange of carbon dioxide in a low-wind
 oligotrophic lake, *43*(4).
- Cole, J. J., Pace, M. L., Carpenter, S. R., & Kitchell, J. F. (2000). Persistence of net heterotrophy
 in lakes during nutrient addition and food web manipulations. *Limnology and Oceanography*, 45(8), 1718–1730. https://doi.org/10.4319/lo.2000.45.8.1718
- Cole, J., Prairie, Y. T., Mcdowell, W. H., & Tranvik, L. J. (2007). Plumbing the Global Carbon
 Cycle : Integrating Inland Waters into the Terrestrial Carbon Budget. *Ecosystems*, *10*(May 2016), 171–184. https://doi.org/10.1007/s10021-006-9013-8
- 441 Coloso, J. J., Cole, J. J., Hanson, P. C., & Pace, M. L. (2008). Depth-integrated, continuous
 442 estimates of metabolism in a clear-water lake. *Canadian Journal of Fisheries and Aquatic*443 *Sciences*, 65(4), 712–722. https://doi.org/10.1139/F08-006
- Coloso, J. J., Cole, J. J., & Pace, M. L. (2011). Short-term variation in thermal stratification
 complicates estimation of lake metabolism. *Aquatic Sciences*, 73(2), 305–315.
 https://doi.org/10.1007/s00027-010-0177-0
- Downing, J. A., McDowell, W. H., Kortelainen, P., Caraco, N. F., Tranvik, L. J., Cole, J. J., ...
 Melack, J. M. (2006). The global abundance and size distribution of lakes, ponds, and
 impoundments. *Limnology and Oceanography*, *51*(5), 2388–2397.
 https://doi.org/10.4319/lo.2006.51.5.2388
- Enríquez, S., Duarte, C. M., & Sand-Jensen, K. (1993). Patterns in decomposition rates among
 photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, 94(4), 457–
 471. https://doi.org/10.1007/BF00566960
- Euliss Jr., N. H., Wrubleski, D. A., & Mushet, D. M. (1999). Wetlands of the Prairie Pothole
 Region: Invertebrate species composition, ecology, and management. In D. P. Batzer, R. B.
 Rader, & S. A. Wissinger (Eds.), *Invertebrates in freshwater wetlands of North America: Ecology and management* (pp. 471–514). John Wiley and Sons. Retrieved from
 http://pubs.er.usgs.gov/publication/85406
- Gelda, R. K., & Auer, M. T. (1996). Development and testing of a dissolved oxygen model for a
 Hypereutrophic Lake. *Lake and Reservoir Management*, *12*(1), 165–179.
 https://doi.org/10.1080/07438149609354006
- Gerten, D., & Adrian, R. (2000). Climate-Driven Changes in Spring Plankton Dynamics and the
 Sensitivity of Shallow Polymictic Lakes to the North Atlantic Oscillation. *Limnology and Oceanography*, 45(5), 1058–1066. Retrieved from http://links.jstor.org/sici?sici=0024-
- 465 3590(200007)45%3A5%3C1058%3ACCISPD%3E2.0.CO%3B2-%23

- Ginger, L. J., Zimmer, K. D., Herwig, B. R., Hanson, M. A., Hobbs, W. O., Small, G. E., &
 Cotner, J. B. (2017). Watershed vs. within-lake drivers of nitrogen: Phosphorus dynamics in
 shallow lakes: Phosphorus. *Ecological Applications*, 27(7), 2155–2169.
 https://doi.org/10.1002/eap.1599
- Greenbank, J. (1945). Limnological Conditions in Ice-Covered Lakes, Especially as Related to
 Winter-Kill of Fish. *Ecological Monographs*, *15*(4), 343–392.
 https://doi.org/10.2307/1948427
- Hagerthey, S. E., Cole, J. J., & Kilbane, D. (2010). Aquatic metabolism in the Everglades:
 Dominance of water column heterotrophy. *Limnology and Oceanography*, 55(2), 653–666.
 https://doi.org/10.4319/lo.2009.55.2.0653
- Hanson, M. A., & Butler, M. G. (1990). Early responses of plankton and turbidity to
 biomanipulation in a shallow prairie lake. *Hydrobiologia*, 200/201, 317–327.
 https://doi.org/10.1139/f94-117
- Hanson, M. A., & Butler, M. G. (1994). Responses of Plankton, Turbidity, and Macrophytes to
 Biomanipulation in a Shallow Prairie Lake. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(5), 1180–1188. https://doi.org/10.1139/f94-117
- Hargeby, A., Blindow, I., & Hansson, L. A. (2004). Shifts between clear and turbid states in a
 shallow lake: Multi-causal stress from climate, nutrients and biotic interactions. *Archiv Fur Hydrobiologie*, *161*(4), 433–454. https://doi.org/10.1127/0003-9136/2004/0161-0433
- Heiskanen, J. J., Mammarella, I., Ojala, A., Stepanenko, V., Erkkilä, K., Miettinen, H., ...
 Nordbo, A. (2015). Effects of water clarity on lake stratification and lake-atmosphere heat
 exchange, 7412–7428. https://doi.org/10.1002/2014JD022938.Received
- Herwig, B. R., Zimmer, K. D., Hanson, M. A., Konsti, M. L., Younk, J. A., Wright, R. W., ...
 Haustein, M. D. (2010). Factors influencing fish distributions in shallow lakes in prairie and
 prairie-parkland regions of Minnesota, USA. *Wetlands*, *30*(3), 609–619.
 https://doi.org/10.1007/s13157-010-0037-7
- Hobbs, W. O., Engstrom, D. R., Scottler, S. P., Zimmer, K. D., & Cotner, J. B. (2013).
 Estimating modern carbon burial rates in lakes using a single sediment sample. *Limnology and Oceanography: Methods*, *11*(JUNE), 316–326.
 https://doi.org/10.4319/lom.2013.11.316
- Hosper, H. (1997). *Clearing Lakes*. Lelystad, The Netherlands: Public Works Water
 Management.
- Hutchinson, G. E. (1957). A Treatise on Limnology. Vol. 1, Geography, Physics, and Chemistry.
 (J. Wiley, Ed.) (Vol. 95). London: Cambridge University Press.
 https://doi.org/10.1017/S0016756800062634
- Jackson, M. B., & Lasenby, D. C. (1982). A Method for Predicting Winter Oxygen Profiles in
 Ice-covered Ontario Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, (Apha
 1965), 1267–1272.
- Jähne, B. J., Münnich, K. O. M., Bösinger, R., Dutzi, A., Huber, W., & Libner, P. (1987). On the
 Parameters Influencing Air-Water Gas Exchange of magnitude lower in the water than in
 the air, information, which in turn has also hindered transfer in the water k +. *Journal of*

- 507 *Geophysical Research*, 92(C2), 1937–1949. https://doi.org/10.1029/JC092iC02p01937
- Jones, I. A. N., George, G., & Reynolds, C. (2005). Quantifying effects of phytoplankton on the
 heat budgets of two large limnetic enclosures, 1239–1247. https://doi.org/10.1111/j.1365 2427.2005.01397.x
- Laas, A., Nõges, P., Kõiv, T., & Nõges, T. (2012). High-frequency metabolism study in a large
 and shallow temperate lake reveals seasonal switching between net autotrophy and net
 heterotrophy. *Hydrobiologia*, 694(1), 57–74. https://doi.org/10.1007/s10750-012-1131-z
- Lasenby, D. C. (1975). Development of oxygen deficits in 14 southern Ontario lakes. *Limnology and Oceanography*, 20(November).
- Li, D., Zhang, J., Huang, D., Wu, Y., & Liang, J. (2002). Oxygen depletion off the Changjiang
 (Yangtze River) Estuary. *Science in China, Series D: Earth Sciences*, 45(12), 1137–1146.
 https://doi.org/10.1360/02yd9110
- Magnuson, J. J., Beckel, A. L., Mills, K., & Brandt, S. B. (1985). Surviving winter hypoxia:
 behavioral adaptations of fishes in a northern Wisconsin winterkill lake. *Environmental Biology of Fishes*, 14(4), 241–250. https://doi.org/10.1007/BF00002627
- Mathias, J. A., & Barica, J. (1980). Factors Controlling Oxygen Depletion in Ice-Covered Lakes.
 Canadian Journal of Fisheries and Aquatic Sciences, 37(2), 185–194.
 https://doi.org/10.1139/f80-024
- Mclean, K. I., Mushet, D. M., & Stockwell, C. A. (2016). From "Duck Factory" to "Fish
 Factory": Climate Induced Changes in Vertebrate Communities of Prairie Pothole Wetlands
 and Small Lakes. *Wetlands*, *36*. https://doi.org/10.1007/s13157-016-0766-3
- Meding, M. E., & Jackson, L. J. (2001). Biological implications of empirical models of winter
 oxygen depletion. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(9), 1727–1736.
 https://doi.org/10.1139/f01-109
- Meding, M. E., & Jackson, L. J. (2003). Biotic, chemical, and morphometric factors contributing
 to winter anoxia in prairie lakes. *Limnology and Oceanography*, 48(4), 1633–1642.
 https://doi.org/10.4319/lo.2003.48.4.1633
- Meijer, M.-L., de Haan, M. W., Breukelaar, A. W., & Buiteveld, H. (1990). Is reduction of the
 benthivorous fish an important cause of high transparency following biomanipulation in
 shallow lakes? *Hydrobiologia*, 200/201, 303–315.
- Moss, B. J., Madgwick, J., & Phillips, G. (1996). *Guide to the restoration of nutrient-enriched shallow lakes*. Norwich, Norfolk: Broads Authority.
- Nürnberg, G. K. (1995). Quantifying anoxia in lakes. *Limnology and Oceanography*, 40(6),
 1100–1111. https://doi.org/10.4319/lo.1995.40.6.1100
- Odum, H. T. (1956). Primary Production in Flowing Waters. *Limnology and Oceanography*,
 1(1), 102–117. https://doi.org/doi:10.4319/lo.1956.1.2. 0102
- Papst, M. H., Mathias, J. A., & Barica, J. (1980). Relationship Between Thermal Stability and
 Summer Oxygen Depletion in a Prairie Pothole Lake. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(9), 1433–1438. https://doi.org/10.1139/f80-183
- 546 Qin, B.-Q., Liu, Z., & Havens, K. (2007). Eutrophication of Shallow Lakes with Special

- 547 *Reference to Lake Taihu, China*. https://doi.org/10.1007/978-1-4020-6158-5
- Scheffer, M, Hosper, S. H., Meijer, M.-L., Moss, B., & Jeppesen, E. (1993). Alternative
 Equilibria in Shallow Lakes. *Reviews*, 11(3), 220–226.
- Scheffer, Marten, & Jeppesen, E. (2007). Regime shifts in shallow lakes. *Ecosystems*, 10(1), 1–3.
 https://doi.org/10.1007/s10021-006-9002-y
- Scheffer, Marten, & Van Nes, E. H. (2007). Shallow lakes theory revisited: Various alternative
 regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, 584(1), 455–466.
 https://doi.org/10.1007/s10750-007-0616-7
- Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., ...
 Stainton, M. P. (1996). The effects of climatic warming on the properties of boreal lakes
 and streams at the Experimental Lakes Area, northwestern Ontario. *Limnology and Oceanography*, 41(5), 1004–1017. https://doi.org/10.4319/lo.1996.41.5.1004
- Sobek, S., Durisch-Kaiser, E., Zurbruğg, R., Wongfun, N., Wessels, M., Pasche, N., & Wehrli,
 B. (2009). Organic carbon burial efficiency in lake sediments controlled by oxygen
 exposure time and sediment source. *Limnology and Oceanography*, 54(6), 2243–2254.
 https://doi.org/10.4319/lo.2009.54.6.2243
- Stefan, H. G., & Fang, X. (1994). Dissolved oxygen model for regional lake analysis. *Ecological Modelling*, 71(1–3), 37–68. https://doi.org/10.1016/0304-3800(94)90075-2
- Theissen, K. M., Hobbs, W. O., Hobbs, J. M. R., Zimmer, K. D., Domine, L. M., Cotner, J. B., &
 Sugita, S. (2012). The altered ecology of Lake Christina: A record of regime shifts, land-use
 change, and management from a temperate shallow lake. *Science of the Total Environment*,
 433, 336–346. https://doi.org/10.1016/j.scitotenv.2012.06.068
- Tonn, W. M., & Magnuson, J. J. (1982). Patterns in the species composition and richness of fish
 assemblages in northern Wisconsin lakes. *Ecology*, 63(4), 1149–1166.
 https://doi.org/10.2307/1937251
- Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R. G., Ballatore, T. J., ...
 Weyhenmeyer, G. A. (2009). Lakes and reservoirs as regulators of carbon cycling and
 climate. *Limnology and Oceanography*, 54(6 PART 2), 2298–2314.
 https://doi.org/10.4319/lo.2009.54.6 part 2.2298
- Turner, R. E., & Rabalais, N. N. (1994). Coastal eutrophication near the Mississippi river delta.
 Nature, *368*(6472), 619–621. https://doi.org/10.1038/368619a0
- Twilley, R. R., Ejdung, G., Romare, P., Kemp, W. M., Twilley, R. R., Ejdung, G., ... Kemp, W.
 M. (1986). A Comparative Study of Decomposition, Oxygen Consumption and Nutrient
 Release for Selected Aquatic Plants Occurring in an Estuarine Environment. *Oikos*, 47(2),
 190–198.
- Van de Bogert, M. C., Carpenter, S. R., Cole, J. J., & Pace, M. L. (2007). Assessing pelagic and
 benthic metabolism using free water measurements. *Limnology and Oceanography: Methods*, 5(5), 145–155. https://doi.org/10.4319/lom.2007.5.145
- Van Der Zwaan, G. J., & Jorissen, F. J. (1991). Biofacial patterns in river-induced shelf anoxia.
 Modern and Ancient Continental Shelf Anoxia, (58), 65–82.

Waiser, M. J., & Robarts, R. D. (2004). Photodegradation of DOC in a Shallow Prairie Wetland :
 Evidence from Seasonal Changes in DOC Optical Properties and Chemical Characteristics.
 Biogeochemistry, 69(2), 263–284.

590 Wang, H. J., Wang, H. Z., Liang, X. M., Pan, B. Z., Kosten, S., Wang, H. J., ... Kosten, S.

- (2018). Macrophyte species strongly affects changes in C, N, and P stocks in shallow lakes
 after a regime shift from macrophyte to phytoplankton dominance Macrophyte species
 strongly affects changes in C, N, and P stocks in shallow lakes after a regime shift . *Inland Waters*, 2041. https://doi.org/10.1080/IW-6.3.837
- Wanninkhof, R. (1992). Relationship between wind speed and gas exchange over the ocean.
 Journal of Geophysical Research, 97(C5), 7373–7382. https://doi.org/10.1029/92JC00188
- Welch, E. B., & Cooke, G. D. (1995). Internal Phosphorus Loading in Shallow Lakes : Importance and Control. *Lake and Reservoir Management*, 2381.
 https://doi.org/10.1080/07438149509354208
- Welch, E. B., & Perkins, M. A. (1979). Oxygen Deficit Phosphorus loading relation in lakes,
 51(12), 2823–2828.
- Zimmer, K. D., Hanson, M. A., Herwig, B. R., & Konsti, M. L. (2009). Thresholds and stability
 of alternative regimes in shallow prairie-parkland lakes of central north America.
 Ecosystems, 12(5), 843–852. https://doi.org/10.1007/s10021-009-9262-4
- Zimmer, K. D., Hobbs, W. O., Domine, L. M., Herwig, B. R., Hanson, M. A., & Cotner, J. B.
 (2016). Uniform carbon fluxes in shallow lakes in alternative stable states. *Limnology and Oceanography*, *61*(1), 330–340. https://doi.org/10.1002/lno.10215

608