PATTERNS AND MECHANISMS OF YEAR-TO-YEAR VARIABILITY

IN WINTER OXYGEN DEPLETION RATES

IN ICE-COVERED LAKES

by

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Ten years of winter oxygen data were analyzed from the North Temperate Lakes, Long Term Ecological Research site in Vilas County, Wisconsin, to characterize the year-to-year variability of oxygen depletion rates and to determine the factors which influence this variability. Mean oxygen depletion rates among the lakes ranged from 0.023 to 0.084 g $O_2 \cdot m^{-3} \cdot d^{-1}$. Depletion rates varied by as much as 50% from year to year. Lakes with similar morphometry exhibited temporal coherence in depletion rates over the ten-year period, suggesting that different mechanisms were influencing the variability in deep and shallow lakes. The sediment area to lake volume ratio best explained the variability in mean depletion rates among lakes, although summer chl a was also a factor. While differences in morphometry and productivity explained the variability in oxygen depletion rates among lakes, these variables did not account for the variability observed among years.

Cover variables, such as snow depth and ice thickness, were correlated to yearly depletion rates for several lakes. There was strong relationship between light extinction coefficients of the ice cover and depletion rates for several lakes

indicating that oxygen production was causing the year-to-year variability in depletion rates. The importance of oxygen production suggests that year-to-year variability in depletion rates is caused by variability in net water column oxygen consumption. Lake-to-lake variability, then, is caused by differences in sediment oxygen consumption related to the morphometric and average productivity characteristics of the lakes.

These observations have implications for assessing the impact of climate change, as changes in lake productivity, morphometry, and winter cover characteristics could affect depletion rates. Variability from year to year is also important for predicting the risk of winterkill over a period of years. Several multiple regression models are presented which combine lake-specific and year-specific variables to make predictions about winter oxygen depletion rates.

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INTRODUCTION

Anoxia in lakes is a concern for lake management, both because of its impact on fish survival (Moore 1942; Greenbank 1945) and the role of low oxygen in releasing phosphorus from the sediments (Mortimer 1941). The hypolimnion in the summer and the whole lake under winter ice cover are isolated from oxygen inputs from the atmosphere. During the late summer or late winter, oxygen depletion can proceed to the extent that large portions of the water column become anoxic, resulting in fish mortality if the fish are unable to find refuges (Coutant 1985; Magnuson et al. 1985). The extent of anoxia is dependent on the length of stratification or ice cover, the initial oxygen concentration at the time of stratification or freeze-up, and the oxygen depletion rate. This paper focuses on this latter mechanism in terms of winter anoxia.

Hutchinson (1938) pioneered the use of the areal hypolimnetic oxygen deficit (AHOD) as a means of comparing productivity among lakes. Since then, numerous authors have used AHOD as a comparative tool and have studied its relationship to morphometry and productivity (e.g. Cornett and Rigler 1980; Charlton 1980). Schindler (1971) maintained that the winter oxygen depletion rate is a more reasonable estimate of lake metabolism than the summer deficit since oxygen production is limited under ice cover. Many studies have compared winter oxygen depletion rates among lake types to predict winter anoxia (Babin and Prepas 1985), oxygen profiles (Jackson and Lasenby, 1982; Molot et al. in press), and winterkill risk (Barica and Mathias 1979).

Lake morphometry and productivity both influence the magnitude of winter oxygen depletion rates among lakes. Depletion rates are primarily related to morphometry, with deeper lakes having higher areal depletion rates (Barica and Mathias 1979). Welch et al. (1976) found that depth was the dominant factor in winter oxygen depletion but that summer chlorophyll a (chl a) and total phosphorus (TP) were also involved. Mathias and Barica (1980) illustrated the interaction of morphometry and productivity by regressing volumetric depletion rates for several lakes against the sediment area to lake volume ratio. Given similar sediment area to volume ratios, oligotrophic lakes had much lower depletion rates than eutrophic lakes. Babin and Prepas (1985), combining data from several different lake districts, proposed an empirical model to predict depletion rates from mean depth and summer total phosphorus.

Studies disagree as to whether winter oxygen depletion rates exhibit interannual variability. Mathias and Barica (1980) mention that depletion rates were fairly similar from year to year, despite five-fold variations in summer chl a concentrations. Others note that sediment oxygen consumption rates in a lake are fairly constant from year to year (Lasenby 1975) and differ little between summer and winter (Linsey and Lasenby 1985). In contrast, Greenbank (1945) and Nickum (1970) observed that winterkill was more likely to occur in years with more snow cover. In addition, Halsey (1968) noted that depletion rates were greater in years with longer periods of snow cover. Others have documented similar relationships between light availability and low oxygen conditions (Prowse and Stephenson 1986;

Catalan 1992), suggesting that depletion rates could vary from year to year depending on the thickness and duration of snow and ice. No studies, however, have explicitly examine the year-to-year variability in rates of winter oxygen depletion.

Variability in winter oxygen depletion could have important implications for assessing the effects of climate change on lakes. Warmer summer temperatures and a longer growing season could result in increased algal biomass leading to increased import of organic matter to the sediments and increased rates of winter oxygen depletion. Snowier, wetter winters also could result in increased oxygen depletion if photosynthesis is blocked by low light conditions. Increased rates of oxygen depletion could have important consequences for fish communities. Tonn and Magnuson (1982) and Rahel (1984) have shown that winterkill frequency determines the structure of fish assemblages in northern Wisconsin lakes. If depletion rates increased due to climate change, then the frequency of winterkill would be expected to increase, leading to alterations in fish assemblages. More frequent winterkill is of concern to lake managers, as they would have to consider artificial aeration and fish stocking to maintain productive fisheries (Patriarche and Merna 1970). Thus, it is important to know how depletion rates vary from year to year and what factors control the variability.

A simple mass balance model illustrates the factors involved in winter oxygen depletion (Fig. 1). A generalized equation for this model is:

$$d[O_2]/dt = SOC + WOC + R - P \tag{1}$$

where $d[O_2]/dt$ is the rate of oxygen depletion, SOC is the sediment oxygen consumption rate, WOC is the water column oxygen consumption rate, R is the algal respiration rate, and P is the algal photosynthetic rate or oxygen production rate.

Consumption by sediments is usually considered the primary source of oxygen depletion in lakes (Mortimer 1941; Hatcher 1986; Baird et al. 1987). Oxygen depletion occurs at the sediment-water interface as a result of microbial decomposition of organic material in the sediments and the oxidation of reduced species, such as iron and sulfur (Mortimer 1941; Hatcher 1986). In dissolved oxygen models, SOC usually is modeled as a temperature-dependent constant, although it is sometimes modeled as a function of the oxygen concentration as well (Bowie et al. 1985; Snodgrass 1986). Sediment oxygen consumption is also thought to be a function of the benthic community composition and the organic and physical characteristics of the sediments (Hatcher 1986; Pamatmat 1986). During the winter, temperatures are generally uniform across lakes and do not vary much among years. Thus different lakes would be expected to have different rates of sediment oxygen consumption depending on the nature of the sediments and dissolved oxygen concentrations.

Dissolved oxygen models usually estimate SOC empirically and assume that continued settling of organic matter balances substrate decay. Thus SOC is considered to be at steady state for a given lake (Bowie et al. 1985). Yearly variability would come only from differences in temperature and dissolved oxygen concentrations. In real systems, however, the amount of organic matter supplied to

the sediments might be a source of variability in the sediment consumption rate from year to year. Summer chl *a* and TP concentrations are correlated to winter oxygen depletion rates, i.e., more productive lakes tend to have higher depletion rates (Mathias and Barica 1980; Babin and Prepas 1985). Extended to year-to-year variations within a lake, increased algal abundance in a given summer could have the potential to increase depletion rates the following winter.

A second source of oxygen depletion is through degradation of dissolved and particulate organic matter in the water column (WOC), both through carbonaceous oxygen demand and nitrification (Bowie et al. 1985; Ellis and Stefan 1989). WOC usually is modeled as a function of temperature and the amount of organic matter in the water column. Water column oxygen consumption can be quite large, particularly in deeper, more productive lakes (Hargrave 1973; Charlton 1980). During the winter, however, water column oxygen consumption has been found to be negligible compared to sediment oxygen consumption (Mathias and Barica 1980), and thus unlikely to exert substantial year-to-year or lake-to-lake differences in winter oxygen depletion.

Algal respiration and photosynthesis comprise the third component of oxygen dynamics in lakes during the winter. Photosynthesis might be the only source of oxygen when lakes are ice-covered because contact with atmospheric oxygen is virtually nonexistent. Stream-flow connections and freeze-out of dissolved gases with ice formation have also been identified as possible sources of oxygen (Welch et al. 1976). Stream connections are limited in the lakes to be considered in this

analysis, however, and freeze-out generally adds oxygen only to the top few centimeters of the water column. These sources are probably negligible compared to photosynthetic oxygen production. Algal respiration is temperature-dependent and can be considered part of the water column consumption. The magnitude of this component depends on the amount of algae present in the water column, but probably has only a minor effect relative to photosynthesis.

If light availability varies from year to year or lake to lake, variations in photosynthetic oxygen production could result and produce variations in winter depletion rates. Algal photosynthetic rates depend on temperature, light availability, and nutrient concentrations (Talling 1957; Bowie et al. 1985). When light is low, however, it becomes the limiting factor (Kirk 1983). Because light conditions are reduced severely by snow and ice during the winter, photosynthetic rates depend directly upon the thickness and opacity of the cover components. Snow, grey ice, and black ice all have different light extinction and reflection characteristics (Adams 1978) and could exert variable influences on the light regime under the ice. Thus, photosynthetic rates could vary both seasonally and among lakes and years, depending on the composition of the snow and ice cover. For example, Wright (1964) noted variations in chl a concentrations and primary production under the ice caused by changes in light intensity following snowfall events. Furthermore, Prowse and Stephenson (1986) documented a direct relationship between light availability and oxygen concentrations under ice cover through the winter. Thus variations in oxygen concentrations can be directly tied to variations in the light

environment.

To summarize, the major potential sources of variability in winter oxygen depletion rates are variations in the sediment consumption rate due to the organic characteristics of the sediments and the oxygen concentration at the sediment surface and variations in net oxygen consumption in the water column caused by variations in algal photosynthetic rates limited by light availability.

Can variability in oxygen depletion rates from year to year be explained by variations in the light environment, and thus by the amount of oxygen production from photosynthesis? Or is the variability due to differences in productivity which drive variations in sediment oxygen consumption? I hypothesize that lake average conditions, such as morphometry and productivity, set the average observed depletion rate for a given lake, primarily through their influence on sediment oxygen consumption processes. Sediment consumption might vary gradually from year to year, but year-to-year variability results mostly from winter-specific light characteristics that modify net oxygen consumption in the water column through variation in photosynthetic oxygen production.

The objectives of my thesis are: 1) to characterize the year-to-year variability in winter oxygen depletion rates for nine lakes in northern Wisconsin; 2) to examine the influence of light availability and productivity on the year-to-year variability in oxygen depletion rates; and 3) to determine the relative contribution of sediment and net water column oxygen consumption to the variability of oxygen depletion rates.

I have used volumetric estimates for oxygen depletion rates in this paper even though the areal rate has been used more commonly in limnology. Hutchinson (1938, 1957) advocated areal estimates for hypolimnetic oxygen depletion, which he felt were more useful than volumetric expressions in comparing the productivity of a large number of lake types, because they were independent of depth. However, Charlton (1980) and Cornett and Rigler (1980) have pointed out that the neither the areal rate nor its volumetric equivalent is depth-independent, and have advocated taking hypolimnetic thickness as well as temperature into account when calculating oxygen deficits.

Winter oxygen depletion rates have usually been reported in areal units as well (e.g. Schindler 1971; Babin and Prepas 1985), although a few studies have used the volumetric rate (Mathias and Barica 1980; Catalan 1992). While not independent of depth, the volumetric depletion rate is a more true measure of lake metabolism and provides information about the amount of oxygen in a given unit volume of water which can be easily compared from lake to lake. Areal rates are reported for comparison with other lake districts, but otherwise the volumetric expression will be used.

METHODS

Data set

Primary study lakes at the North Temperate Lakes, Long Term Ecological
Research (LTER) site in northern Wisconsin (Kratz et al. 1986) provided a ten-year
data set (1982 to 1991), and several lakes with which to assess temporal variability
in winter oxygen depletion rates. Lakes include Allequash Lake (north basin), Big
Muskellunge Lake, Crystal Lake, Crystal Bog, Sparkling Lake, Trout Bog, Trout
Lake (southeast basin) and the two basins of Little Rock Lake (north and south).
Limnological data have been collected routinely from these lakes since the spring of
1981, including temperature, oxygen, pH, Secchi, chl a, light irradiance,
zooplankton, phytoplankton, fish, and an exhaustive list of organic and inorganic
compounds (anions, cations, metals, dissolved carbon, TP; Kratz et al. 1986).
Sampling was begun on Little Rock Lake in the fall of 1983 as part of the Little
Rock Lake Acidification Project. The lakes represent a variety of morphometric and
trophic states, ranging in size from 0.5 to 750 ha, with summer chl a in the euphotic
zone ranging from 2.8 to 28.3 μg/L (Table 1). The lakes all freeze in mid- to late
November and stay frozen for four to five months.

Data collection

Oxygen data were collected three times each winter on the LTER lakes,
usually every five weeks beginning in mid-January. On each sampling date, vertical
profiles of dissolved oxygen (DO), temperature, chl a, dissolved and total organic
carbon (DOC and TOC), and light irradiance were obtained. Average snow depth

and thickness of the grey and clear ice cover were also measured. DO was measured at 1 m depth intervals from the surface to within 1 m of the bottom of the lake at its deepest point. During ice cover, the surface DO reading was taken at the ice-water interface, but the deeper readings were taken relative to the water surface. DO concentration was measured with a YSI yoltmeter and Clark-type membrane electrode over the entire period of data collection. The electrode was calibrated quarterly using the standard Winkler method with azide modification (APHA 1985). Methods used to collect the other variables are documented elsewhere (Kratz et al. 1986).

Oxygen data were available for the first few weeks of ice cover for Little Rock Lake only. To estimate the initial oxygen concentration at the time of freeze-up for the LTER lakes, I used the oxygen profile from the last ice-free sampling date, which usually occurred two to four weeks before the onset of ice cover. Sometimes the lakes were not completely mixed at this time or were still several degrees above freezing, especially if there was a long time interval between the sampling date and freeze-up. Such situations could have led to oxygen concentrations that were 2 to 3 mg/L lower than the initial concentration at freeze-up. Usually, though, these ice-free oxygen concentrations likely approximated conditions at freeze-up within 1 mg/L.

Calculations

I calculated oxygen depletion rates from the oxygen profiles following the techniques of Barica and Mathias (1979) and Babin and Prepas (1985). First, the

oxygen concentrations at each depth were multiplied by the volume of the corresponding horizontal 1 m depth interval. The surface (0 m) value was multiplied by the interval from the bottom of the ice to 0.5 m, while the deepest value represents the interval from 0.5 m above its depth to the bottom of the lake. Then the oxygen masses were summed across depth intervals, yielding an oxygen mass for the whole lake. This value was then divided by the volume of the lake (corrected for ice thickness) or the area of the lake at the ice-water interface, resulting in a weighted average volumetric (g O_2/m^{-3}) or areal (g O_2/m^{-2}) oxygen concentration. Next, the weighted average concentration for each sampling date was regressed against the number of days since freeze-up (with the last ice-free estimate set at 0 days). The slope represents the winter oxygen depletion rate, expressed volumetrically as g $O_2 \cdot m^{-3} \cdot d^{-1}$ and areally as g $O_2 \cdot m^{-2} \cdot d^{-1}$.

The limited number of samples collected on the LTER lakes during winter presents some potential problems when calculating depletion rates. Depletion rates have been observed to be nonlinear, particularly later in the season because of oxygen inputs (Babin and Prepas 1985) or low oxygen concentrations (Ellis and Stefan 1989). Thus the depletion rate should either be calculated before the relation becomes nonlinear (Barica and Mathias 1979), or be expressed as a nonlinear function (Babin and Prepas 1985). Because the third sampling date was usually near the end of ice-covered period, a linear regression fit through three data points may not have reflected the true depletion rate. Including the last ice-free oxygen concentration was an attempt to provide more confidence in the estimate of the

depletion rate. Thus, most estimates are based on four sampling dates. In some cases either the ice-free or the late March oxygen concentration was dropped if a better fit resulted from its omission. In a few cases an estimate could not be made because of the poor fit of the regression. Most fits were quite good; 85% of the depletion rates had $R^2 > 0.90$, and the lowest R^2 was 0.71. Depletion rate estimates and relevant statistics are given in the Appendix.

Light attenuation was expressed in two ways, as percent transmission through the ice and snow cover (cover transmission) and as an extinction coefficient, after Adams et al. (1984). Cover transmission was calculated by dividing the light irradiance at the ice-water interface by the incident light irradiance at the surface of the ice and snow cover and multiplying by 100. The extinction coefficient (μ) was calculated as the natural log of the cover transmission divided by the thickness of the ice and snow cover. At low cover transmission ($< 10\%$) there is a wide range of extinction coefficients (> 5 m^{-1}) , while at extinction coefficients ≤ 5 m^{-1}, cover transmission increases linearly with decreasing extinction coefficient. Neither of these parameters were corrected for albedo or reflectance. Rather they express the capacity of the lake cover to prevent light from reaching the water column, whether through attenuation or reflection.

I estimated oxygen production rates for each lake and year to determine whether the amount of oxygen that could have been produced by photosynthesizing algae was great enough to offset the observed depletion rate, and to see whether variations in oxygen depletion rates could have been explained by variations in

oxygen production rates. I used an equation developed by Prowse and Stephenson (1986) for under-ice conditions to calculate oxygen production from light irradiance and chl *a* concentrations:

$$d[O_2]/dt = 2.67 \cdot s \cdot I \cdot [chl\ a] \qquad (2)$$

where $d[O_2]/dt$ is in mg·m^{-3}·h^{-1}, *2.67* is the molar ratio of oxygen produced to C fixed during photosynthesis, *s* is a slope term which describes the relationship of light to photosynthesis, an empirical value $\leq$ 0.2 (Jassby and Platt 1976), *I* is the irradiance in W/m^2, and *[chl a]* is in mg/m^3. This equation is derived from a more complex photosynthesis/irradiance curve which is linear under low light conditions (Jassby and Platt 1976). This equation assumes that at low light levels, such as those found under ice in winter, the photosynthetic rate is basically light limited. I used a value of 0.1 for *s*, which gives a conservative estimate of the oxygen production rate (Prowse and Stephenson 1986).

Using Equation 2, I determined production rates for the whole lake using volume-weighted average chl *a* concentrations and light irradiance measured at each sampling date. In addition, I estimated surface oxygen production rates by multiplying the chl *a* concentration at the surface by the light irradiance at the ice-water interface. As LTER light data were measured in μE·m^{-2}·sec^{-1}, I converted these units into irradiance units of W/m^2 using the relationship 1 W = 4.6 μE/sec, an average value for the wavelengths of photosynthetically active radiation, 380-720 nm (Wetzel and Likens 1991).

In order to make the volume-weighted oxygen production rate directly comparable to the volumetric depletion rate, I assumed six hours of light per day and divided by 1000 mg/g to get a rate of oxygen production in units comparable to the depletion rates. Since the depletion rates I have reported represent net depletion, the sum of this depletion rate and the oxygen production rate for a particular year and lake could be thought of as the "true" depletion rate. The effect of oxygen production rates can then be determined by calculating the percent reduction in oxygen depletion due to oxygen production.

Data analysis

Analysis of variance (ANOVA) was used to assess the importance of among-year and among-lake variability in depletion rates, chl a concentrations, and light levels. Years and lakes were considered treatments, while samples within a lake and year were treated as replicates. Since depletion rates are basically slope estimates, an analysis of covariance technique (ANCOVA) for testing the homogeneity of slopes was used to test whether depletion rates were significantly different from year to year within individual lakes (Wilkinson 1989). There are some problems with using analysis of variance for non-experimental data, most importantly the assumption of independence (Ott 1988). Thus the results presented here should not be taken as statistical proof, but as supporting evidence for sources of variability.

Coherence among lakes was examined by correlation of yearly depletion rates among lake pairs. Lakes can be considered coherent if they show similar patterns of variability in some variable over time, suggesting that some factor is affecting the

lakes uniformly (Magnuson et al. 1990). I determined coherence by performing a simple correlation between the yearly depletion rates for each pair of lakes. A high correlation coefficient indicated that a pair of lakes was temporally coherent in oxygen depletion rates.

Least-squares regression was used to examine the relationship between oxygen depletion rates and variables related to morphometry, productivity, and cover characteristics. Lake-to-lake differences were assessed by regressing depletion rates averaged over the ten-year period for each lake against corresponding means of the different variables. Year-to-year relationships were assessed for each lake using yearly depletion rates and yearly averages of the variables. In general, regressions with p-values ≤ 0.10 were considered to indicate a significant relationship. Multiple regression models were also fit using data from all lakes and years together.

Unless otherwise noted, volume-weighted averages were used for concentrations of the variables. Summer chl a concentrations were calculated for the euphotic zone, defined as that portion of the water column with $\geq 1\%$ of the surface light irradiance (Babin and Prepas 1985). In general, winter variables were averaged over the three winter sampling dates to obtain a year-specific value for each lake. Values for most variables were available for all years and lakes. Light data and DOC were not collected during the winter until 1985. DOC information was unavailable for Little Rock Lake and volume-weighted data were not available for Little Rock Lake for 1990-1991.

RESULTS

<u>Inter-lake variability</u>

Oxygen depletion rates averaged over the ten-year study period ranged from 0.084 g $O_2 \cdot m^{-3} \cdot d^{-1}$ for Crystal Bog to 0.023 g $O_2 \cdot m^{-3} \cdot d^{-1}$ for Trout Lake (Table 2; Fig. 2). Areal rates ranged from 0.154 to 0.404 g $O_2 \cdot m^{-2} \cdot d^{-1}$, similar to those reported for other lake districts (Table 3). The mean areal depletion rate for the LTER lakes (0.295 g $O_2 \cdot m^{-2} \cdot d^{-1}$) was most similar to the lakes in southern Ontario (0.232 g $O_2 \cdot m^{-2} \cdot d^{-1}$), and the prairie pothole lakes of Manitoba (0.256 g $O_2 \cdot m^{-2} \cdot d^{-1}$). The Experimental Lakes in northwest Ontario had a much lower average depletion rate (0.164 g $O_2 \cdot m^{-2} \cdot d^{-1}$), while the Albertan lakes had a higher depletion rate than the LTER lakes (0.470 g $O_2 \cdot m^{-2} \cdot d^{-1}$). Ranges of depletion rates for all lake districts overlapped with the range of values for the LTER lakes.

Lake-to-lake variance in mean depletion rates was significantly greater than the within-lake variance (ANOVA, Table 4a). The significance of the "Day X Lake" interaction ($p < 0.001$) indicates that depletion rates differed among lakes. Mean depletion rates for Big Muskellunge, Crystal Lake, Sparkling, Trout Bog, and Trout Lake were not significantly different from each other, but were lower than those of the other four lakes (Scheffe t-test for multiple comparisons, Fig. 2). Of these four lakes, the depletion rates for Crystal Bog and the two Little Rock Lake basins were similar, while that for Allequash was different from Crystal Bog and Little Rock-South. In general the shallower lakes had higher depletion rates and less variability than the deeper lakes (Tables 1 and 2; Fig. 2). Trout Bog was the

exception; although only 7 m deep, it had a mean rate more similar to the deeper lakes.

Examination of oxygen profiles from 1991 for four lakes provided further insights into the differences in oxygen depletion among lakes (Fig. 3). Three of the lakes, Allequash, Sparkling, and Big Muskellunge, had relatively high and vertically uniform oxygen concentrations just before the onset of ice cover. Allequash then showed steady depletion at all depths throughout the winter, with a fairly linear decrease in oxygen with depth. In Sparkling, oxygen depletion occurred most extensively below 8 m, and then only between the last two sampling dates. Big Muskellunge, which is the same depth as Sparkling, also exhibited more depletion during the last time interval, but with quite extensive depletion at all depths. Trout Bog, which began the winter with uniformly low oxygen concentrations, became depleted to zero oxygen quite rapidly from 2 to 7 m, but had an increase in oxygen concentrations just under the ice. Thus, although depletion occurred in all lakes, the pattern of depletion varied among the lakes, both vertically in the water column and over the course of the winter.

Morphometric variables best explained the variance in depletion rates among the nine lakes (Table 5). The best predictors were the log of the sediment area to lake volume ratio (A_s/V; Fig. 4) and log mean depth (Fig. 5) with $R^2 > 0.80$. Other variables were correlated to the depletion rate, including total ice thickness, grey ice thickness, and summer epilimnetic temperatures (Table 5); however, they were also highly correlated to mean depth and/or A_s/V (Table 6). Productivity

variables were not correlated with depletion rates unless Trout Bog was excluded (Table 5), in which case summer euphotic zone chl *a* and summer Secchi depth were significantly correlated to the depletion rate. Again, these variables were strongly correlated to mean depth and the sediment area to volume ratio (Table 6). Deep lakes tended to be less productive than shallow lakes.

Cover transmission and extinction coefficients were correlated fairly strongly with cover characteristics, particularly grey ice and snow + grey ice thickness (Table 6). Lakes with thicker snow and grey ice tended to have lower light levels. However, these light parameters were inversely related to winter chl *a* concentrations, such that lakes with more light available had lower winter chl *a* concentrations. The bogs strongly affected this relationship, as they had comparatively low light conditions, yet high winter chl *a* concentrations.

Inter-year variability

The LTER lakes exhibited substantial variability in depletion rates from year to year (Table 2). Coefficients of variation ranged from 11% for Crystal Bog to 71% for Trout Lake. Analysis of variance indicated that year-to-year variability was not significant compared to lake-to-lake variability (Table 4b). Yearly variability was significant, however, within particular lakes (Table 4c). Testing the homogeneity of slopes assumption for each lake individually, I found that Allequash, Big Muskellunge, Trout Lake, and Little Rock-North had significant differences in their depletion rates from year to year with 95% probability. Depletion rates in Sparkling were significantly different from year to year at 90%.

While not all lakes had statistically significant variability in depletion rates from year to year, depletion rates on several lakes appeared to be temporally coherent (Fig. 6). For example, depletion rates in 1982 were high for Sparkling, Crystal Lake, and Trout Lake, while depletion rates in 1986 and 1990 were rather high for Crystal Bog, Little Rock-South, Allequash and Trout Bog. Years with low depletion rates were not as uniform across lakes, although several lakes had low depletion rates in 1987. Using the paired correlation analysis, depletion rates for Allequash, Crystal Bog, and Little Rock-South were significantly correlated with each other, as were those for Crystal Lake, Sparkling, and Trout Lake (Table 7). Other significant correlations included Little Rock-North and Allequash, Trout Bog and Allequash, and Big Muskellunge and Trout Lake.

Two groups of coherent lakes can be identified, one consisting of the four deepest lakes, and the other of the remaining shallower lakes (Fig. 6). Within each of these groups, the lakes have similar patterns in the variability of their depletion rates over time, but the two groups have different patterns from each other. Lakes with relatively similar depths tended to have higher correlations (median r = 0.93 for deep lakes and 0.67 for shallow lakes), while pairings of deep and shallow lakes tended to have lower correlations (median r = 0.20; Table 7). This distinction can be illustrated by plotting the correlation coefficient for each lake pair against the difference in maximum depth of the two lakes (Fig. 7).

Comparing oxygen profiles from 1990 (Fig. 8) to those from 1991 (Fig. 3) on four lakes provides further evidence for the differences that can occur in

depletion rates from winter to winter. The oxygen concentrations were generally lower at all depths during 1990, indicating higher depletion rates (Table 8). Another difference is that the three mid-winter profiles were much closer together in 1990 than those for 1991, indicating that most of the depletion occurred before the January sampling date. Also, gains in oxygen at certain depths were apparent in the late March profile for three of the lakes: from 3 to 5 m in Allequash, 2 to 7 m in Big Muskellunge, and 4 to 10 m in Sparkling. In 1991, steady depletion occurred at all depths over the course of the sampling period. Other variables showed differences between 1990 and 1991 as well (Table 8). Chl a concentrations were generally lower in 1990, as was light availability. Interestingly, the total cover thickness between the two years was fairly similar, but snow and grey ice were much thicker in 1990.

Factors controlling inter-year differences

Regressing yearly depletion rate estimates against a variety of other yearly variables revealed no consistent predictors of depletion rates across all lakes (Table 9). Winter chl a was weakly correlated to the depletion rate on Crystal Bog (p = 0.06). Snow depth, total cover, and ice thickness were fairly good predictors for several lakes. Indeed, thicker snow or ice cover was associated with higher depletion rates on all lakes except Sparkling. Light transmission through the cover was related to depletion rates for Crystal Bog (p = 0.07), while the most consistent variable was the cover extinction coefficient, which was significant for Allequash (p = 0.03), Crystal Bog (p = 0.07), Crystal Lake (p = 0.05), and Trout Bog (p =

0.01). Higher depletion rates occurred in years with greater extinction coefficients (Fig. 9).

There is little evidence that interannual differences in summer production had an influence on oxygen depletion rates, illustrated by summer euphotic zone chl a concentrations for three lakes (Fig. 10). Peak depletion rate years were not generally associated with high chl a concentrations the previous summer, although they were weakly related on Trout Lake (Table 9). Spring TP and summer Secchi disk depth were not correlated to depletion rates for any of the lakes. Summer epilimnetic temperatures were related to depletion rates on Little Rock-North and Sparkling, but with different signs. Regional climate data, such as annual precipitation and cumulative snowfall, were not related to depletion rates, but summer air temperature was negatively related to the following winter's depletion rate on three lakes. No correlations were found between depletion rates and the length of the ice-free season. To combine effects of lake-specific variables, such as morphometry, with yearly variable parameters, I performed multiple regressions using a data set comprised of yearly parameters for eight of the lakes. Trout Bog was excluded because of its unexpectedly low depletion rates given its depth and chl a concentrations (Tables 1 and 2). I used A_s/V as the morphometric term in all of the regressions, and mean snow depth (sn), cover extinction coefficient (μ), winter chl a ([chl $a]_w$), and summer euphotic zone chl a ([chl $a]_{su}$) as the yearly variable terms. I used only data from lakes and years with depletion rate estimates and values for all of the variables (n = 43).

With this data set, A_s/V alone explained 74% of the variability in depletion rates (Table 10). Coefficients were similar to those found using ten-year mean depletion rates (Table 5). [Chl $a]_{su}$ also had a relatively good fit. Adding any of the yearly variable parameters to A_s/V slightly improved the R^2 of the model (additional variables were significant at $p \leq 0.10$). Snow depth had the greatest effect, increasing R^2 from 0.74 to 0.79.

Three-term models were fit using A_s/V, a chlorophyll term and the light or snow term. All models had R^2 between 0.80 and 0.82, with the models incorporating snow depth slightly better than those incorporating μ. The models including [chl $a]_{su}$ were slightly better than those with [chl $a]_w$. Overall the model with the best fit was:

$$WODR = 0.003 + 0.093(A_s/V) + 0.001(S) + 0.001([chl\ a]_{su}) \quad R^2 = 0.82 \tag{3}$$

The mass balance model presented in the introduction (Equation 1) can be modified to incorporate rate constants (k_n) and state variables, such that:

$$WODR = k_1(A_s/V) + (k_2-k_3)(chl\ a) + k_4(DOC) \tag{4}$$

where:

k_1 = sediment oxygen consumption rate, g $O_2 \cdot m^{-2} \cdot d^{-1}$

k_2 = algal respiration rate, g $O_2 \cdot mg\ chl\ a^{-1} \cdot d^{-1}$

k_3 = algal photosynthetic rate, g $O_2 \cdot mg\ chl\ a^{-1} \cdot d^{-1}$

k_4 = organic matter oxidation rate, g $O_2 \cdot g\ C^{-1} \cdot d^{-1}$

To determine coefficients for this equation, I fit a multiple regression model using A_s/V, [chl $a]_w$, and DOC. There were only 28 data points available for this

regression because of the limited number of DOC measurements. The resulting

equation was:

$$WODR = 0.138(A_s/V) - 0.002([chl\ a]_w) + 0.0002(DOC) + 0.016 \qquad R^2 = 0.84 \quad (5)$$

The A_s/V and chl a terms were both significant, but the DOC term was not (p =

0.67 when added as the final variable). The negative [chl a]$_w$ term indicates net

oxygen production by the algal component.

To illustrate the effects of sediment oxygen consumption versus that of water

column processes, I divided Equation 5 into a sediment oxygen consumption term

(SOC) and a water column consumption term (WOC), such that:

$$SOC = 0.138(A_s/V) \qquad\qquad\qquad (6)$$

$$WOC = 0.016 - 0.002[chl\ a]_w + 0.0002(DOC) \qquad\qquad (7)$$

I used these equations to calculate sediment and water column oxygen consumption

for all the lakes except Little Rock using yearly [chl a]$_w$ and DOC values. Mean

SOC and WOC for each of the seven lakes were then plotted as a function of depth

in terms of their percent contribution to the overall depletion rate (Fig. 11). SOC

accounted for nearly 100% of the overall depletion rate in the shallowest lake,

dropping to $\leq$ 50% in the three deepest lakes. WOC represented an increasing

proportion of the depletion rate with increasing depth reaching almost 60% in the

deepest lake.

Oxygen production

Mean whole-lake oxygen production rates ranged from 0.7 to 7.7 mg $O_2 \cdot m^{-3} \cdot$

h^{-1} for the LTER lakes over the period 1984 to 1991 (Table 11). Mean surface rates

varied from 1.6 to 25.0 mg $O_2 \cdot m^{-3} \cdot h^{-1}$. Oxygen production rates varied considerably from year to year as evidenced by the large standard deviations (Table 11). Indeed yearly oxygen production rates ranged from < 0.1 to 91.5 mg $O_2 \cdot m^{-3} \cdot h^{-1}$. As a result of this large variability, oxygen production values reported here should probably be considered order of magnitude estimates at best. For comparison, Prowse and Stephenson (1986) report values of 0.44 mg $O_2 \cdot m^{-3} \cdot h^{-1}$ under white ice conditions up to 19.0 mg $O_2 \cdot m^{-3} \cdot h^{-1}$ under black ice with no snow, assuming a chl a concentration of 0.5 μg/L.

Oxygen production reduced the "true" depletion rate by as little as 0.1% in some years to as much as 38% for Trout Bog and 68% for Big Muskellunge (Table 12). On average, oxygen production offset the "true" depletion rate by 12% for Allequash up to 30% for Trout Lake. Thus even for a conservative estimate, oxygen production could have a fairly significant impact on the "apparent" oxygen depletion rate in a given year.

Averaging over seven years, whole-lake oxygen production rates were positively correlated to depletion rates $(R^2 = 0.56)$, meaning that lakes with high production rates also had high depletion rates (Table 13). This was primarily the result of the different trophic states of the lakes as evidenced by the relationship between oxygen production and chl a. Oxygen production was positively correlated to chl a on a lakewide basis $(R^2 = 0.80, p = 0.003$ without Trout Bog), but not related to light irradiance (Table 14). Thus lakes with less light available had higher production rates because of the amount of chl a. These high chl a lakes also tended

to have high depletion rates.

Yearly depletion rates were significantly related to surface oxygen production rates on Crystal Bog and Trout Bog (R^2 = 0.73 and 0.75; Table 13). Years with high oxygen production were associated with low depletion rates, as shown for Trout Bog (Fig. 12). Crystal Lake had a significant negative correlation between oxygen depletion and whole-lake oxygen production, but this was based on just four data points. Little Rock-South showed weak negative correlations between both measures of oxygen production and depletion rates (Fig. 13) as did Trout Lake and Big Muskellunge. Allequash, Little Rock-North, and Sparkling showed no relationship between oxygen production and depletion. Light availability appeared to explain the variability in oxygen production rates from year to year for most lakes (Table 14). Big Muskellunge, Crystal Lake, Little Rock-North, and Little Rock-South had significant correlations between oxygen production and light levels, but not with chl *a* levels. Crystal Bog had correlations between oxygen production and both chl *a* and light. Allequash, Sparkling, and Trout Lake also showed correlations to both chl *a* and light, but were dominated by chl *a*. Trout Bog was related to chl *a* concentrations, but not light.

DISCUSSION

Winter oxygen depletion rates can be thought of as having two major

consumption components: sediment oxygen consumption and net water column

oxygen consumption (including the net effects of decomposition of organic matter,

algal respiration, and photosynthesis). If sediment and water column oxygen

consumption are affected by different mechanisms, they could show differences in

their patterns of variability among lakes and years leading to the differences

observed in the variability of depletion rates. The different mechanisms seem to be

related to the morphometry and productivity of lakes and to climate as expressed

through snow and ice cover. Each of these sources of variability affects depletion

rates differently, and thus will be considered separately. Since morphometry and

productivity are related in the study lakes, I will discuss these two factors together.

The final section deals with integrating the different sources of variability through

multiple regression.

Morphometry and productivity

The LTER lakes exhibited considerable variability from one lake to another

in their mean volumetric depletion rates over the period of study. The differences

among lakes were most apparent between the shallow lakes and the deep lakes (Fig.

2). The deeper lakes (Sparkling, Crystal Lake, Big Muskellunge, and Trout Lake)

all had similar mean depletion rates that were lower than those of the shallower

lakes (Allequash, Crystal Bog, and the Little Rock basins).

Other researchers have reported a link between depth and the areal depletion rate (Welch et al. 1976; Barica and Mathias 1979; Babin and Prepas 1985). The relationship is the reverse of that with volumetric depletion rates in that deeper lakes have higher areal depletion rates. Welch et al. (1976) attribute the relationship to higher amounts of oxygen storage in shallow lakes, or the fact that shallow lakes respire more of their organic production in the summer when temperatures are high. However, the relationship might also be simply the result of morphometry. Deep lakes have a higher volume of water per unit surface area, and so exhibit larger rates of oxygen depletion per unit area, given a constant volumetric rate (Welch and Bergmann 1985).

Regardless of the reason for the relationship between depth and depletion rates, depth is not directly involved in the mechanisms of oxygen depletion. A more relevant morphometric expression is A_s/V. Although inversely related to mean depth for the LTER lakes (Table 6), A_s/V seems a more appropriate predictor from a mechanistic point of view and in fact had a better fit to depletion rates than mean depth (Fig. 4). This ratio describes the relative importance of the sediment surface to a given volume of water. Since most of the observed oxygen depletion is thought to occur at or near the sediment-water interface (Mortimer 1941; Mathias and Barica 1980; Baird et al. 1987), it makes sense that those lakes with higher ratios exhibited higher depletion rates.

Mathias and Barica (1980) also demonstrated the importance of the sediment area to volume ratio for a variety of Canadian lakes. They regressed volumetric

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depletion rates (WODR) against A_s/V for two sets of lakes, one oligotrophic and one eutrophic. The slopes of the regression lines can be thought of as mean sediment oxygen consumption rates (SOC) for the two sets of lakes, while the intercepts can be thought of as the water column oxygen consumption rates (WOC). They found that the sediments in eutrophic lakes consumed oxygen three times more rapidly than oligotrophic lakes (0.226 and 0.075 g $O_2 \cdot m^{-2} \cdot d^{-1}$ respectively). WOC in both cases was 0.01 g $O_2 \cdot m^{-3} \cdot d^{-1}$. The similar regression for the LTER lakes (Fig. 4) produced a mean SOC of 0.121 g $O_2 \cdot m^{-2} \cdot d^{-1}$, closer to the oligotrophic grouping of the Canadian lakes. WOC was somewhat higher (0.019 g $O_2 \cdot m^{-3} \cdot d^{-1}$), indicating that respiration in the water column may have been more important in the LTER lakes.

The clear differences in the patterns of variability from year to year between the shallow lakes and the deep lakes (Fig. 6) suggest that different mechanisms influence the yearly variability of depletion rates among deep and shallow lakes or that there are depth-dependent differences in the relative importance of the various components of the depletion rate. Shallow lakes are likely to be more influenced by sediment oxygen consumption because these lakes have high sediment area to volume ratios and a large proportion of the water column is within a few meters of the sediment-water interface. Deep lakes, in contrast, have much more water volume per unit area of sediment, and so might be more influenced by oxygen consumption in the water column than in the sediments. A higher proportion of organic matter is consumed in the water column of deep lakes, resulting in less organic matter available for sediment consumption (Hargrave 1973; Charlton 1980).

Thus, deeper lakes might have lower rates of sediment oxygen consumption, leading to less of an impact on the variability of the overall depletion rate.

The profiles from 1990 and 1991 (Figs. 3 and 8) further illustrate the differences between deep and shallow lakes. In all four lakes, oxygen levels are rather low in the bottom few meters by late March. In addition, oxygen was depleted more rapidly at lower depths in 1990 than in 1991, indicating that sediment oxygen consumption was variable between the two years. In Allequash and Trout Bog, however, these bottom few meters represent a larger proportion of the water column than in the two other lakes. Thus the sediment consumption rate had a large effect in these lakes. By contrast, the majority of the water column remained well-oxygenated in the two deeper lakes (Big Muskellunge and Sparkling). Depletion was most apparent only in the bottom quarter of these lakes (Figs. 3 and 8). Thus, even if the sediment consumption rate was variable in the deep lakes, its overall effect on the whole-lake depletion rate would have been much less than in the shallow lakes. Also, because depletion rates are volume-weighted, small differences in oxygen concentrations in the upper part of the water column can have a large effect on depletion rates (Linsey and Lasenby 1985). Water column oxygen consumption thus seems to be a more important factor in year-to-year variability of depletion rates in deep lakes.

The regression equation incorporating A_s/V, winter chl a, and DOC provides further information about the relative importance of water column oxygen consumption and sediment oxygen consumption in deep and shallow lakes (Equation

5). As lakes deepened, WOC represented an increasing proportion of the overall depletion rate, representing over half of the total depletion in the three deepest lakes (Fig. 11). In contrast, SOC was more dominant in the shallow lakes. These differences could have caused the different patterns of variability exhibited among deep lakes and shallow lakes (Fig. 6). Variability from year to year in shallow lakes might have been caused by variability in sediment oxygen consumption processes, while variations in water column oxygen consumption might have had more of an influence in deep lakes.

Productivity has been identified as another factor governing variability in depletion rates among lakes (Welch et al. 1976; Babin and Prepas 1985). Highly productive lakes tend to exhibit higher depletion rates in the summer because of the increased amount of organic matter being exported to the sediments (Hutchinson 1938, 1957), which results in higher sediment respiration rates (Hargrave 1973). For a given level of primary production, however, deeper lakes tend to have lower sediment respiration rates, because more of the organic material is decomposed in the water column (Hargrave 1973). Babin and Prepas (1985) found that productivity-related variables were good predictors of the areal depletion rate over a wide range of lake types during the winter. A model incorporating summer TP and mean depth explained the most variability for their data set. Welch et al. (1976) found that summer chl a and TP were good predictors of the areal depletion rate but that the effect of morphometry was much more significant when both parameters were included in a multiple regression model.

The interaction of morphometry and productivity is illustrated by the comparison of areal depletion rates for five different lake districts (Table 3). The mean depletion rates found for the LTER lakes were most similar to those reported for southern Ontario (Welch et al. 1976) and Manitoba (Barica and Mathias 1979), even though lakes in these districts are much·different in depth. The Canadian Shield lakes of Ontario are deeper and would be expected to have had high areal depletion rates, but are much more oligotrophic than the LTER lakes, and so had similar depletion rates. The Manitoban prairie lakes are the opposite - shallow, but very productive. These lakes had higher than expected depletion rates based on depth alone. In contrast, the Experimental Lakes (Schindler 1971) and the Albertan lakes (Babin and Prepas 1985), which are similar in depth to the LTER lakes, had very different ranges of depletion rates. The Albertan lakes are more productive on average than the LTER lakes, thus even though similar in morphometry, their depletion rates were higher. Similarly, the ELA lakes are more oligotrophic and thus exhibited lower depletion rates than those found in the LTER lakes. Thus, both productivity and morphometry seemed to influence depletion rates over a range of lake types.

Among the LTER lakes, productivity-related variables were not correlated to volumetric depletion rates (Table 5). Babin and Prepas (1985) mention that within a group of lakes of similar productivity, morphometry was the dominant predictor of depletion rates, and that productivity only became important when considering a diverse set of trophic conditions. The LTER lakes did have a fairly narrow range of

productivity (Table 1). The mean summer chl *a* biomass for the seven lakes ranged from 2.8 to 13.1 μg/L, while the bogs had somewhat higher concentrations (17.3 μg/L for Crystal Bog and 28.3 μg/L for Trout Bog).

Depletion rates and productivity parameters were related, however, when Trout Bog was excluded (Table 5). The confounding factor is that summer chl *a* in the LTER lakes was strongly correlated to mean depth and A_s/V (Table 6). Deep lakes, with low sediment area to volume ratios, had lower chl *a* concentrations than shallow lakes. This relationship made it difficult to distinguish the effect of productivity on depletion rates from the effect of morphometry. Both productivity and morphometry likely influence depletion rates in the LTER lakes, but morphometry is likely more controlling because of the narrow range of productivity.

As indicated throughout the preceding discussion, Trout Bog did not fit into the general patterns of the other LTER lakes. Although it had high chl *a* concentrations and is relatively shallow, the mean depletion rate for Trout Bog was comparable to those for deeper lakes (Table 2). As a result, when the mean depletion rate for Trout Bog was excluded from the regressions with depth, A_s/V, and the productivity variables, there was generally a better fit (Table 5). The reason for this discrepancy has to do with the nature of Trout Bog. First, because it is a bog, it has a high organic content and consumes oxygen rapidly to the point of being nearly anoxic by the end of the summer. Second, because of its fairly small surface area relative to its volume, complete mixing in the fall is uncommon. Crystal Bog, which also has a high oxygen demand, does not exhibit this behavior, because it is

fairly shallow and does not stratify. Thus, when Trout Bog freezes in the fall, it is rarely 100% saturated with oxygen, unlike the other lakes which are 90 to 100% saturated at freeze-up. For example, in the winter of 1990, Trout Bog was about 50% saturated at all depths just six days before freeze-up (Fig. 8). Thus oxygen depletion rates would have been much lower than if the lake had started out fully saturated (Trimbee and Prepas 1988). In addition, because of its high oxygen demand, much of the oxygen may have become depleted before the lake was sampled in January, making the apparent depletion rates lower than expected (Figs. 3 and 8).

As we have seen, sediment oxygen consumption appears to drive variability in depletion rates among lakes. Productivity influences the rate of sediment oxygen consumption, while morphometry determines the relative effect of sediment oxygen consumption over the whole lake. Morphometry is relatively uniform from year to year, but productivity could potentially cause year-to-year variability within a lake. Higher productivity in the summer might lead to greater influx of organic matter to the sediments, resulting in higher depletion rates the following winter.

Summer productivity variables, however, were poor predictors of year-to-year variations in winter oxygen depletion (Table 9). Neither summer Secchi depth, spring TP, or summer chl a was correlated with depletion rates. There was no evidence that increased chl a levels in the summer resulted in increased depletion rates the following winter (Fig. 10).

One explanation for this lack of correspondence is that sediment oxygen

consumption integrates several years of sedimentation so that annual differences in chl *a* production and subsequent flux to the sediments over a particular summer do not influence winter oxygen depletion (Graneli 1978; Mathias and Barica 1980). In fertilization experiments, Welch and Bergmann (1985) observed a time lag on the order of years between increased productivity from fertilization and increased winter oxygen depletion rates. Thus, one might expect to see long-term changes in sediment and whole-lake oxygen consumption with changes in trophic conditions caused by eutrophication, water quality improvement, or global warming. Random fluctuations in productivity from year to year, however, appear to be smoothed out by the sediment oxygen consumption rate.

A second explanation may be that the amount of organic matter in the sediments does not limit sediment oxygen consumption during the winter. Graneli (1978) noted that addition of fresh organic matter to sediment cores did not cause increases in oxygen depletion under lab conditions. The limiting factors could be low oxygen levels in combination with low temperatures, which would limit sediment oxygen demand during the winter (Bowie et al. 1985; Hatcher 1986). Sediment oxygen consumption rates have been noted to diminish when oxygen concentrations at the sediment/water interface fall below 3 mg/L (Bowman and Delfino 1980; Ellis and Stefan 1989). Thus, even a large influx of organic matter in a given summer would not result necessarily in increased oxygen depletion the following winter if the amount of organic matter is already in excess of the amount that can be oxidized.

Light availability and oxygen production

In contrast with summer production-related variables, sources of oxygen during the winter appeared to influence year-to-year patterns in winter oxygen depletion rates. Linsey and Lasenby (1985) measured water column and sediment oxygen consumption directly from water samples and obtained an estimate of the depletion rate that greatly exceeded the depletion rate estimated from oxygen profiles. This observation suggests that oxygen production through photosynthesis might be an important source of variability in depletion rates.

The most consistent predictors of depletion rates over several lakes were those having to do with modification of light availability, providing evidence for the importance of photosynthetic oxygen production. Different variables were important for the different lakes: snow depth for Allequash and Big Muskellunge; total cover thickness for Crystal Bog, Crystal Lake, and Trout Lake; and grey ice or grey ice and snow for Little Rock and Trout Bog (Table 9). These differences have to do with the relative importance of the various components on different lakes and their optical characteristics. Prowse and Stephenson (1986) and others (Bolsenga 1969; Adams 1978) have shown that grey ice reflects much more light than black or clear ice, while snow reflects an even greater amount. Thus grey ice thickness had a great effect on the light penetration in those lakes where grey ice was rather conspicuous, such as on the bogs and both basins of Little Rock Lake (Fig. 14). Similarly, Crystal Lake and Trout Lake, which usually had relatively little snow or grey ice cover (Fig. 14), were likely dominated by fluctuations in clear ice

thickness, explaining the correlation between total cover and depletion rates on these lakes.

Prowse and Stephenson (1986) also observed a relationship between oxygen depletion, cover thickness, and light penetration. They found that the timing and magnitude of oxygen depletion within a particular winter were linked to temporal changes in the snow and ice cover, due to its modification of light availability for photosynthetic oxygen production. Although they focused on seasonal changes, the relationship could be extended to yearly differences. For example, lower depletion rates observed in 1991 were accompanied by less snow, thinner grey ice cover, and lower extinction coefficients than in 1990 (Table 8). Over the ten-year study period, higher depletion rates were observed in those years that had higher mean extinction coefficients for several lakes (Fig. 9). The close correspondence between light availability and the depletion rate suggests that, at least for these lakes, oxygen inputs substantially influenced the variability of depletion rates from year to year.

A note should be made about the influence of light on the lake-to-lake variability in oxygen depletion rates. When Trout Bog was excluded, depletion rates were strongly correlated to total and grey ice thickness, the extinction coefficient of the cover, and percent light transmission (Table 5). Further, cover thickness and light penetration were strongly correlated to lake depth and the sediment area to volume ratio (Table 6), such that deeper lakes had more light penetration. It would appear then that deeper lakes, with more light available, had higher oxygen production rates which could have led to the lower depletion rates observed on these

lakes. As we will see in the next section, however, lakes with more light available actually had lower oxygen production rates because of low chl a levels. Thus, even though light and depletion rates were correlated on a lake-to-lake basis, morphometry and productivity still best explain the lake-to-lake variability in depletion rates.

Direct calculation of oxygen production provided further insights about the importance of photosynthesis in determining the year-to-year variability in depletion rates. Oxygen production rates were highly variable from year to year (Table 11) but on average could have offset the "true" depletion rate by 12% to 30% depending on the lake (Table 12). Yearly depletion rates, however, were strongly correlated to oxygen production rates for just two of the lakes, e.g. Trout Bog (Fig. 12). Several of the other lakes, such as Little Rock-South (Fig. 13), exhibited weak correlations between oxygen production and depletion, such that the year with highest oxygen production had the lowest depletion rate, and the years with no oxygen production had higher depletion rates. Oxygen production appeared to have offset oxygen depletion in these lakes, but the lack of a consistent linear relationship from year to year suggests that there may have been other sources of variability.

Chl a concentrations had the biggest effect on oxygen production among lakes (Table 14). Lakes with high chl a concentrations tended to have higher oxygen production rates, regardless of the light availability. Shallow lakes tended to have more chl a during the winter, but less light penetration, due to greater snow and grey ice cover (Fig. 14). Even though light was limited, the amount of chl a in

these shallow lakes was great enough to produce relatively high mean oxygen production rates. As we have seen, shallow lakes also tended to have the highest depletion rates (Fig. 5). Thus the more productive and shallower lakes had both higher oxygen depletion rates and higher oxygen production rates than the deeper and less productive lakes. Indeed, mean depletion rates were positively correlated to mean oxygen production rates (Table 13).

Though chl a concentrations dominated differences in oxygen production among lakes, yearly variations for most lakes appeared to be influenced by light levels (Table 14). Almost all of the lakes had significant negative correlations between average light irradiance and depletion rates, indicating that in years with low light availability there was also low oxygen production. Variations in chl a concentrations partially explained the variability in oxygen production for three lakes, but only Trout Bog showed no relationship to light levels.

To summarize, it seems that year-to-year variability in oxygen production can be attributed to variations in light availability, while lake-to-lake variability has to do with chl a concentrations. The explanation is fairly straightforward. As evidenced by analysis of variance (Table 15), winter chl a concentrations were more variable from lake to lake than year to year, while light irradiance at the surface was much more variable from year to year than among lakes. Whole-lake light irradiance had neither significant inter-year nor inter-lake variability. In other words, light levels were fairly similar among the LTER lakes under the ice, but were variable from year to year at the surface depending on the snow and ice conditions. In contrast,

chl *a* concentrations varied among the lakes because of their different trophic conditions, but varied little from year to year. Extended to depletion rates, the year-to-year variability of under-ice light levels seems to explain at least part of the variability exhibited by oxygen depletion rates, while the differences among lakes can be attributed in part to differences in productivity.

Integrating light, productivity and morphometry

We have seen that morphometry, productivity, and light availability under the ice each influence oxygen depletion rates for a given lake and the variability observed over time. Multiple regression models which incorporated those variables explained more than 75% of the overall variance exhibited in oxygen depletion rates among lakes and years (Table 10). Morphometry alone, specifically A_s/V, explained a good portion of the variance in depletion rates among lakes. However, including one or two potentially year-specific parameters significantly improved the fit of the model (Table 10). The models with the highest R^2 were those that included both winter or summer chl *a* and either snow depth or the cover extinction coefficient. These models provide further evidence that variations in the light environment under ice cover coupled with the amount of algal biomass could determine at least part of the yearly variability observed in oxygen depletion rates.

The inclusion of chl *a* in the multiple regression models indicates that productivity does affect depletion rates, but it is unclear whether it explains lake-to-lake or year-to-year variability. Summer chl *a* levels have a positive effect on depletion rates in that increased chl *a* biomass results in higher depletion rates. By

contrast, the winter chl *a* term is negative; more chl *a* in a given winter reduces the depletion rate. The difference is that summer chl *a* reflects the overall productivity of the lakes, so that lakes with higher chl *a* biomass tended to have higher depletion rates due to more organic matter to be decomposed. During the winter, chl *a* levels could reflect the amount of oxygen production that occurs, and thus higher chl *a* levels would result in lower depletion rates. Note, however, that neither chlorophyll term was significantly correlated with depletion rates for individual lakes over time, except Crystal Bog where higher winter chl *a* was correlated with lower depletion rates (Table 9). Also, winter chl *a* became a positive term in the multiple regression equations if Crystal Bog was left out. These observations all suggest that the influence of chl *a* is more of a lake effect than a year effect.

The light term, on the other hand, seems to reflect year effects, as extinction coefficients and snow depth were correlated with depletion rates on individual lakes (Table 9). As demonstrated previously, more attenuation of light combined with less chl *a* allows less photosynthesis to occur and less oxygen to be produced by algae. Snow depth and the cover extinction coefficient are both positive terms in the multiple regression models, indicating that years with less light availability result in higher depletion rates. However, the inclusion of the light term could mean simply that lakes with lower light had higher depletion rates, as depth and productivity were correlated with cover and light variables. It is unclear, then, whether the multiple regression models were able to distinguish lake effects from year effects.

Given information about the variability of chl a, light penetration, or cover characteristics, the multiple regression equations listed in Table 11 could be used to predict the mean rate of oxygen depletion in a lake and its potential range of variability. The most practical model for making predictions about the likelihood of winter anoxia might be the one incorporating A_s/V and mean snow depth as these variables are easily determined. A_s/V can be approximated by dividing the surface area of the lake by its volume, while mean snow depth can be measured easily and monitored over several years. With this information, one could then predict the expected mean depletion rate given a lake's surface area and volume, and the probable variability from year to year given the observed variability in snow cover. Coupled with measurement of the initial oxygen concentration at the time of freeze-up, one could predict the probability of dangerous oxygen depletion later in the winter, depending on the amount of snowfall.

CONCLUSION

Morphometry and productivity produce variability in winter oxygen depletion rates among lakes, while light availability and cover characteristics explain variations from year to year. These different sources of variability also affect different components of oxygen depletion. Morphometry and productivity primarily influence the sediment oxygen consumption rate. The productivity of the lake determines the composition and amount of organic material in the sediments, and thus sets the rate of sediment oxygen consumption, while the morphometry of the lake (A_s/V) determines the effect of sediment oxygen consumption on the whole-lake depletion rate. Light availability, in contrast, primarily affects the amount of oxygen produced in the upper part of the water column, and thus the amount of net water column oxygen consumption. While water column oxygen consumption may be less significant compared to sediment oxygen consumption, it appears to be the driving source of variability from year to year. Sediment oxygen consumption is relatively constant and set by morphometry and average productivity, while net water column consumption is variable and depends upon the amount of snow and ice in a given winter.

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TABLE HEADINGS

Table 1. Selected characteristics of study lakes. Data for Allequash are from the north basin only. Means and standard deviations (in parentheses) were calculated for the period 1982 to 1991, except for the light parameters, which were measured from 1984 to 1991. Data for Trout Lake are from the southeast basin only. No spring total phosphorus (TP) data were available for Little Rock Lake.

Table 2. Means, standard deviations (SD), and coefficients of variation (CV) for volumetric and areal depletion rates (WODR) for the study lakes from 1982 to 1991. "n" represents the number of years for which a depletion rate was calculated. Depletion rates were not calculated if a regression line could not be fit to the available data.

Table 3. A comparison of areal depletion rates and other characteristics for five lake districts. Means for each lake district are given, with ranges in parentheses. The original publications are given in parentheses under the lake district.

Table 4. ANOVA tables for year-to-year and lake-to-lake variability in oxygen concentrations. a) Lakes as treatments; b) years as treatments; c) years and lakes as treatments. Data used are volume-weighted oxygen concentrations for each sampling date, year, and lake (n = 348). Inclusion of the "Day" term allows

comparisons of depletion rates. The R^2 given are for the overall model.

Table 5. Statistical summary of linear regressions of mean volumetric depletion rates against morphometric, winter, and ice-free season variables. Results are presented for all lakes (n = 9) and with Trout Bog excluded (n = 8). Slopes and intercepts of the regression equation are given if $p \leq 0.05$.

Table 6. Correlation coefficients (r) for lake specific variables against sediment area to volume, mean depth, cover light transmission, and the cover extinction coefficient. Values in parentheses are the correlation coefficients calculated without Trout Bog.

Table 7. Correlation coefficients (r) for testing temporal coherence of depletion rates between lake pairs. Lake pairs are divided into three groups: shallow/shallow, shallow/deep, and deep/deep. Shallow lakes (< 6 m mean depth) include Allequash, Crystal Bog, Little Rock-North, Little Rock-South, and Trout Bog. Deep lakes (> 6 m) include Big Muskellunge, Crystal Lake, Sparkling, and Trout Lake. Abbreviations are identified in the caption for Fig. 2. Significant correlations ($p \leq 0.10$) are highlighted in bold. The mean, standard deviation, median and range of r are given for the three groups of lake pairings.

Table 8. Comparison of winter variables for 1990 and 1991 for Allequash, Big Muskellunge, Sparkling, and Trout Bog. A depletion rate was not calculated for Big Muskellunge in 1991 because of the poor fit of a linear regression line.

Table 9. Statistical summary of linear regressions of yearly depletion rates against yearly winter and ice-free variables. Only those regressions with $p \leq 0.10$ are listed. Slope refers to the sign of the relationship: "+" if there is a positive relationship between depletion rate and the variable, "-" if it is a negative relationship.

Table 10. Multiple regression models for predicting the depletion rate given a lake-specific variable (sediment area to volume ratio, A_s/V) and at least one year-specific variable (mean snow depth, sn, extinction coefficient, μ, winter chl a, $[chl\ a]_w$, or summer euphotic zone chl a, $[chl\ a]_{su}$). All variables were significant when added as the final variable at $p \leq 0.10$.

Table 11. Oxygen production rates: a) at the surface; and b) for the whole-lake. Rates are listed in mg $O_2 \cdot m^{-3} \cdot h^{-1}$. Means, standard deviations (SD), and ranges (Min. and Max.) are given for seven years of calculated oxygen production. Lakes are ranked in order of decreasing mean production rate.

Table 12. Percent reduction in "true" depletion rate due to oxygen production. Oxygen production rates were converted to daily rates and divided by the "true" depletion rate which is the sum of the measured depletion rate and the oxygen production rate. Means, standard deviations (SD), and ranges are given for seven years of calculated oxygen production for each lake. Lakes are ranked in order of decreasing mean % reduction.

Table 13. Linear regression results for whole-lake and surface oxygen production rates against depletion rates. Regressions of yearly rates are given for each lake as well as for lake averages. Regressions with $p \leq 0.10$ are in bold. NS = not significant at $p \leq 0.35$.

Table 14. Results for whole-lake oxygen depletion rates regressed against winter chl a and light irradiance. Results for year-to-year regressions for each lake are given as well as for lake averages. p-values ≤ 0.05 are in bold, NS = not significant at $p \leq 0.10$.

Table 15. ANOVA tables for assessing variability of light and chl a parameters: a) surface chl a; b) whole-lake chl a; c) surface light irradiance; d) whole-lake light irradiance. Data are surface and volume-weighted values from each winter sampling date, lake, and year. R^2 and n are given for each model.

Table 1

	Allequash-N	Big Muskell.	Crystal Bog	Crystal Lake	Little Rock-N	Little Rock-S	Sparkling	Trout Bog	Trout Lake-SE
Volume (10^3 m^3)	4304	29900	9	3799	372	251	8843	62	132000
Surface area (ha)	112.4	396.3	0.5	36.7	9.8	8.1	81.4	1.1	769.8
Sediment area/volume (m^-1)	0.26	0.13	0.63	0.10	0.26	0.32	0.09	0.19	0.06
Mean depth (m)	3.8	7.5	1.7	10.4	3.8	3.1	10.9	5.6	17.1
Maximum depth (m)	8	21.3	2.5	20.4	10.3	6.5	20	7.9	35.7
Length ice cover (d)	148 (7)	144 (5)	153 (8)	142 (4)	149 (7)	149 (7)	139 (6)	156 (8)	136 (7)
Total ice thickness (cm)	45.2 (7.6)	45.7 (6.2)	33.8 (5.3)	39.5 (9.6)	34.1 (5.5)	32.9 (5.6)	42.6 (6.2)	36.4 (6.8)	44.2 (6.2)
Snow depth (cm)	11.6 (6.6)	10.4 (5.4)	10.5 (3.1)	9.6 (5.2)	9.5 (5.3)	11.2 (8.5)	8.4 (4.8)	11.8 (6.5)	6.5 (3.4)
Grey ice thickness (cm)	14.5 (10.7)	11.6 (6.5)	20.9 (6.7)	10.8 (6.8)	18.2 (8.1)	15.6 (5.1)	13.1 (8.3)	17.8 (7.1)	10.3 (9.7)
Cover extinction coef. (m^-1)	6.48 (2.32)	5.74 (2.15)	10.37 (3.00)	6.55 (1.96)	8.84 (2.51)	8.50 (2.01)	6.20 (1.74)	10.43 (3.27)	5.61 (2.25)
Cover transmission (%)	12.5 (12.6)	16.8 (11.4)	3.9 (4.2)	13.8 (10.9)	10.5 (10.7)	10.2 (7.0)	14.2 (9.9)	3.3 (3.1)	18.4 (12.6)
Winter chl a (µg/L)	1.1 (0.9)	0.9 (0.6)	10.2 (5.8)	1.0 (0.5)	2.1 (1.3)	2.9 (1.5)	2.0 (1.2)	7.8 (4.3)	1.9 (0.8)
Summer Secchi (m)	3.9 (0.7)	8.0 (0.6)	2.0 (0.3)	8.6 (1.5)	5.7 (0.6)	4.9 (0.1)	7.5 (0.6)	1.7 (0.2)	5.6 (0.4)
Spring epilimnetic TP (µg/L)	32.4 (3.8)	15.9 (1.3)	18.2 (6.1)	5.3 (4.3)	-	-	11.6 (5.7)	22.7 (1.7)	11.1 (2.7)
Summer euphotic chl a (µg/L)	10.4 (4.8)	4.0 (2.4)	17.3 (14.1)	2.8 (1.2)	13.1 (3.2)	8.7 (5.5)	3.9 (1.4)	28.3 (17.6)	3.2 (1.2)
Summer epilimnetic temp. (°C)	20.8 (1.5)	19.7 (0.7)	21.1 (1.2)	19.8 (0.7)	20.7 (1.0)	21.0 (1.4)	19.9 (0.6)	20.6 (1.1)	19.7 (1.3)

Table 2

Lake	n	Vol. WODR (g O2/m^3•d)			Areal WODR (g O2/m^2•d)		
		Mean	SD	CV	Mean	SD	CV
Allequash	10	0.055	0.010	17.4	0.220	0.040	18.0
Big Muskellunge	8	0.026	0.009	34.1	0.200	0.067	33.3
Crystal Bog	9	0.084	0.009	11.3	0.154	0.016	10.5
Crystal Lake	5	0.029	0.009	30.3	0.312	0.089	28.4
Little Rock N	7	0.065	0.017	25.6	0.252	0.064	25.6
Little Rock S	6	0.079	0.009	11.0	0.248	0.025	10.3
Sparkling	7	0.029	0.013	45.1	0.332	0.142	42.8
Trout Bog	10	0.032	0.010	32.5	0.180	0.056	31.1
Trout Lake	7	0.023	0.017	71.4	0.404	0.284	70.2

Table 3

Lake District	n	Areal Depletion Rate (g O2/m^2•d)	Mean Depth (m)	Surface Area (hectares)	Summer Chl a (µg/L)
ELA Lakes - NW Ontario (Schindler 1971) †	11	0.164 (0.036 - 0.253)	6.4 (1.5 - 15.0)	19.1 (1.7 - 56.1)	3.4 (1.0 - 11.3)†††
Shield Lakes - S Ontario (Welch et al. 1976) †	16	0.232 (0.080 - 0.390)	12.4 (3.5 - 27.2)	351 (71 -1272)	1.3 (0.8 - 2.1)
Prairie Lakes - Manitoba (Barica and Mathias 1979) †	10	0.295 (0.220 - 0.420)	2.5 (1.6 - 4.2)	11.9 (2.3 - 28.7)	25.0 (5.0 - 102.4)
Central Albertan Lakes (Babin and Prepas 1985) ††	11	0.470 (0.243 - 0.848)	7.5 (3.7 - 19.4)	177 (41 - 443)	17.7 (3.3 - 73.5)
LTER lakes - N Wisconsin (this study)	9	0.256 (0.154 - 0.404)	7.1 (1.7 - 17.1)	157 (0.5 - 770)	10.1 (1.4 - 67.2)

† Area and chl a data reported in Mathias and Barica (1980). Depletion rate and depth data reported in Babin and Prepas (1985).

†† Area and chl a data from Prepas and Vickery (1984).

††† Chl a data do not include Lake 227, which received large nutrient additions.

Table 4

a. $R^2 = 0.90$

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Days since freeze	784.90	1	784.90	559.28	<0.001
Lakes	586.31	8	73.29	52.22	<0.001
Days x Lakes	371.00	8	46.38	33.05	<0.001
Error	463.12	330	1.40		

b. $R^2 = 0.29$

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Days since freeze	1127.70	1	1127.70	109.29	<0.001
Years	75.32	9	8.37	0.81	0.606
Days x Years	62.34	9	6.93	0.67	0.735
Error	3384.47	328	10.32		

c. $R^2 = 0.93$

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Days since freeze	690.40	1	690.40	642.99	<0.001
Lakes	583.89	8	72.99	67.97	<0.001
Years	46.18	9	5.13	4.78	<0.001
Days x Lakes	46.28	9	5.14	4.79	<0.001
Days x Years	385.64	8	48.21	44.90	<0.001
Error	335.00	312	1.07		

Table 5

	All lakes (n=9)*			Trout Bog excluded (n=8)		
	R^2	p-value	Slope ; int.	R^2	p-value	Slope ; int.
<u>Morphometric variables</u>						
Volume	0.23	0.199	-	0.29	0.170	-
Surface area	0.29	0.133	-	0.39	0.096	-
Sediment area/volume	0.78	0.002	(0.121;0.019)	0.80	0.003	(0.120;0.021)
Mean depth	0.64	0.010	(-0.004;0.075)	0.74	0.007	(-0.004;0.079)
Maximum depth	0.61	0.013	(-0.002;0.073)	0.80	0.003	(-0.002;0.081)
<u>Winter variables</u>						
Total ice thickness	0.52	0.029	(-0.003;0.178)	0.66	0.014	(-0.004;0.197)
Snow depth	0.19	0.248	-	0.36	0.116	-
Grey ice thickness	0.58	0.017	(0.005;-0.027)	0.83	0.002	(0.006;-0.039)
Extinction coefficient of cover	0.39	0.075	-	0.85	0.001	(0.013;-0.048)
% light transmission	0.32	0.111	-	0.82	0.002	(-0.503;0.112)
Winter chl a	0.19	0.238	-	0.44	0.070	-
<u>Ice-free variables</u>						
Summer Secchi	0.26	0.161	-	0.62	0.020	(-0.009;0.10)
Spring epilimnetic TP	0.25	0.252	-	0.35	0.218	-
Summer euphotic zone chl a	0.11	0.390	-	0.81	0.003	(0.004;0.016)
Length ice-free season	0.41	0.065	-	0.79	0.003	(-0.004;0.834)
Summer epilimnetic temp.	0.81	0.001	(0.037;-0.697)	0.96	0.000	(0.039;-0.745)

* n=7 for TP data

Table 6

Variables	Sediment area / volume	Mean depth	Cover transmission	Extinction coefficient
Mean depth	-0.77 (-0.79)			
Cover transmission	-0.71 (-0.94)	0.72 (0.81)		
Extinction coefficient	0.71 (0.91)	-0.69 (-0.75)	-0.97 (-0.95)	
Maximum depth	-0.78 (-0.82)	0.96 (0.97)	0.84 (0.89)	-0.78 (-0.80)
Surface area	-0.48 (-0.52)	0.76 (0.76)	0.71 (0.74)	-0.64 (-0.63)
Length ice-free season	-0.70 (-0.85)	0.90 (0.98)	0.88 (0.84)	-0.86 (-0.81)
Snow depth	0.46 (0.54)	-0.84 (-0.87)	-0.64 (-0.54)	0.53 (0.40)
Total ice thickness	-0.63 (-0.66)	0.59 (0.59)	0.75 (0.79)	-0.86 (-0.90)
Grey ice thickness	0.84 (0.91)	-0.81 (-0.81)	-0.90 (-0.93)	0.92 (0.94)
Winter chl a	0.73 (0.89)	-0.45 (-0.46)	-0.87 (-0.83)	0.85 (0.80)
Summer euphotic zone chl a	0.48 (0.92)	-0.57 (-0.81)	-0.91 (-0.90)	0.88 (0.90)
Summer Secchi	-0.66 (-0.84)	0.52 (0.55)	0.81 (0.72)	-0.78 (-0.68)
Summer epilimnetic temp.	0.83 (0.86)	-0.87 (-0.87)	-0.79 (-0.87)	0.79 (0.85)

Table 7

Shallow Lakes		Shallow /Deep		Deep Lakes	
Lake pair	r	Lake pair	r	Lake pair	r
CBxLRS	**0.81**	CBxBM	0.02	BMxCR	†
CBxTB	0.51	CBxCR	**0.81**	BMxSP	0.52
CBxAL	**0.67**	CBxSP	0.45	BMxTR	**0.98**
CBxLRN	0.51	CBxTR	0.53	CRxSP	**0.92**
LRSxLRN	0.69	LRSxBM	0.49	CRxTR	**0.93**
LRSxAL	**0.94**	LRSxCR	†	SPxTR	**0.92**
LRSxTB	0.54	LRSxSP	0.22		
LRNxAL	**0.74**	LRSxTR	0.12		
LRNxTB	0.57	LRNxBM	0.17		
ALxTB	**0.67**	LRNxCR	†		
		LRNxSP	0.05		
		LRNxTR	0.35		
		ALxBM	0.19		
		ALxCR	0.13		
		ALxSP	0.14		
		ALxTR	0.06		
		TBxBM	0.23		
		TBxCR	0.12		
		TBxSP	0.41		
		TBxTR	0.25		
Mean	0.67		0.26		0.85
SD	0.14		0.21		0.19
Median	0.67		0.20		0.92
Minimum	0.51		0.02		0.52
Maximum	0.94		0.81		0.98

† correlations with $n < 4$

Table 8

	Allequash		Big Muskell.		Sparkling		Trout Bog	
	1990	1991	1990	1991	1990	1991	1990	1991
Winter chl a (µg/L)	0.7	1.4	1.3	0.6	1.4	1.4	5.8	11.9
Cover transmission (%)	0.2	10.5	0.4	16.7	1.0	18.0	0.2	7.3
Cover extinction coefficient (m^-1)	9.36	6.00	9.85	5.87	7.95	5.49	16.42	7.86
Date freeze-up	21-Nov	2-Dec	21-Nov	2-Dec	26-Nov	14-Dec	14-Nov	25-Nov
Snow depth (cm)	15.3	10.5	10.4	7.6	10.6	5.8	10.6	11.5
Grey ice thickness (cm)	7.0	6.3	11.2	2.0	16.7	4.3	20.7	8.7
Clear ice thickness (cm)	38.7	37.0	32.3	42.0	25.3	44.4	18.8	28.0
Total cover thickness (cm)	61.0	53.9	53.9	51.6	52.6	54.5	50.1	48.2
WODR (g O2/m^3•d)	0.070	0.061	0.025	-	0.044	0.020	0.050	0.035

Table 9

	Allequash				Big Muskellunge				Crystal Bog				Crystal Lake				Little Rock N			
	R^2	p	n	slope	R^2	p	n	slope	R^2	p	n	slope	R^2	p	n	slope	R^2	p	n	slope
Winter variables*																				
Total cover thickness									0.73	0.003	9	+	0.88	0.019	5	+				
Ice thickness									0.34	0.099	9	+	0.73	0.065	5	+				
Snow depth	0.49	0.024	10	+	0.60	0.042	7	+												
Grey ice thickness					0.49	0.080	7	-												
Snow + grey ice thickness													0.78	0.047	5	+	0.49	0.079	7	+
Extinction coefficient of cover	0.67	0.025	7	+					0.51	0.072	7	+	0.91	0.046	4	+				
% light transmission									0.51	0.071	7	-								
Winter chl a									0.42	0.057	9	-								
Ice-free variables																				
Summer Secchi													ND†				ND			
Spring epilimnetic TP													ND				ND			
Summer euphotic zone chl a																				
Summer epilimnetic temp.													ND				0.81	0.038	5	-
Length ice-free season																				
Summer air temp.	0.42	0.060	9	-													0.59	0.044	7	-

	Little Rock S				Sparkling				Trout Bog				Trout Lake			
	R^2	p	n	slope	R^2	p	n	slope	R^2	p	n	slope	R^2	p	n	slope
Winter variables																
Total cover thickness													0.91	0.001	7	+
Ice thickness									0.33	0.080	10	+	0.83	0.004	7	+
Snow depth																
Grey ice thickness	0.59	0.074	6	+												
Snow + grey ice thickness									0.37	0.065	10	+				
Extinction coefficient of cover									0.75	0.012	7	+	0.63	0.108	5	+
% light transmission																
Winter Chl a					0.43	0.109	7	+								
Ice-free variables																
Summer Secchi	ND															
Spring epilimnetic TP	ND				ND											
Summer euphotic zone Chl a													0.46	0.093	7	+
Summer epilimnetic temp.					0.88	0.062	4	+								
Length ice-free season																
Summer air temp.									0.32	0.089	10	-				

* Italics represent maximum thickness for a particular year, rather than mean thickness.

† ND = n<4

Table 10

Variables	Equation	R^2	p
Sediment area:volume (As/V)	WODR = 0.122(As/V) + 0.019	0.74	<0.001
Extinction coefficient (μ)	WODR = 0.007(μ) + 0.0003	0.43	<0.001
Mean snow depth (sn)	WODR = 0.002(sn) + 0.031	0.11	0.028
Winter chl a ([Chl a]w)	WODR = 0.004([Chl a]w) + 0.041	0.26	0.001
Summer chl a ([Chl a]s)	WODR = 0.004([Chl a]s) + 0.022	0.52	<0.001
As/V, μ	WODR = 0.101(As/V) + 0.003(μ) + 0.005	0.78	<0.001
As/V, sn	WODR = 0.118(As/V) + 0.001(sn) + 0.007	0.79	<0.001
As/V, [Chl a]w	WODR = 0.157(As/V) - 0.002([Chl a]w) + 0.017	0.78	<0.001
As/V, [Chl a]s	WODR = 0.098(As/V) + 0.001([Chl a]s) + 0.016	0.77	<0.001
As/V, μ, [Chl a]w	WODR = 0.133(As/V) + 0.002(μ) - 0.002([Chl a]w) + 0.007	0.80	<0.001
As/V, μ, [Chl a]s	WODR = 0.077(As/V) + 0.003(μ) + 0.001([Chl a]s) + 0.001	0.81	<0.001
As/V, sn, [Chl a]w	WODR = 0.144(As/V) + 0.001(sn) - 0.002([Chl a]w) + 0.008	0.81	<0.001
As/V, sn, [Chl a]s	WODR = 0.093(As/V) + 0.001(sn) + 0.001([Chl a]s) + 0.003	0.82	<0.001

Table 11

a.

Lake	Surface O2 production (in mg/m^3•h)			
	Mean	SD	Min.	Max.
Trout Bog	25.0	35.8	0.3	91.5
Crystal Bog	17.7	22.1	0.1	52.1
Trout Lake	15.0	14.7	2.1	39.1
Allequash	14.7	26.4	0.0	72.1
Little Rock - S	5.7	11.7	0.0	32.1
Little Rock - N	5.5	6.0	0.0	15.7
Crystal Lake	4.9	7.5	0.1	21.0
Sparkling	4.5	3.2	0.6	7.6
Big Muskellunge	1.6	1.7	0.2	4.6

b.

Lake	Whole-lake O2 production (in mg/m^3•h)			
	Mean	SD	Min.	Max.
Crystal Bog	7.7	10.5	0.0	28.1
Little Rock - S	4.6	7.1	0.0	16.9
Sparkling	3.7	5.4	0.1	15.4
Little Rock - N	3.6	6.2	0.0	14.5
Big Muskellunge	2.5	3.5	0.0	9.5
Crystal Lake	2.2	1.6	0.1	4.1
Trout Lake	1.9	2.1	0.2	6.0
Allequash	1.7	2.6	0.0	7.3
Trout Bog	0.7	0.7	0.1	1.8

Table 12

Lake	% Reduction of "true" depletion rate			
	Mean	SD	Min.	Max.
Trout Lake	29.6	23.5	6.2	59.6
Crystal Bog	25.3	28.6	0.1	66.4
Big Muskellunge	21.3	27.6	0.3	67.7
Crystal Lake	20.4	22.2	1.0	42.5
Little Rock - S	19.6	24.6	0.1	59.8
Sparkling	18.3	20.8	0.8	52.2
Little Rock - N	17.0	22.7	0.1	56.2
Trout Bog	14.0	13.9	0.9	38.1
Allequash	12.1	14.9	0.1	41.7

Table 13

	Whole-lake				Surface			
	R^2	p	slope	n	R^2	p	slope	n
Allequash		NS		7		NS		7
Big Muskellunge	0.43	0.230	-	5	0.44	0.220	-	5
Crystal Bog	0.22	0.290	-	7	**0.73**	**0.014**	-	7
Crystal Lake	**0.86**	**0.070**	-	**4**	0.48	0.300	-	4
Little Rock - N		NS		5		NS		6
Little Rock - S	0.58	0.130	-	5	0.42	0.160	-	6
Sparkling		NS		5		NS		5
Trout Bog	0.28	0.220	-	7	**0.75**	**0.012**	-	7
Trout Lake	0.33	0.320	-	5	0.47	0.200	-	5
Lake averages	**0.56**	**0.020**	+	**8**		NS		8

Table 14

	Chl a			Light		
	R^2	**p**	**slope**	**R^2**	**p**	**slope**
Allequash	0.82	0.005	+	0.54	0.060	+
Big Muskellunge		NS		0.49	0.080	+
Crystal Bog	0.51	0.070	+	0.54	0.060	+
Crystal Lake		NS		0.67	0.024	+
Little Rock - N		NS		0.97	0.002	+
Little Rock - S		NS		0.93	0.008	+
Sparkling	0.91	0.001	+	0.68	0.022	+
Trout Bog	0.70	0.020	+		NS	
Trout Lake	0.84	0.004	+	0.66	0.030	+
Lake averages	0.80	0.003	+		NS	

Table 15

a. Surface chl a: $R^2 = 0.27$, n = 165

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Years	2762.24	6	460.37	1.03	0.411
Lakes	21752.99	8	2719.12	6.06	<0.001
Error	67329.73	150	448.87		

b. Whole-lake chl a: $R^2 = 0.46$, n = 158

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Years	235.36	6	39.23	2.39	0.032
Lakes	1741.85	8	217.73	13.24	<0.001
Error	2351.36	143	16.44		

c. Surface light: $R^2 = 0.14$, n = 167

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Years	394656.46	6	65776.08	2.37	0.033
Lakes	294109.53	8	36763.69	1.32	0.236
Error	4223723.90	152	27787.66		

d. Whole-lake light: $R^2 = 0.13$, n = 158

SOURCE	SUM-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Years	28365.57	6	4727.59	1.57	0.161
Lakes	35013.74	8	4376.72	1.45	0.181
Error	431624.25	143	3018.35		

FIGURE LEGENDS

Figure 1. Mass balance diagram for sources and sinks of oxygen during the wintertime. [O_2] is the ambient oxygen concentration. Arrows refer to the direction of O_2 flux, except for the light arrow. k_n refer to the various rate coefficients for the different components.

Figure 2. Mean volumetric depletion rates (WODR, in g $O_2 \cdot m^{-3} \cdot d^{-1}$) from 1982 to 1991 for each of the LTER lakes with error bars of one standard deviation. Lakes are ranked in order of decreasing mean WODR. The lines below the graphs connect lakes not significantly different at 95% probability using Scheffe t-test (Ott 1988). AL = Allequash, BM = Big Muskellunge, CB = Crystal Bog, CR = Crystal Lake, LRN = Little Rock-North, LRS = Little Rock-South, SP = Sparkling, TB = Trout Bog, TR = Trout Lake.

Figure 3. Dissolved oxygen profiles for a) Allequash, b) Sparkling, c) Trout Bog, and d) Big Muskellunge in the winter of 1991. November profiles measured previous to ice formation. Freeze dates are listed in Table 8.

Figure 4. Mean WODR (g $O_2 \cdot m^{-3} \cdot d^{-1}$) vs. sediment area to volume ratio (m^{-1}) for the nine LTER lakes. Regression lines and equations are given for linear and log expressions of A_s/V.

Figure 5. Mean WODR (g $O_2 \cdot m^{-3} \cdot d^{-1}$) vs. mean depth (m) for the nine LTER lakes. Regression lines and equations are given for linear and log expressions of mean depth.

Figure 6. Yearly WODR for a) shallow lakes (mean depth < 6 m), and b) deep lakes (mean depth > 6 m) over time. Big Muskellunge and Little Rock-North are not plotted for clarity. Note similarities in patterns of depletion over time within the two lake groupings. Lake abbreviations are as in Fig. 2.

Figure 7. Correlation coefficients for yearly depletion rates of lake pairs vs. difference in maximum depth. Lake pairs which are similar in depth have high correlation between depletion rates from year to year. Shallow/shallow, deep/deep, and shallow/deep pairings are distinguished (see Table 7).

Figure 8. Dissolved oxygen profiles for a) Allequash, b) Sparkling, c) Trout Bog, and d) Big Muskellunge in the winter of 1990. November profiles measured prior to ice formation. Freeze dates are listed in Table 8. (Compare with Fig. 3).

Figure 9. Time plots of yearly WODR and mean extinction coefficients (μ) for a) Allequash, b) Crystal Bog, and c) Trout Bog, showing high temporal coherence between variables. Regression results are summarized in Table 9. Note difference in scale for the three graphs.

Figure 10. Time plots of yearly WODR and mean summer euphotic zone chl *a* concentrations ([chl *a*]$_{su}$) for a) Allequash, b) Crystal Bog, and c) Trout Bog, showing little temporal coherence between variables. Regression results are summarized in Table 9. Note difference in scale for the three graphs.

Figure 11. Relative contribution of sediment (SOC) and water column (WOC) oxygen consumption to overall depletion rates for lakes of different depths. Based on Equations 6 and 7 in text. Values plotted are means for each lake from 1985 to 1991. Little Rock Lake basins not included because no DOC data were available.

Figure 12. Surface oxygen production rates (bars) and WODR (line) for Trout Bog from 1984 to 1991. Note that depletion rates are daily rates, while production rates are hourly.

Figure 13. Whole-lake oxygen production rates (bars) and WODR (line) for Little Rock-South from 1985 to 1990. Note that depletion rates are daily rates, while production rates are hourly.

Figure 14. Mean relative proportions of snow, grey ice, and clear ice for the LTER lakes. Proportions are averages for 1982 to 1991. Lakes are listed in order of increasing mean depth. Abbreviations for lakes are as in Fig. 2.
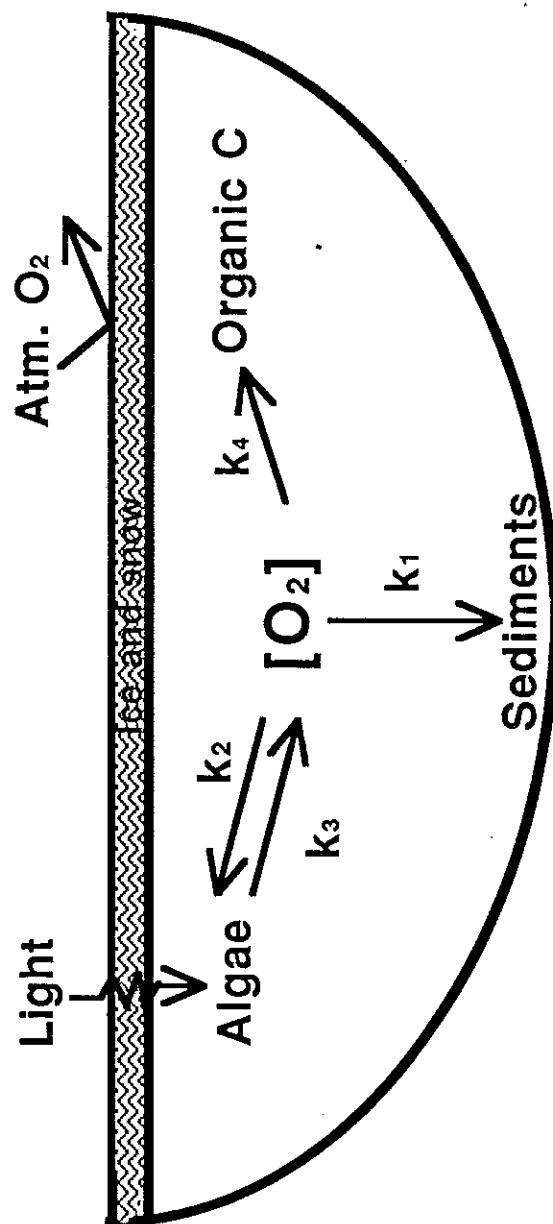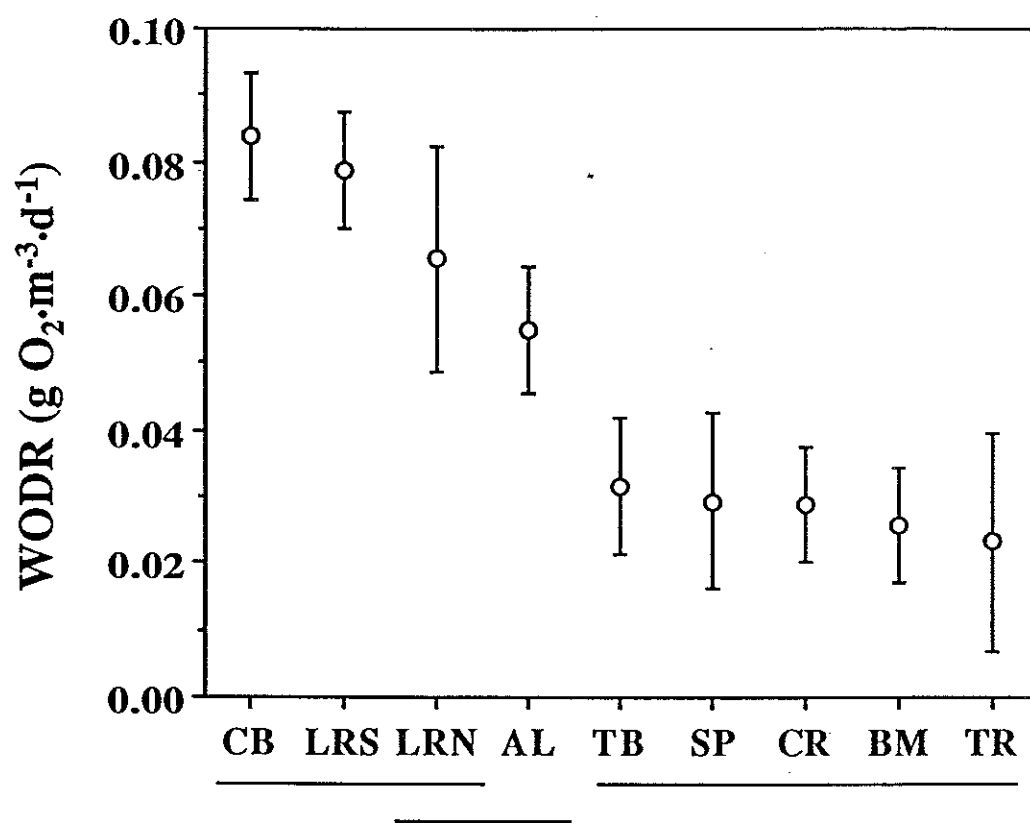
70

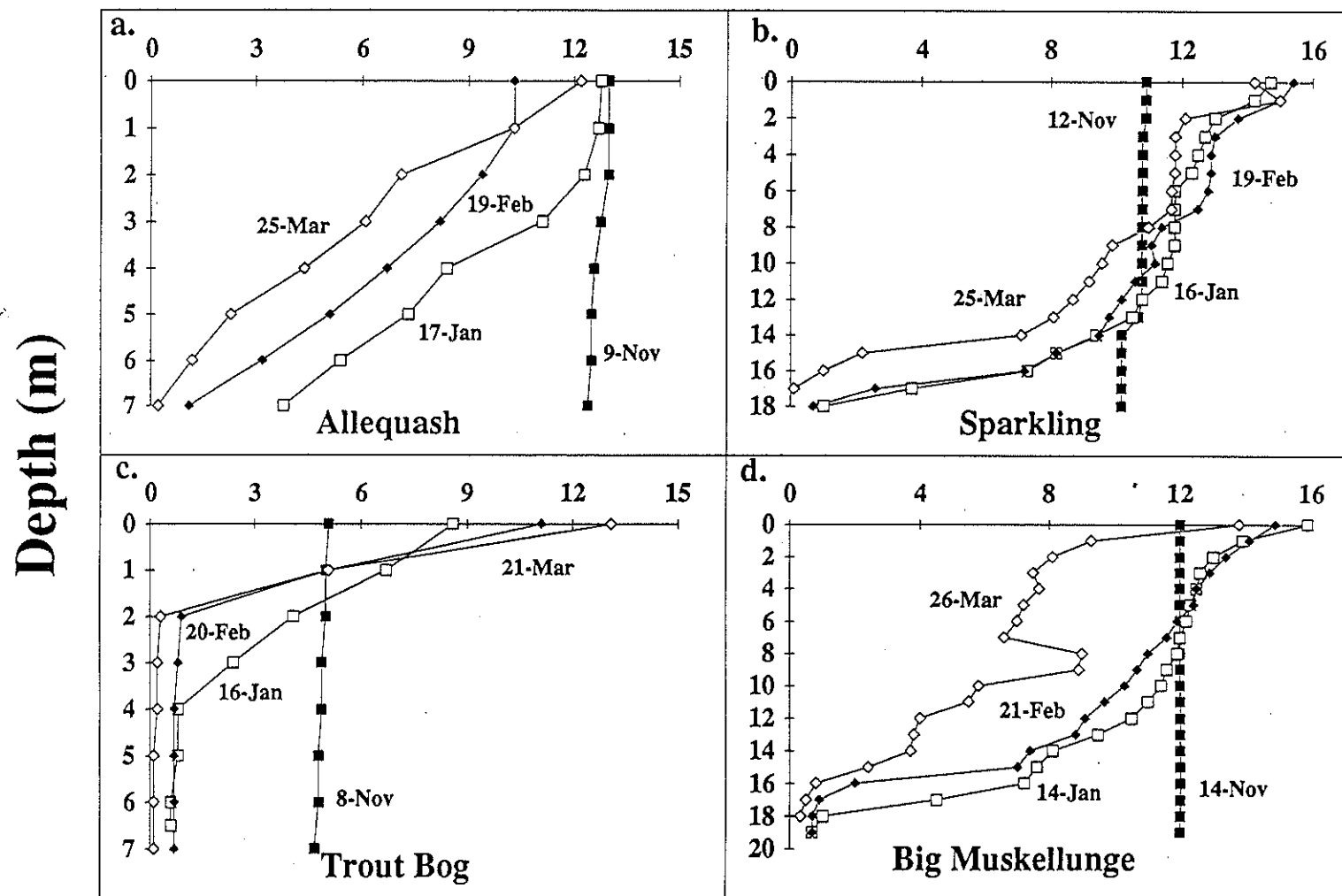Fig. 1

Fig. 2

Fig. 3

Dissolved oxygen (mg/L)
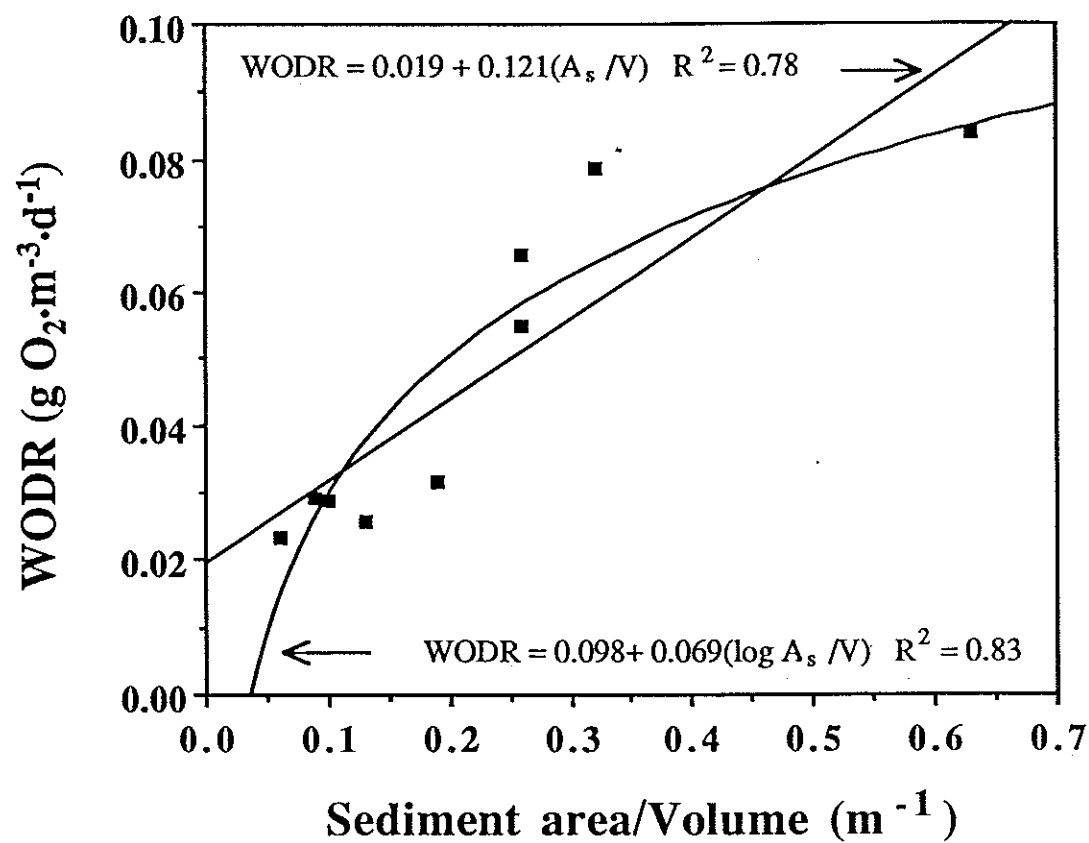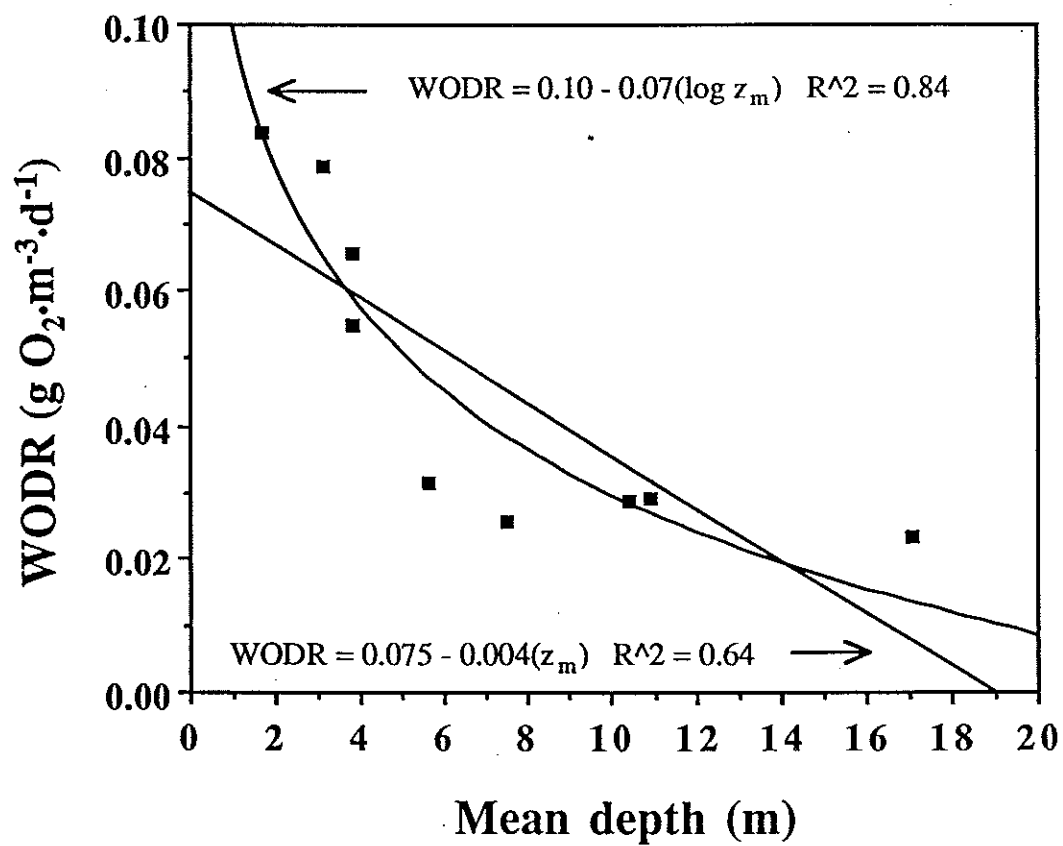
Depth (m)

a. Allequash
25-Mar
19-Feb
17-Jan
9-Nov

b. Sparkling
12-Nov
19-Feb
25-Mar
16-Jan

c. Trout Bog
21-Mar
20-Feb
16-Jan
8-Nov

d. Big Muskellunge
26-Mar
21-Feb
14-Jan
14-Nov

Fig. 4

Fig. 5

WODR = 0.10 - 0.07(log z_m)   R^2 = 0.84

WODR = 0.075 - 0.004(z_m)   R^2 = 0.64

Fig. 6   **a.**
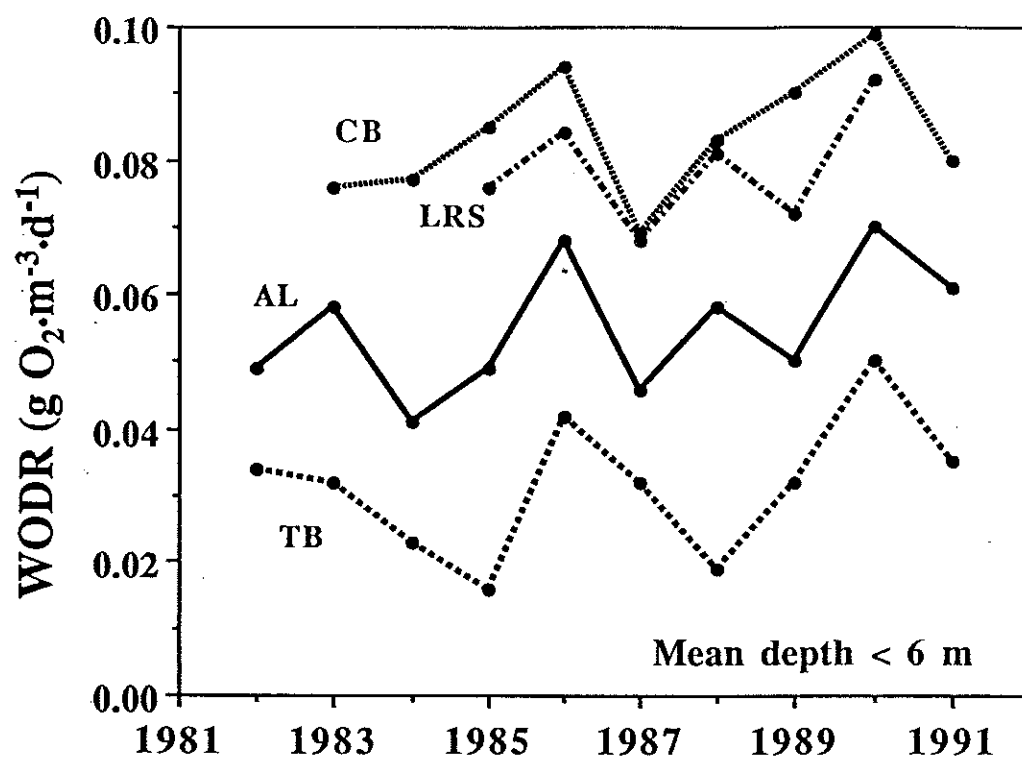
b.
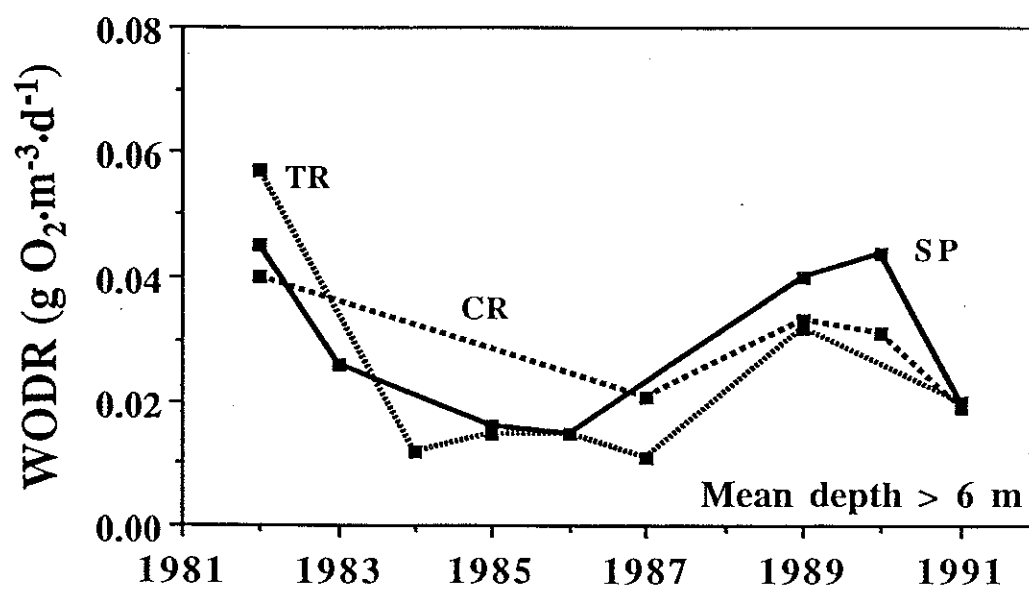
Fig. 7

Fig. 8

Dissolved oxygen (mg/L)

a. Allequash

b. Sparkling

c. Trout Bog

d. Big Muskellunge

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Fig. 9

WODR (g O$_2$·m^{-3}·d^{-1})

μ (m^{-1})
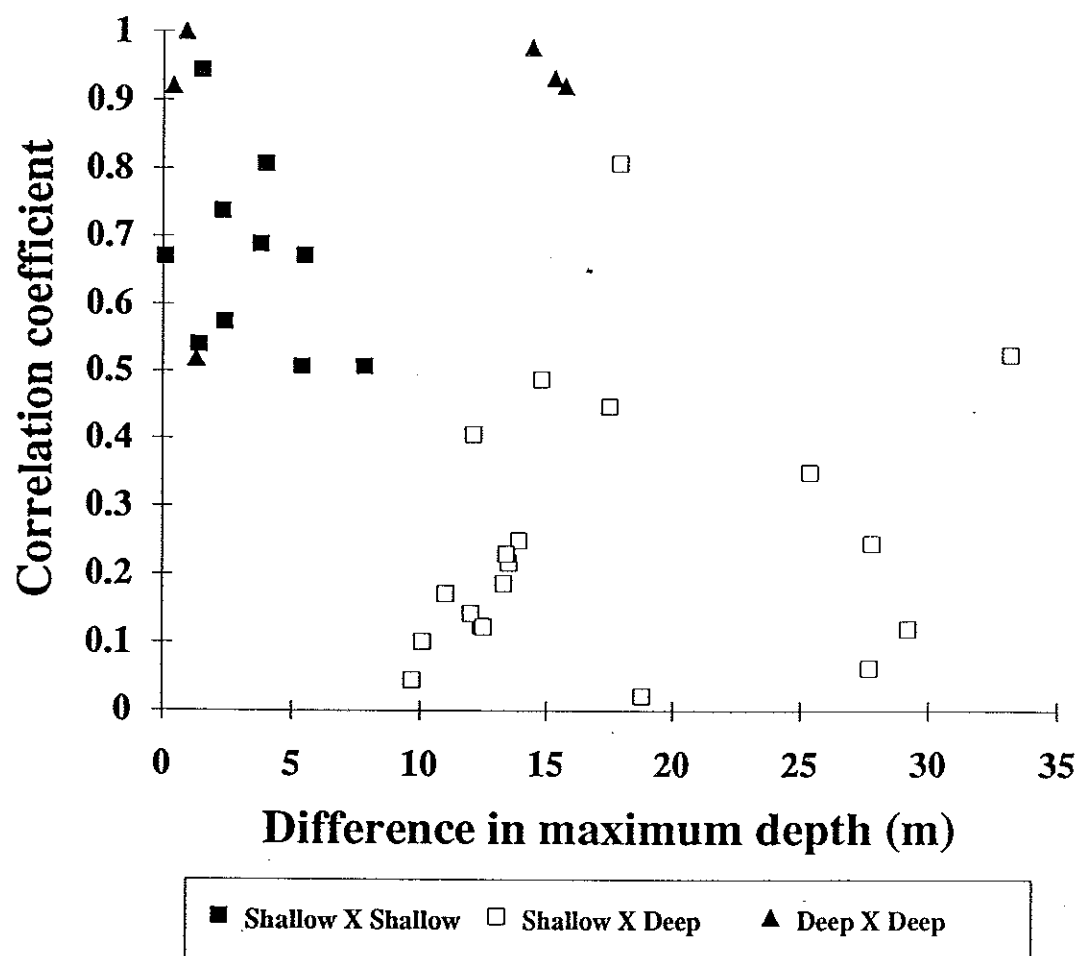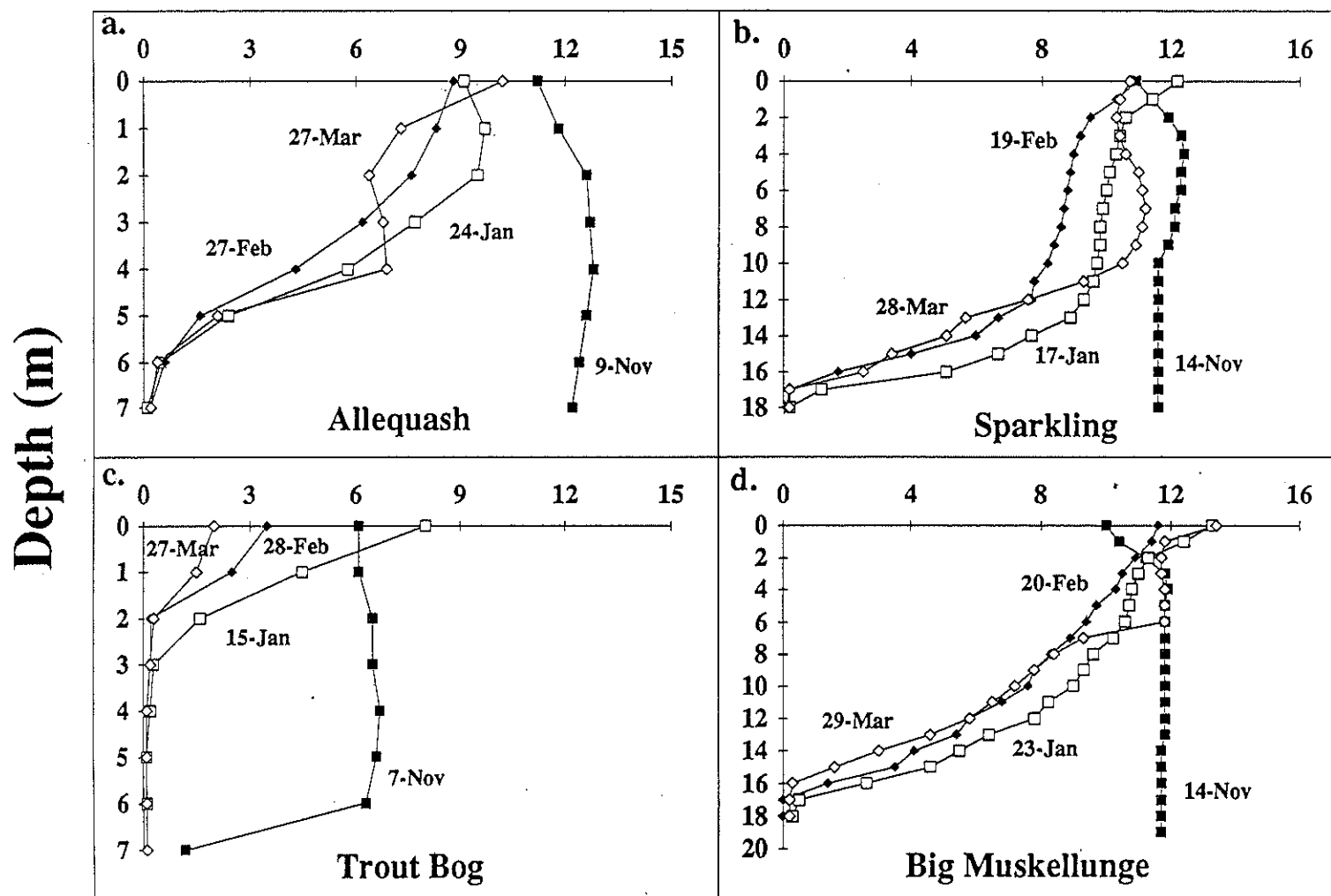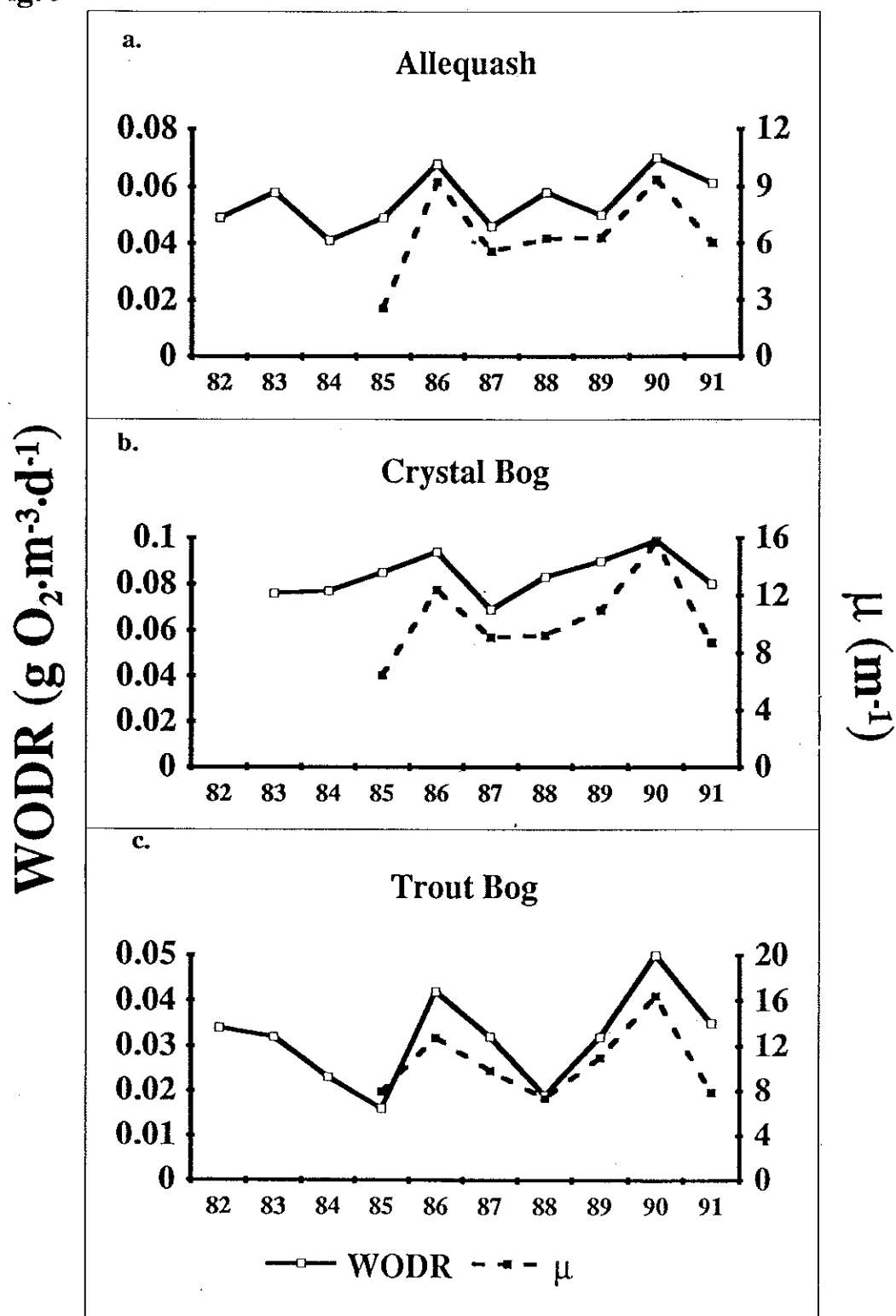
Fig. 10
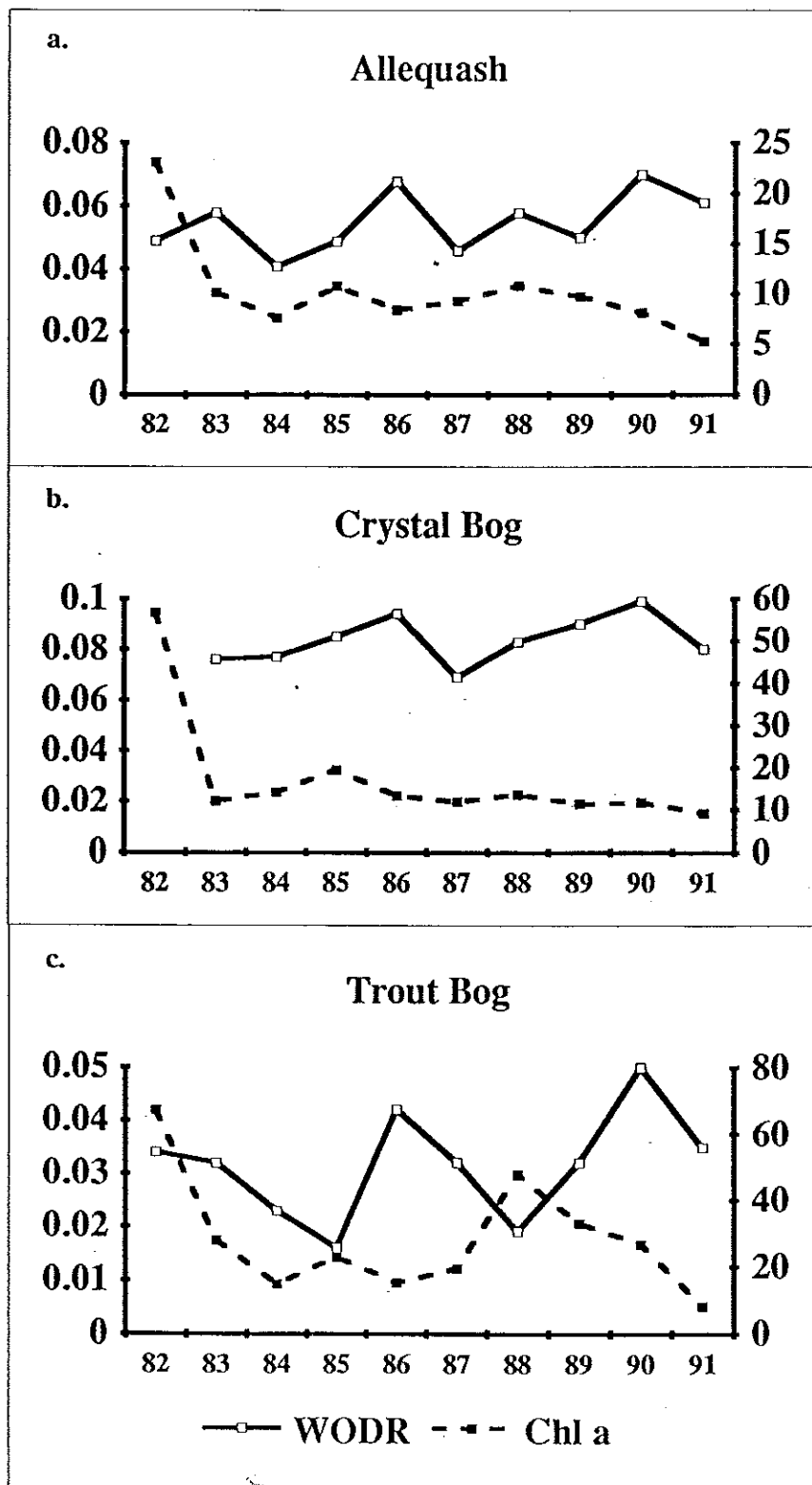
Fig. 11
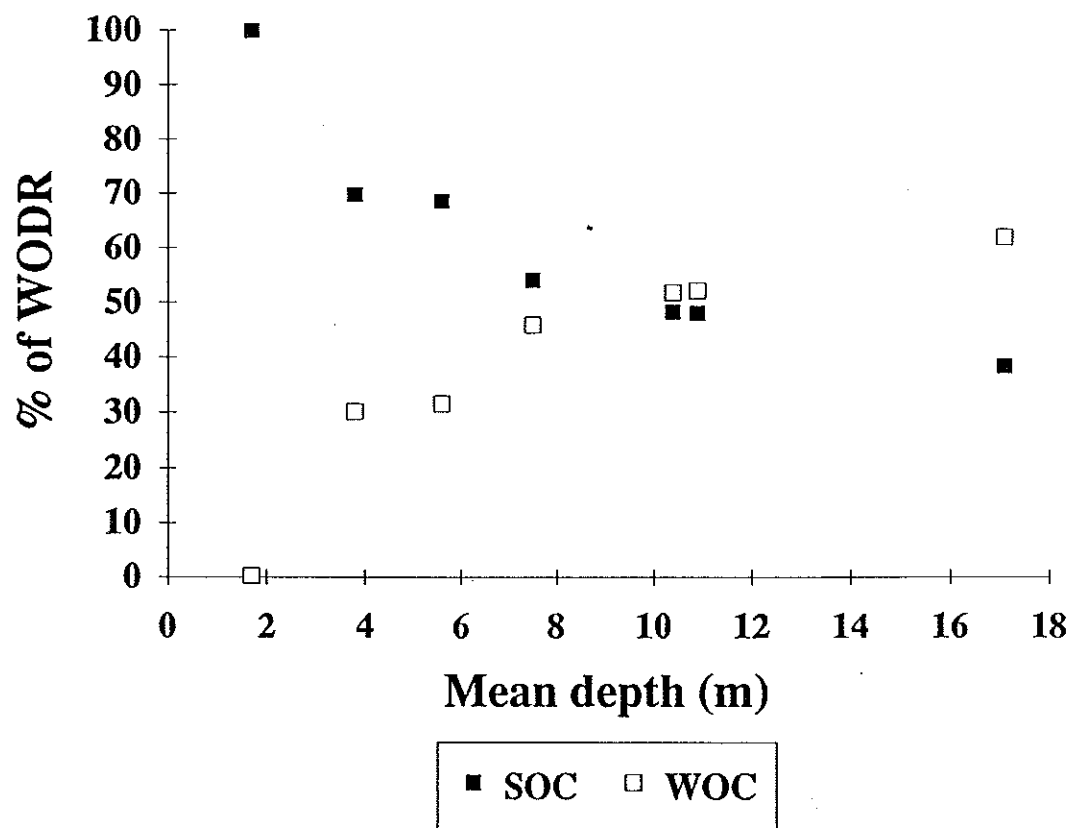
Fig. 12

Fig. 13
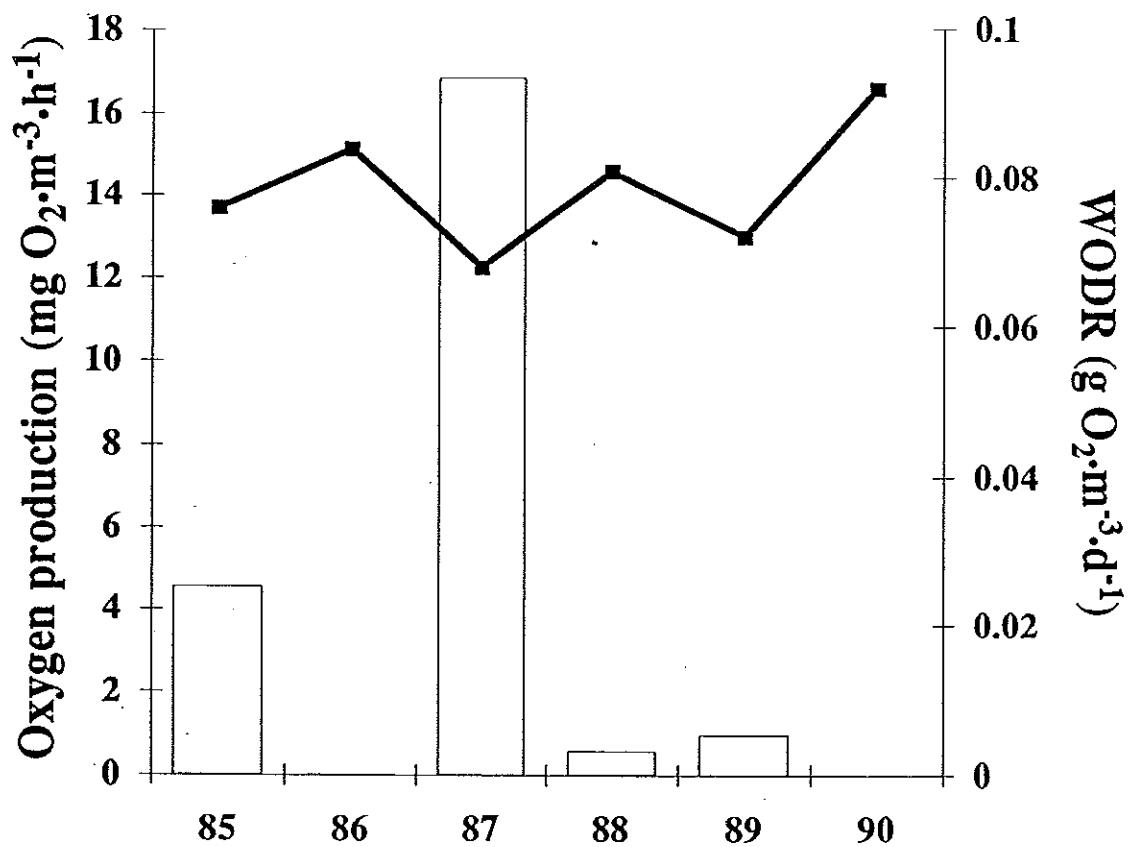
Fig. 14
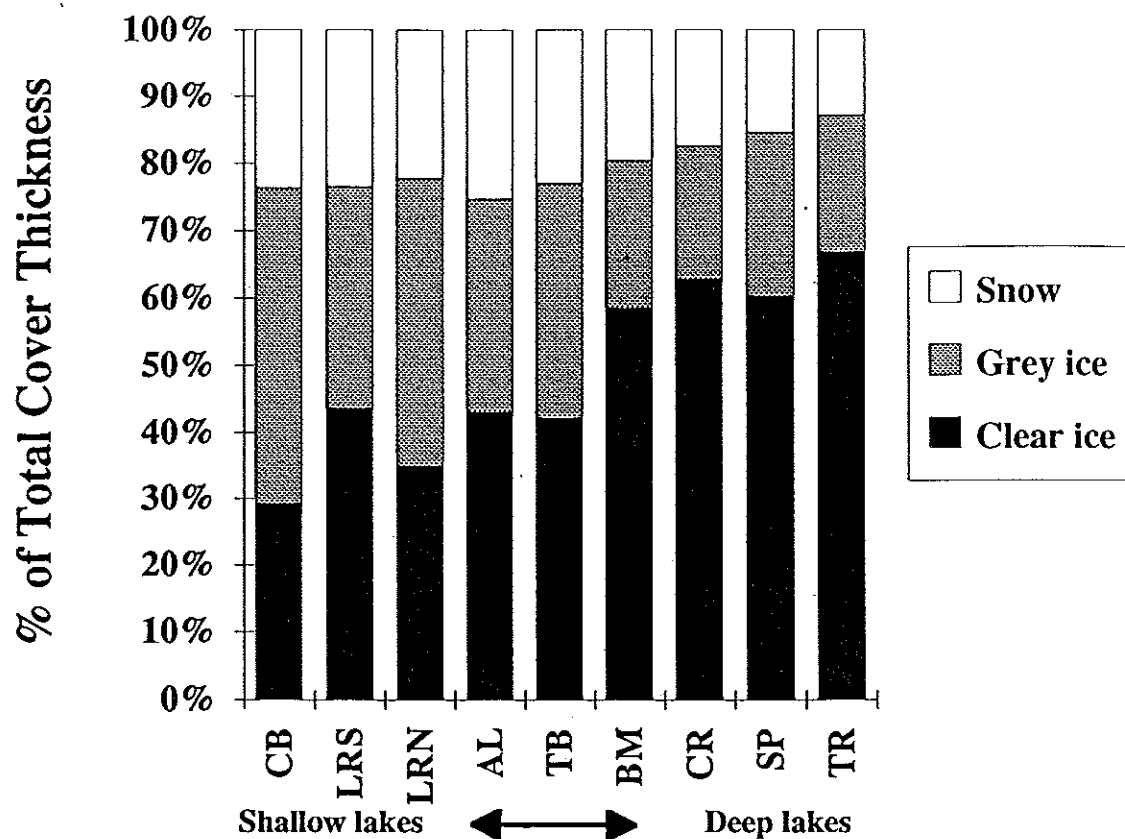
APPENDIX

Table A.1. Oxygen depletion rates as estimated by linear regression for each year and lake. "Slope" refers to the estimate of the depletion rate (in g $O_2 \cdot m^{-3} \cdot d^{-1}$) as fit through "n" data points. "Dates used" refers to which oxygen profiles were used t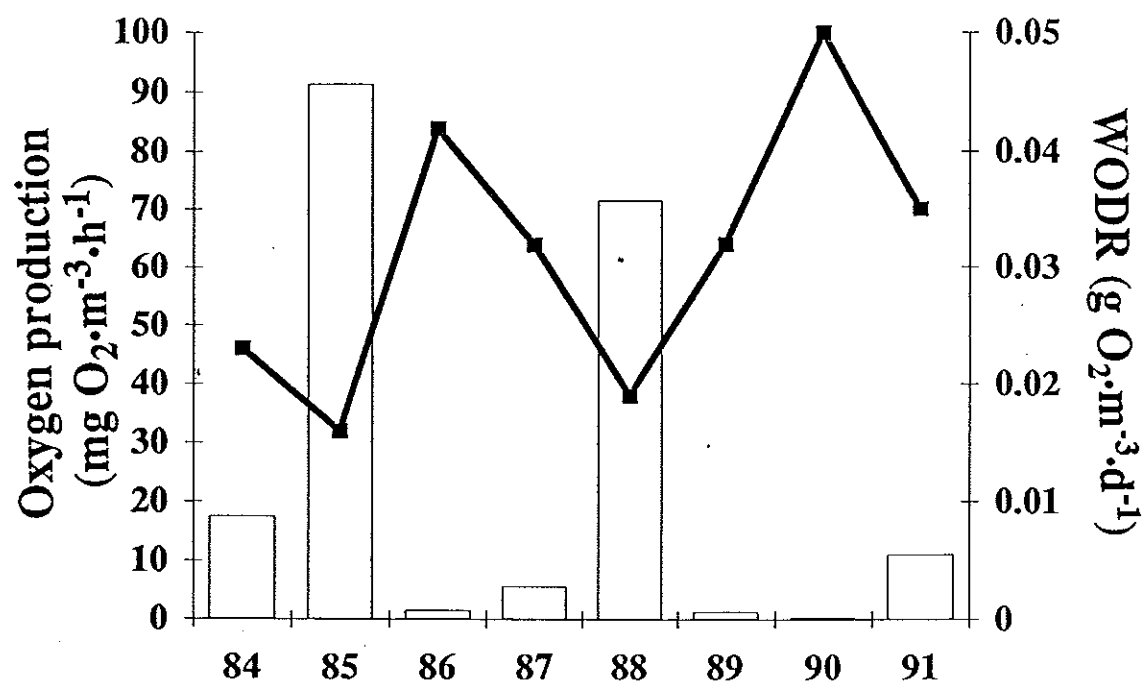o calculate the regression: a = all profiles including last ice-free profile; b = all profiles except last winter profile; c = all profiles except ice-free profile; and d = no late winter or ice-free profile. The dates that were chosen represented the best linear fit of the data. Additional regression statistics (standard error of the slope (SE), intercept, and R^2) are also given.

Table A.1

Lake	Year	n	Dates used	Intercept	Slope	SE	R^2
Allequash	1982	3	c	10.5	-0.049	0.009	0.97
Allequash	1983	3	c	12.2	-0.058	0.003	0.99
Allequash	1984	4	a	10.5	-0.041	0.005	0.97
Allequash	1985	4	a	11.7	-0.049	0.004	0.99
Allequash	1986	3	b	10.5	-0.068	0.005	0.99
Allequash	1987	4	a	10.3	-0.046	0.003	0.99
Allequash	1988	4	a	11.0	-0.058	0.005	0.98
Allequash	1989	4	a	11.9	-0.050	0.005	0.98
Allequash	1990	3	b	11.9	-0.070	0.011	0.97
Allequash	1991	4	a	12.8	-0.061	0.003	0.99
Big Muskellunge	1983	3	c	13.2	-0.033	0.005	0.97
Big Muskellunge	1984	3	c	11.3	-0.022	0.003	0.98
Big Muskellunge	1985	3	c	12.5	-0.025	0.002	0.99
Big Muskellunge	1986	3	c	11.3	-0.021	0.002	1.00
Big Muskellunge	1988	3	c	11.1	-0.013	0.001	1.00
Big Muskellunge	1989	3	c	14.6	-0.040	0.002	1.00
Big Muskellunge	1990	3	b	11.4	-0.025	0.004	0.98
Crystal Bog	1983	4	b	8.5	-0.076	0.012	0.95
Crystal Bog	1984	3	b	8.9	-0.077	0.026	0.90
Crystal Bog	1985	3	b	9.8	-0.085	0.019	0.95
Crystal Bog	1986	3	b	8.9	-0.094	0.037	0.86
Crystal Bog	1987	3	b	7.7	-0.069	0.013	0.97
Crystal Bog	1988	3	b	8.0	-0.083	0.025	0.92
Crystal Bog	1989	3	b	9.5	-0.090	0.010	0.99
Crystal Bog	1990	3	b	9.6	-0.099	0.035	0.89
Crystal Bog	1991	3	b	8.1	-0.080	0.009	0.99
Crystal Lake	1982	3	c	14.2	-0.040	0.018	0.83
Crystal Lake	1987	3	b	12.1	-0.021	0.006	0.94
Crystal Lake	1989	3	c	14.1	-0.033	0.000	1.00
Crystal Lake	1990	3	b	12.1	-0.031	0.004	0.98
Crystal Lake	1991	3	c	12.7	-0.019	0.004	0.95

Table A.1 (cont.)

Lake	Year	n	Dates used	Intercept	Slope	SE	R^2
Little Rock - N	1984	3	c	11.1	-0.042	0.005	0.99
Little Rock - N	1985	4	d	13.2	-0.074	0.008	0.98
Little Rock - N	1986	3	c	11.2	-0.075	0.014	0.97
Little Rock - N	1987	4	b	11.1	-0.068	0.004	0.99
Little Rock - N	1988	4	c	11.5	-0.059	0.004	0.99
Little Rock - N	1989	4	c	12.3	-0.049	0.001	1.00
Little Rock - N	1990	3	d	13.9	-0.091	0.005	1.00
Little Rock - S	1985	4	d	13.7	-0.076	0.008	0.98
Little Rock - S	1986	4	a	10.8	-0.084	0.008	0.98
Little Rock - S	1987	4	b	10.9	-0.068	0.003	1.00
Little Rock - S	1988	3	c	13.0	-0.081	0.009	0.98
Little Rock - S	1989	5	a	13.0	-0.072	0.004	0.99
Little Rock - S	1990	4	b	12.3	-0.092	0.006	0.99
Sparkling	1982	3	c	13.1	-0.045	0.012	0.94
Sparkling	1983	3	c	11.5	-0.026	0.010	0.88
Sparkling	1985	3	b	11.0	-0.016	0.006	0.87
Sparkling	1986	3	b	10.1	-0.015	0.006	0.88
Sparkling	1989	3	c	13.3	-0.040	0.000	1.00
Sparkling	1990	3	b	11.7	-0.044	0.000	1.00
Sparkling	1991	3	c	12.4	-0.020	0.013	0.71
Trout Bog	1982	3	c	5.3	-0.034	0.001	1.00
Trout Bog	1983	3	b	4.9	-0.032	0.004	0.98
Trout Bog	1984	3	b	3.9	-0.023	0.004	0.96
Trout Bog	1985	3	b	3.9	-0.016	0.001	0.99
Trout Bog	1986	3	b	3.9	-0.042	0.018	0.85
Trout Bog	1987	3	b	3.4	-0.032	0.011	0.89
Trout Bog	1988	4	a	4.0	-0.019	0.001	1.00
Trout Bog	1989	4	a	7.8	-0.032	0.005	0.95
Trout Bog	1990	3	b	5.4	-0.050	0.014	0.92
Trout Bog	1991	3	b	4.9	-0.035	0.000	1.00
Trout Lake	1982	3	c	14.8	-0.057	0.018	0.91
Trout Lake	1984	3	c	11.5	-0.012	0.003	0.93
Trout Lake	1985	3	c	13.3	-0.015	0.003	0.96
Trout Lake	1986	3	c	11.8	-0.015	0.001	1.00
Trout Lake	1987	3	c	12.9	-0.011	0.002	0.96
Trout Lake	1989	3	c	13.7	-0.032	0.001	1.00
Trout Lake	1991	3	c	13.3	-0.020	0.005	0.95