



This is to certify that the thesis entitled

t

SEASONAL VARIATION IN RATIOS OF COMMUNITY **RESPIRATION TO GROSS PHOTOSYNTHESIS** DETERMINED BY STABLE ISOTOPES AND CONCENTRATIONS OF DISSOLVED OXYGEN IN GRAND TRAVERSE BAY, LAKE MICHIGAN

presented by

AMANDA LEIGH FIELD

has been accepted towards fulfillment of the requirements for the

M.S.

Environmental Geosciences degree in

Major Professor's Signature

Apr. 1 30 2004

Date

MSU is an Affirmative Action/Equal Opportunity Institution



PLACE IN RETURN BOX to remove this checkout from your record. TO AVOID FINES return on or before date due. MAY BE RECALLED with earlier due date if requested.

DATE DUE	DATE DUE	DATE DUE

6/01 c:/CIRC/DateDue.p65-p.15

_ - ___

SEASONAL VARIATION IN RATIOS OF COMMUNITY RESPIRATION TO GROSS PHOTOSYNTHESIS DETERMINED BY STABLE ISOTOPES AND CONCENTRATIONS OF DISSOLVED OXYGEN IN GRAND TRAVERSE BAY, LAKE MICHIGAN.

By

Amanda Leigh Field

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Geological Sciences

ABSTRACT

SEASONAL VARIATION IN RATIOS OF COMMUNITY RESPIRATION TO GROSS PHOTOSYNTHESIS DETERMINED BY STABLE ISOTOPES AND CONCENTRATIONS OF DISSOLVED OXYGEN IN GRAND TRAVERSE BAY, LAKE MICHIGAN.

By

Amanda Leigh Field

Dissolved oxygen concentrations (O_2) were used in conjunction with stable oxygen isotopes ($\delta^{18}O-O_2$) to determine the ratio of community respiration to gross photosynthesis (R:P ratios) in 2000 and 2001 in Grand Traverse Bay (GTB), Lake Michigan. Average R:P ratios in 2000 (1.2 ± 0.03 SE) and 2001 (1.1 \pm 0.04 SE) indicate that GTB is net heterotrophic on an annual basis and requires an allochthonous source or non-contemporaneous autochthonous source of organic carbon to support excess heterotrophic activity. On a seasonal basis, the system fluctuated between periods of net heterotrophy (R:P > 1) in early spring and late fall and net autotrophy (R:P < 1) in late spring and early summer. Periods of net autotrophy coincided with the onset of stratification. As stratification progressed, R:P ratios near unity were observed in the epilimnion indicating that heterotrophic activity in GTB is strongly dependent upon autochthonous inputs of organic carbon during periods of stratification. We suggest that the temporal discontinuity between the introduction and utilization of organic carbon drives metabolism towards net heterotrophy.

In memory of James E. Field:

Pancakes and coffee are not the same without you.

I wish you were still here with us.

ACKNOWLEDGMENTS

This work was sponsored by the Michigan Sea Grant College Program, project number R/ES-18, under grant number 1997-99 NA76RG0133 from the Office of Sea Grant, National Oceanic & Atmospheric Administration (NOAA), U.S. Department of Commerce, and funds from the State of Michigan. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation appearing hereon. I thank the Grand Traverse Band of Ottawa and Chippewa Indians and the officers and crew of the Inland Seas for their dedicated assistance and good humor that made sampling both possible and enjoyable. This work is indebted to the efforts of my advisor. Dr. Nathaniel Ostrom, and my committee members. Dr. Peggy Ostrom and Dr. Jan Stevenson. I thank Dr. Hasand Gandhi and Brian Roberts for their assistance with sample analysis. A special thank you to Kim Frendo who aptly conducted the sampling in 2000 and took the time to demonstrate everything to the newcomer. I truly owe Dr. Mary Russ for her patient assistance and encouragement throughout my graduate career, not to mention her honesty and fabulous humor. Thank you to all those faculty and staff at Michigan State University who have provided encouragement and generous assistance: Dr. Cambray, Dr. Patino, Dr. Sibley, Mr. Todd Tarrant, Mr. Gabe Ording, and Mrs. Marsha Walsh. I especially thank my mother and father who put up with a tremendous influx of 'stuff' when I moved back and even a larger mess once I began writing. Your trust and courage in the face of adversity has given me more strength than anything or anyone else ever could - thank you.

iv

TABLE OF CONTENTS

vi
vii
1
6
6 7
9
13
17
25
27
29
39

LIST OF TABLES

Table 1:	Summary of measurements collected at station GT3, 2000	27
Table 2 :	Summary of measurements collected at station GT3, 2001	28

LIST OF FIGURES

Figure 1: Station GT3, Grand Traverse Bay, Lake Michigan (modified from http://www.glerl.noaa.gov)	29
Figure 2: Temperature (° C, bold line) and Fluorescence (RFU, thin line) as a function of depth (m) and sampling date in 2000	30
Figure 3: Temperature (° C, bold line) and Fluorescence (RFU, thin line) as a function of depth (m) and sampling date in 2001	31
 Figure 4: Fraction of O₂ saturation (O_{2sat}) as a function of depth at station GT3 in Grand Traverse Bay in (a) April – June 2000, (b) July and October – November 2000, (c) April – June 2001, and (d) August and October 2001. 	32
Figure 5: δ^{18} O-O ₂ as a function of depth at station GT3 in Grand Traverse Bay in (a) April – June 2000, (b) July and October – November 2000, (c) April – June 2001, and (d) August and October 2001	33
Figure 6: R:P ratios as a function of depth at station GT3 in Grand Traverse Bay in (a) April – June 2000, (b) July and October – November 2000, (c) April – June 2001, and (d) August and October 2001.	34
Figure 7: (a) Fraction of O ₂ saturation (O _{2sat}), (b) δ^{18} O-O ₂ , and (c) R:P ratios as a function of depth (m) and sample date at station GT3 in Grand Traverse Bay in 2000 and 2001. The bold horizontal line represents (a) 100% O ₂ saturation, (b) air-water gas exchange (δ^{18} O = 0.7‰), and (c) community respiration equal to gross photosynthesis (R:P = 1).	35
Figure 8. δ^{18} O-O ₂ (‰, wrt air) as a function of the fraction of O ₂ saturation (O _{2sat}) and sampling date for the upper 30 m at station GT3. The bold vertical line represents 100 % saturation. Airwater gas exchange (0.7 ‰) is indicated by the bold horizontal line. The equilibrium locus represents the initial conditions of an aquatic system at equilibrium with the atmosphere and when biological activity is negligible. Quadrants I and III indicate O ₂ input and utilization, II suggests O ₂ utilization, and IV represents O ₂ input. (a.) All data points for the upper 30 m are plotted and	

data representing R:P ratios greater than, less than, and approximately equal to one are encircled to more clearly display

seasonal trends. (b.) Mean δ^{18} O-O ₂ and O _{2sat} values for the upper 30 m are plotted for each month.	
Figure 9: Fraction of O ₂ saturation (O _{2sat}) as a function of δ^{18} O - O ₂	
(‰, wrt air). Open squares are data for Lake Kinneret published	
by Luz et al. (2002), open triangles are data from Amazon floodplain lakes published by Quay et al. (1995), and filled circles	
are from the present study. The bold vertical line represents 100	
% saturation. Air-water gas exchange (0.7 ‰) is indicated by	
the bold horizontal line. Quadrants I and III indicate O_2 input and	
utilization, II suggests O_2 utilization and IV represents O_2 input.	
The majority of data for each study are encircled for ease of	
identification.	37
Figure 10: The progression of thermal stratification with depth over	
time. The bottom of the thermocline (epi + meta) is indicated by a	
dotted line. Two vertical dashed line boxes indicate the start and	
end of thermostratification (mid-May - Oct/Nov). Values depicted	
for O _{2set} , δ^{18} O-O ₂ , and R:P ratios were averaged for the upper	
water column and the hypolimnion during the stratified period	

INTRODUCTION

The balance between community respiration and gross primary production (R:P ratio) in an aquatic ecosystem is influenced by the fixation of organic carbon from in situ primary production (autochthonous production) and influx of external carbon transported into a system from surrounding aquatic and terrestrial environments (allochthonous production). In a system driven by autochthonous production, community respiration is equal to or less than gross primary production ($R \le P$) and the system is net autotrophic. Conversely, community respiration in excess of gross primary production (R > P) results if additional sources of organic carbon to autochthonous production are available to respiring organisms. Such systems are net heterotrophic. The degree to which net heterotrophy is expressed in an aquatic system, and thus the degree to which allocthonous production influences a system, has been shown to vary with lake productivity (Odum and Prentki 1978, del Giorgio and Peters 1994, del Giorgio et al. 1997, Cole et al. 2000).

In the majority of measured oligotrophic temperate lakes, community respiration exceeds gross primary production (del Giorgio and Peters 1994, Coveney and Wetzel 1995, del Giorgio et al. 1997, Cole et al. 2000). Such observations led to the conclusion that allochthonous inputs of organic carbon play a significant role in the metabolism of unproductive systems (del Giorgio and Peters 1994, Coveney and Wetzel 1995, del Giorgio et al. 1997). Recently, however, this interpretation was challenged when gross primary production was observed to exceed community respiration in oligotrophic Laurentian Shield lakes

(Carignan et al. 2000). Subsequent research has indicated that elevated DOC concentrations result in net heterotrophy and lower concentrations result in net autotrophy (Praire et al. 2002, Hanson et al. 2003). Such observations imply that DOC concentration, and ultimately that watershed characteristics controlling DOC influx (del Giorgio and Peters 1993, Praire et al. 2000), control the balance between net allochthonous and autochthonous organic carbon in lake ecosystems.

Current assessments of the balance between R and P in lacustrine environments are generally restricted to the epilimnetic and metalimnetic waters during periods of thermostratification (del Giorgio 1994, Carignan et al. 2000, Praire et al. 2002, Hanson et al. 2003). Thermally stratified layers restrict the vertical movement of nutrients and organic matter and significantly affect the metabolic balance of a system. For example, physically forced sediment resuspension events during isothermal conditions stimulated heterotrophic activity in Southeastern Lake Michigan (Cotner et al. 2000). This is in contrast to indications that nutrient regeneration, not external sources of organic carbon, supports metabolism in the upper water column during late summer and fall stratification in Lake Michigan (Van Mooy et al. 2001). Meanwhile, metabolism in the hypolimnion during the stratified period is strongly influenced by sediment resuspension events (Eadie et al. 1984, Scavia and Laird 1987, Cotner et al. 2000, Schneider et al. 2002) and sedimenting particles from the epilimnion (Schneider et al. 2002). With measurements restricted to stratified periods and

to epilimnetic/metalimnetic depths, a gap exists in our current understanding of the seasonal and depth trends in the balance between R and P.

The occurrence of net autotrophy and heterotrophy was investigated as a function of time and depth in Grand Traverse Bay (GTB), Lake Michigan, based upon the variations in R:P ratios over time. Ratios of R to P were determined from in situ measurements of oxygen concentrations [O₂] and stable oxygen isotopes (δ^{18} O-O₂) utilizing a model developed for Amazon Basin floodplain lakes and rivers (Quay et al. 1995). Values of δ^{18} O-O₂ are expressed with respect to air (wrt air) where δ^{18} O = 0.0‰ wrt air is equal to 23.5‰ V-SMOW (international standard for O) in per mil (‰) notation.

(1)
$$\delta^{18}O = (({}^{18}O/{}^{16}O)_{sample}/({}^{18}O/{}^{16}O)_{standard} - 1) * 1000$$

The model takes advantage of the quantifiable effects that photosynthesis, respiration, and gas exchange have on $[O_2]$ and $\delta^{18}O-O_2$. Effects of photosynthesis, respiration, and gas exchange on $\delta^{18}O-O_2$ values are a result of kinetic fractionation processes whereby small differences in the mass of an isotope (¹⁶O or ¹⁸O) influence the rate at which a reaction occurs (Kroopnick 1975, Kiddon et al. 1993, Quay et al. 1995). During respiration, ¹⁶O-¹⁶O is utilized at a faster rate than ¹⁶O-¹⁸O and the residual O₂ is enriched in ¹⁸O relative to the initial substrate (Lane and Dole 1956, Bender and Grande 1987, Kiddon et al. 1993, and Quay et al. 1995). During the splitting of water molecules in photosynthesis, H₂¹⁸O and H₂¹⁶O are utilized at approximately the same rate and the O₂ released has a δ^{18} O value that is equal to that of the water

(Stevens et al. 1975, Guy et al. 1993). In GTB, the average isotopic signature of the water is -28.8‰ wrt air and a predominance of photosynthesis over respiration results in δ^{18} O-O₂ values approaching -28.8‰ wrt air. Fractionation during the exchange of O₂ between the atmosphere and surface waters results in a slight enrichment in ¹⁸O of surface waters by 0.7‰ (Kiddon et al. 1993, Benson and Krause 1984). As a result, δ^{18} O-O₂ values greater than air (0.7‰) indicate that the rate of respiration is greater than that of photosynthesis while values less than air indicate a predominance of photosynthesis relative to respiration (Bender and Grande 1987, Quay et al. 1995).

The primary objective of the current study was to investigate the balance between R and P (R:P ratios) as a function of season and depth in Grand Traverse Bay (GTB). Station GT3 is located in the upper west arm of Grand Traverse Bay (GTB), a lobed inlet of Lake Michigan (Figure 1). Northern Lake Michigan is characterized as oligotrophic to mesotrophic (Stoermer et al. 1972, Auer et al. 1976, and Tarapchack and Stoermer 1976). Surface waters from northern Lake Michigan flow into the west arm of GTB (Lauff 1957) and water quality is correspondingly similar (Auer et al. 1976). The glacially formed Bay is large (total area is equal to 681.6 km²) and deep (mean depth for the bay is 55 m; Lauff 1957). It is expected that deep, oligotrophic systems such as GTB will be strongly impacted by allochthonous material from the surrounding watershed due to the relatively low contribution of organic matter from established macrophyte communities that impact shallow systems (del Giorgio and Peters 1993). However, low riverine and groundwater inputs (Smith 1973, Schneider et al. 2002) and average C/N ratios previously measured at station GT3 imply that terrestrial inputs of organic carbon into GTB are low (McCusker et al. 1999). As a result, we expected that metabolism would be predominately supported by insitu primary production and would be reflected on an annual basis by R:P ratios near unity.

METHODS

Field and Laboratory Methods

Station GT3 (Figure 1, 44°59.00 N, 85°34.80 W, Z = 112 m) was sampled six times between April and November in 2000 and five times between April and October in 2001 (Table 1 and 2). Sampling was conducted between 800 and 1100 hours to reduce error resulting from diurnal variations in photosynthesis and respiration. A SeaBird Electronics SBE25 CTD profiler equipped with a fluorometer (Seatech) was deployed to characterize temperature and to approximate the chlorophyll a (Chl *a*) abundance of the water column. In 2000, three to five depths were chosen for sampling dissolved O₂. Sampling depths were based upon the fluorescence depth profile of the water column. Five fixed depths (5, 15, 25, 50, and 100 m) were chosen in 2001. Water (3 - 5 L) was collected from these depths using standard and lever-action Niskin bottles (General Oceanics). A modified Winkler method was employed to determine dissolved O₂ concentrations (Carpenter 1965, Emerson et al. 1999).

The collection procedure for δ^{18} O-O₂ followed that of Emerson et al. (1991 and 1999). Approximately 100 mL of sample water was slowly introduced into pre-evacuated 200 mL glass vessels fitted with high vacuum stopcocks that contained dried mercuric chloride (1 mL HgCl₂, saturated solution) to eliminate biological activity. Prior to and after introducing the sample, the arm on the vessel was flushed with CO₂ gas to prevent air contamination. Following equilibration in a constant temperature bath (8 hours, 28°C), water was removed by vacuum until approximately 1 mL remained. Determination of δ^{18} O-O₂

followed the gas chromatograph-isotope ratios mass spectrometry (GC-IRMS) technique of Roberts et al. (2000). Briefly, the sample was introduced into an evacuated inlet system consisting of LiOH (to remove CO₂ and H₂O) and carried by He on a GC column. As the sample passed through the GC column, the molecular sieve trapped any remaining CO₂ and H₂O. The resulting sample was then allowed to flow into the mass spectrometer. Values of δ^{18} O-O₂ were determined on a GV Instrument Prism mass spectrometer with an analytical precision of ± 0.3‰ (Roberts et al. 2000).

Determination of R:P ratios

The ratio of the community respiration rate (R) to gross primary production (P) for a system at steady state (assumed) was calculated from the measured values of δ^{18} O-O₂ and [O₂] (Quay et al. 1995):

(2) R:P =
$$({}^{18:16}O_w\alpha_p - {}^{18:16}O_g)/({}^{18:16}O\alpha_r - {}^{18:16}O_g)$$

and

(3)
$${}^{18:16}O_g = \alpha_g [{}^{18:16}O_a \alpha_s - (O_2/O_{2s}){}^{18:16}O]/[1-(O_2/O_{2s})]$$

where O_2 is the concentration of dissolved oxygen (measured), O_{2s} is the concentration of dissolved oxygen at atmospheric saturation (Benson and Krause 1984, Garcia and Gordon 1992), ^{18:16} O_a is equal to the isotopic composition of O_2 in the atmosphere (0‰ wrt air, Kroopnick and Craig 1972), ^{18:16}O is the isotopic

composition of O₂ in solution (measured), ^{18:16}O_w is the isotopic composition of water (measured, -28.8‰ wrt air), ^{18:16}O_g is the isotopic composition of the gas invasion flux (calculated), α_g is the ratio of the ¹⁸O-¹⁶O to ¹⁶O-¹⁶O gas transfer velocities (0.9972, Knox et al. 1992), α_s is the ratio of the solubilities of ¹⁸O-¹⁶O to ¹⁶O-¹⁶O gases in water (1.0007, Kroopnick and Craig, 1972), α_p is the ratio of the photosynthetic reaction rates of H₂¹⁸O and H₂¹⁶O (1.000 ± 0.003; Stevens et al. 1975, Guy et al. 1993), and α_r is the ratio of ¹⁸O-¹⁶O to ¹⁶O-¹⁶O reaction rates during respiration (estimated 0.9770; Luz et al. 2002). Samples for the determination of δ^{18} O-H₂O were analyzed by Mountain Mass Spectrometry (Evergreen, Colorado) via a MultiPrep and reduction furnace system.

The net respiratory-fractionation factor, α_r , reflects the combined isotope effects associated with the Mehler, photorespiration, cytochrome oxidase, and alternative oxidase respiration pathways for an aquatic community (Kroopnick and Craig 1972, Kroopnick 1975, Guy et al. 1989). Previously measured values range between 0.9780 for ocean surface waters (Kroopnick 1975, Quay et al. 1993) to 0.9820 for Amazon rivers dominated by bacterial respiration (Quay et al. 1995). Recently, Luz et al. (2002) determined the respiratory fractionation factors as a function of season in the epilimnion of a phytoplankton-dominated lacustrine environment, Lake Kinneret. As the community in GTB resembles the community present in Lake Kinneret, we used the average epilimnetic respiratory fractionation factor reported by Luz et al. (2002) of 0.9770 in our calculations of R:P ratios.

RESULTS

The expected seasonal progression in thermal structure for a temperate lake was evident at station GT3 in GTB by isothermal conditions in spring. thermostratification in the summer, breakdown of stratification in fall, and a return to isothermal conditions in late fall (Figures 2 - 3). Sampling in May and June of 2001 occurred several weeks later than in May and June of 2000 and temperatures were 1 - 2 °C higher in the upper 20 m in the latter portion of each month in 2001. The water column was isothermal in May 2000 and weakly stratified in May 2001 (Figures 2 - 3). Surface water temperatures continued to rise throughout the summer stratification period with the maximum epilimnetic temperatures observed in July of 2000 (20°C, Figure 2) and August of 2001 (~22°C, Figure 3). By October, epilimnetic temperatures had decreased signaling the breakdown of thermostratification. However, a cooler (~ 14°C) and well-developed mixed layer extending to 25 m in depth was evident in October of 2000 whereas a warmer (~16°C) and shallow mixed layer extending to 5 m in depth was present in October 2001 (Figure 2 - 3). The variability in the breakdown of stratification between years was likely the result of the intensity and timing of storm events.

Chlorophyll *a* (chl *a*) abundance in 2000 and 2001 ranged from 0.2 to 2.0 relative fluorescence units (RFU). A deep chlorophyll layer (DCL) was present throughout the stratified period in 2000 and a weak DCL was evident in late summer and fall 2001. A DCL was not present in early spring (April and May, Figure 2 - 3) and epilimnetic decreases in fluorescence toward the surface were

likely due to interference from sunlight with the fluorometer. The DCL was most prominent in June of 2000 and consequently deteriorated throughout the summer and fall. In June 2001, as a broad fluorescence layer existed from 30 m to 80 m (Figure 2 - 3). Dual florescence peaks were evident in August of 2001, when an epilimnetic florescence maxima coincided with a equally strong DCL (Figure 2 -3). By October of both years, the DCL was no longer present, and a strong epilimnetic peak was evident between 5 - 25 m in depth (Figure 2 - 3). The water column florescence profile in November was relatively uniform reflecting mixing.

Values of O_{2sat} ranged from 0.82 - 1.05 in 2000 and 0.76 -1.05 in 2001 (Figure 4). Early spring was consistently undersaturated in O_2 and indicated that O_2 utilization by respiring organisms exceeded O_2 input by primary production and/or atmospheric introduction (Figures 4a and 4c). With the onset of thermostratification in June, the upper 30m became supersaturated with respect to O_2 reflecting photosynthetic and/or atmospheric input in excess of O_2 utilization by heterotrophic activity (Figure 4a and 4c). Excluding near saturation conditions at 25 m in July of 2000, the water column was increasingly undersaturated from mid-summer to fall reflecting a predominance of respiration during the stratified period (Figure 4b and 4d). Thus, despite a brief period when supersaturation was observed in the eplimnion, the water column at GT3 was predominately undersaturated reflecting a predominance of respiration over photosynthesis and/or atmospheric exchange.

Observed values of δ^{18} O-O₂ ranged between -1.5 and 1.7 and are driven by seasonal variations in the relative importance of photosynthesis, respiration,

and gas exchange (Figure 5). Spring δ^{18} O-O₂ values were near 0.7‰ (Figure 5a and 5c), thereby reflecting atmospheric input of O_2 (Kiddon et al 1993). After the onset of thermostratification in late spring, isotope values for O₂ in the upper 25 to 50 m were predominately less than 0.7‰ (Figure 5a - d) thus indicating the predominance of photosynthesis over respiration (Stevens et al. 1975, Bender and Grande 1987). In general, the lowest monthly δ^{18} O-O₂ values were observed as a single minimum at 15 m (Figure 5a - d) that rarely coincided with the observed fluorescence maxima (Figure 2 - 3). The exception was August of 2001 when low δ^{18} O-O₂ values at 5 m and 25 m, reflecting a predominance of photosynthesis over respiration, were observed within the epilimnetic (~0 - 15 m) and hypolimnetic (> 20 m) fluorescence maxima (Figure 2 - 3, Table 2). By October 2000 and 2001, low δ^{18} O-O₂ values were restricted to the upper 25-30m (Figure 5b and 5d). Deeper waters (> 30 m) in October 2000 and 2001 and all depths in November 2000 were characterized by δ^{18} O-O₂ values greater than 0.7‰ (Figure 5b and 5d), indicating a prevalence of respiration over photosynthesis (Lane and Dole 1956, Kroopnick 1975, Bender and Grande 1987, Quay et al. 1995). At 100 m, δ^{18} O-O₂ values were generally greater than 0.7‰. indicating that respiration consistently exceeded photosynthesis in the deep hypolimnion (Figure 5a - d).

Ratios of community respiration to gross primary production (R:P) ranged from 0.8 to 1.4 in 2000 and 0.6 to 1.3 in 2001 (Figure 6). While R:P ratios at depths greater than 80 m were consistently above 1.0 and varied little between seasons and years (1.3 - 1.4 in 2000 and 1.1 - 1.3 in 2001), values varied

seasonally in the upper 50 m (1.2 - 1.4 in 2000 and 1.0 - 1.3 in 2001, Figure 6). Observed R:P ratios during the isothermal period of early spring were greater than 1 thereby indicating that community respiration exceeded gross primary production. From late spring (May 2001) and early summer (June 2000 and 2001), R:P ratios less than 1 indicated that gross primary production was greater than community respiration in the upper 20-30 m (Figure 6a and 6c). Values were near unity (R:P = 1) in summer and increased in the fall when the highest R:P ratios were observed (Figure 6b and 6d). The overall predominance of community respiration over gross photosynthesis in both 2000 and 2001 provided a strong indication that station GT3 is net heterotrophic.

DISCUSSION

The balance between community respiration (R) and gross primary production (P) in an aquatic system can be understood by the measurements of O₂ concentrations and stable isotopes. Values less than O₂ saturation in temperate oligotrophic to mesotrophic lakes reflect respiration in excess of atmospheric and photosynthetic O₂ introductions (Quay et al. 1995, Praire et al. 2002). In Grand Traverse Bay (station GT3), the water column was predominantly undersaturated, as indicated by O_{2sat} values less than 1, throughout the sampling periods in 2000 and 2001 (Figure 7a). A brief period of supersaturation in the upper 25 m in May 2001 and June 2000 and 2001 indicated that the introduction of O₂ into the water column exceeded that utilized by heterotrophic activity. Solely based upon values of O_{2sat}, it is difficult to discern if supersaturation is the result of primary production or increased atmospheric introduction of O₂. Despite this uncertainty, the predominance of undersaturated conditions is an indication that station GT3 was predominately net heterotrophic.

Previously, δ^{18} O-O₂ values have been used to qualitatively evaluate the relative importance of atmospheric exchange, P, and R on water column O₂ (Bender and Grande 1987, Quay et al. 1995). Oxygen isotope values reveal which process is most influential based upon the following criteria: (1) atmospheric exchange is suggested by δ^{18} O-O₂ values equal to 0.7 (Benson and Krause 1984, Kiddon et al. 1993), (2) R by values greater than 0.7 (Kroopnick 1975, Bender and Grande 1987, Quay et al. 1995), and (3) P by values less than

0.7 (Stevens et al. 1975, Guy et al. 1993). Variations in δ^{18} O-O₂ with depth and season at station GT3 therefore reflect changes in the relative importance of P, R, and gas exchange over time. During the isothermal periods (April and November 2000, 2001, and May 2000), water column δ^{18} O-O₂ values were near, but greater than 0.7‰ indicating that the predominant metabolic process was O₂ utilization by the respiring community (Figure 7b). Values did not deviate far from 0.7%, however, and suggested a significant influx of atmospherically derived O_2 to the water column occurred in early spring and late fall. When GTB was stratified, values of δ^{18} O-O₂ less than 0.7‰ were observed in the upper 25 m from late May to October and in the upper 50 m in June and July (Figure 7b). Therefore, the primary metabolic process in the upper water column during the stratified period was P. At 100 m, δ^{18} O-O₂ values ranged from 0.8 – 1.5‰ indicating that the primary process influencing O₂ at depth was R (Figure 7b). Consequently, δ^{18} O-O₂ values reveal that primary production provided a significant input of O₂ into the upper water column during the stratified period and that R was the predominant process in the hypolimnion and during isothermal Furthermore, δ^{18} O-O₂ values indicated that the system was net periods. autotrophic from late spring/early summer to fall and net heterotrophic in early spring and late fall. This conclusion, however, is in contrast to the interpretation of O_{2sat} data where undersaturation indicated that R predominates during the Although O_{2sat} and $\delta^{18}O-O_2$ each provide independent stratified months. indications of the balance between R and P, there are instances when these two measures yield conflicting results.

To better understand the relationship between O_{2sat} and $\delta^{18}O-O_2$ in the upper water column, these two parameters were plotted against one another (Figure 8). The intersection of the vertical saturation line ($O_{2sat} = 1.0$) and the horizontal 0.7‰ line, hereafter referred to as the equilibrium locus, represents a point where the flux of O2 is primarily due to atmospheric exchange and the biological fluxes are negligible (Figure 8). The equilibrium locus theoretically represents the initial conditions of a system at equilibrium with the atmosphere. Initial system conditions were assumed to originate at the equilibrium locus in order to provide a point of comparison with measured values. To better understand the relative importance of G, P and R, the figure is broken into four quadrants indicating that O₂ is input and/or consumed (Figure 8). Interpretations of the relative importance of R and P based upon O_{2sat} and $\delta^{18}O-O_2$ are contradictory in guadrants I and III. Interestingly, data that were plotted within quadrant III were measured when the water column was thermally stratified. Measurements made at this time indicated that the water column was undersaturated yet isotope values indicated а predominance of photosynthetically produced O₂. This discrepancy likely represents a system in which the equilibrium locus is not the initial condition; but rather offset by an influence from biological activity. Therefore, the apparent contradiction between O_{2sat} and $\delta^{18}O-O_2$ is likely the result of a biologically influenced shift away from air-water equilibrium conditions and demonstrates that a combination of O_{2sat} and δ^{18} O-O₂ is needed to understand variations in the balance between R and P.

In order to frame the trends observed at station GT3 into a larger context, the distribution of $\delta^{18}\text{O-O}_2$ and O_{2sat} for all depths and times at station GT3 was compared with values reported for the floodplain lakes of the Amazon Basin (Quay et al. 1995) and Lake Kinneret (Luz et al. 2002; Figure 9). The Amazon lakes and Lake Kinneret display contrasting metabolic balances and organic carbon inputs. Amazon Basin floodplain lakes are considered to be strongly net heterotrophic due to high bacterial biomass and high allochthonous inputs of organic carbon (Quay et al. 1995 and references within). Lake Kinneret, however, is characterized by high primary production and high autochthonous inputs (Dubowski et al. 2002). In comparison to the Amazon Basin lakes and Lake Kinneret, the data from station GT3 are narrowly distributed around the equilibrium locus (Figure 9). Therefore, biological activity (P and R) must be low in GTB relative to that in the Amazon lakes or Lake Kinneret. The proximity of GT3 data to the equilibrium locus indicates that the abundance of O₂ within GTB is closer to atmospheric equilibrium. Data points from the Amazon Basin lakes and Lake Kinneret data are skewed to the left and right, respectively, of the equilibrium locus. The distribution of GT3 data indicate that GTB is closer to atmospheric equilibrium at all times and that atmospheric exchange consistently dominates O₂ fluxes in a deep, oligotrophic-mesotrophic, temperate lake to a greater extent than in systems characterized by high biological activity like the Amazon Basin floodplain lakes and Lake Kinneret.

<u>R:P ratios</u>

At station GT3, R:P ratios observed for all depths and times (mean = 1.2 ± 0.03 SE) were significantly greater than one (student t-test, p < 0.001) and indicated that the system on an annual basis was net heterotrophic (Figure 8). Net heterotrophy was expected as respiration rates exceed primary production in the majority of systems characterized as oligotrophic to mesotrophic (Quay 1995, del Giorgio et al. 1994 and 1997, Cole et al. 2000). As net heterotrophy was observed, the contribution of organic materials by the autotrophic community cannot be the sole support to heterotrophic activity. Thus, an additional source to autochtonous organic carbon production is required to support the observed excess respiration.

Within net heterotrophic lakes, additional sources to new in situ primary production are largely presumed to be of terrestrial origin introduced into a system by groundwater or rivers (del Giorgio and Peters 1994, Coveney and Wetzel 1995, del Giorgio et al. 1997, Cole et al. 2000). However, allochthonous inputs of organic carbon are considered low in Lake Michigan (Scavia et al. 1986) and GTB (Smith 1973, McCusker et al. 1999, and Schneider et al. 2002) and additional sources of organic carbon must be considered in order to explain the observance of net heterotrophy. Another possibility of organic carbon introduction exists in Lake Michigan in the form of autochthonously produced material that accumulates within the system and is metabolized at a later point in time (Scavia et al. 1986, Scavia and Laird 1987, Cotner and Biddanda 2002, and Biddanda and Cotner 2002). In Lake Michigan, organic carbon is hypothesized

to accumulate in the upper water column and hypolimnion during periods of low bacterial respiration (Scavia and Laird 1987, Cotner et al. 2000), rapid sedimentation (Biddanda and Cotner 2002), and high phytoplankton productivity in the spring (Scavia et al. 1986, Cotner et al. 2000). Three possible internal sources of organic carbon to the upper water column are the deep chlorophyll layer (DCL), benthic nephloid layer (BNL), and sediments. The DCL is a common feature in Lake Michigan during the stratified summer months (Figure 2 and 3: Brooks and Torke 1977. Mortonson 1977. Moll and Stoermer 1982. Barbiero and Tuchman 2001b, Fahnenstiel and Scavia 1987) and may provide up to 70% of net primary production (Moll and Stoermer 1982). Material introduced to the upper water column from the DCL includes autochthonously produced organic carbon that may have been retained within the system for days or months. Another common feature when Lake Michigan is thermally stratified is the development of a BNL; a concentrated layer of small particles 5 - 30 m above the sediments (Eadie et al. 1984, Hicks and Owens 1991, McCusker et al. 1999, Schneider et al. 2002). The BNL is composed of particulate matter from the water column (Schneider et al. 2002) and from sediment resuspension (Eadie et al. 1984). Thus, the BNL potentially represents a source of organic carbon that is retained within the system for days to years. Sediment resuspension events occur throughout the year in GTB (Schneider et al. 2002) although the largest sediment resuspension events are observed in the winter months when lake ice is not present (Eadie et al. 1984, Cotner et al. 2000, Schneider et al. 2002). Although sedimentary organic carbon is often refractory, such organic

carbon can be altered by solar electromagnetic radiation to biologically available forms (Biddanda and Cotner 2003). Material within the sediments may have been deposited recently to decades ago. For purposes of this discussion, the sources will be grouped under the term non-contemporaneous organic carbon as they represent material that has been retained for some time within the system and respired at a later point in time.

The observed range of R:P ratios, 0.6 to 1.4 (Table 1 and 2), at station GT3 demonstrates that this system alternates between periods of net autotrophy and net heterotrophy. Whereas net autotrophy implies that autochthonously produced organic material is produced in excess and may be retained within the system, net heterotrophy implies that an external or non-contemporaneous organic carbon substrate is utilized within the water column. An imbalance between R and P signifies that heterotrophic activity and autotrophic production are temporally uncoupled. As previously suggested, the metabolism of noncontemporaneous organic carbon provides one mechanism that may result in periods of uncoupling between R and P (Scavia et al. 1986, Cole et al. 2000). The relationship between carbon inputs and the balance between R and P is not unidirectional, however. Temporal uncoupling between R and P may result in the retention of organic matter within a system that is then utilized at a later time (Scavia et al. 1986, Scavia and Laird 1987, Cole et al. 2000, Biddanda and Cotner 2002). Whether R and P are uncoupled or coupled at one point in time is quantitatively expressed by R:P ratios. As a result, the R:P ratio indicates when accumulation of organic carbon within the system occurs (due to excess

phytoplankton production) and when additional sources to autotrophic production of organic carbon are required to satisfy excess heterotrophic consumption of carbon. At station GT3, the alternation between net autotrophy and net heterotrophy implies that this system shifts between periods of accumulation and periods of organic carbon introduction and utilization.

Throughout this study, R exceeded P in the hypolimnion (Figure 6 - 7). While R is expected to be elevated at depths below 30 - 50 m, P is expected to be greatly reduced or absent due to low light conditions. Consequently, it was expected that the R:P values would greatly exceed unity. This was not the case (Figure 6, 7, and 10). The presence of O_2 in the hypolimnion is likely the result of mixing and diffusion of atmospheric and/or photosynthetic O₂ from the upper water column to the lower water column. However, respiration in the hypolimnion also requires a source of organic carbon. While sedimentation of photosynthetically reduced carbon may support hypolimnetic respiration during periods of net autotrophy in the epilimnion, net heterotrophic conditions in the epilimnion indicate that additional inputs to sedimenting products of photosynthesis are required to support R at other times. Sediment resuspension is likely an important source of autochthonously and allochthonously produced organic carbon and nutrients (Cotner et al. 2000) to the water column. Although the largest sediment resuspension events are observed in the winter months when lake ice is not present (Eadie et al. 1984, Cotner et al. 2000, Schneider et al. 2002), significant resuspension events resulting from seiche activity also occur periodically in GTB during stratified periods (Schneider et al. 2002). Such

events in southeastern Lake Michigan result in increased bacterial productivity, decreased phytoplankton productivity, and ultimately in an uncoupling between autotrophic and heterotrophic activity (Cotner et al. 2000). Therefore, diffusion of O_2 from the epilimnion and resuspension of sedimentary material into the hypolimnion likely explain the strong net heterotrophy observed in the hypolimnion throughout both years observed in this study.

Net heterotrophy was observed at station GT3 when the water column was unstratified (November and April - May, Figures 2 - 3 and 6 - 7). The occurrence of net heterotrophy in early spring and fall indicates that allochthonous and non-contemporaneous inputs to the water column exceed autotrophic inputs. Vertically uniform oxygen isotope values (δ^{18} O-O₂ near 0.7‰) and isothermal conditions in early spring and fall indicate total water column turnover. Mixing conditions imply that sediment resuspension may be an important source for heterotrophic activity in early spring and late fall. Sediment resuspension events occur more often during unstratified periods (Schneider et al. 2002) and would support the introduction of non-contemporaneous organic carbon into the upper water column. Therefore, our observation of net heterotrophic activity is uncoupled and that excess respiration may be stimulated by sediment resuspension events.

Net autotrophy was observed in the upper water column at station GT3 during the onset of thermostratification in May of 2001 and June in both years (Figure 2 - 3 and 6 - 7). Late spring and early summer have been reported to be

periods of high P in GTB (Stoermer et al. 1972). However, the observation of strong net autotrophy (R:P ratios as low as 0.6; Table 2) was not expected during this period. Rates of primary production in the west arm of GTB indicate that primary production typically peaks in late summer/fall and spring values are only slightly elevated above winter rates (Auer et al. 1976). Low R:P ratios (< 1) observed at station GT3 imply that either P rates are elevated or R rates are reduced. A reduction in R rates in spring/summer relative to early spring is unlikely as rising water temperatures stimulate bacterial activity and an increase in R is expected to occur (Pomeroy and Deibel 1986, Scavia and Laird 1987). However, the expected magnitude of R may reduced as diatoms dominate in spring (Auer et al. 1972, Barbiero and Tuchman 2001a) and are able to competitively depress the heterotrophic consumption of DOC when Si is available (Havskum et al. 2003). Therefore, the low R:P ratios observed in the transition from late spring to early summer are likely the result of an increase in both R and P; however, P is likely increasing more rapidly than R.

In July of 2000 and August of 2001, community respiration and gross photosynthesis were approximately in balance in the upper 25 m at station GT3. After the period of net autotrophy in late spring/early summer, the water column was undersaturated with respect to O_2 by nearly 10% for the remainder of the summer. Although $\delta^{18}O-O_2$ values revealed an increasing significance of photosynthetic input into the upper water column in the late summer (Figure 6), R:P ratios approaching unity indicate that the increased autotrophic input was accompanied by elevated heterotrophic utilization (Figure 8 and 10).

Consequently, a strong coupling between autotrophic and heterotrophic communities was implied as the autotrophic input of O₂ did not return the system to saturation. The occurrence of R:P ratios approaching unity (Figure 6) during a period when organic matter substrate limitation (Gardner et al. 1989) and nutrient depletion are expected (Fahnenstiel and Scavia 1987, Conley et al. 1998), indicates that heterotrophic activity must be increasingly dependent upon photosynthetic metabolites in the upper water column as stratification persists. Our results are consistent with previous studies conducted in southeastern Lake Michigan where similar patterns in bacterial cell production and net primary production provides evidence that autochthonous production could potentially meet the bacterial organic carbon demand during summer stratification (Scavia et al. 1986). As the R:P ratios presented in this study represent the balance between community respiration and gross primary production, bacterial metabolic demands are included within the R:P ratio. Our results demonstrate that R:P ratios approach unity and indicate that epilimnetic heterotrophic consumption of organic carbon is coupled to autotrophic production in late summer.

Net heterotrophy was strongly indicated in the upper 25 m in October of both years as R:P ratios were equal to 1.2 (Figure 6 - 7, Table 1 and 2). As the water column was still stratified, sources of organic carbon to the epilimnion from the hypolimnion are restricted. Autotrophic and heterotrophic activity in the upper water column in the fall is likely supported by epilimnetic nutrient recycling (Van Mooy et al. 2001) and the metabolic utilization of organic matter from the DCL as the mixing layer increases in depth (Mortonson 1977, Brooks and Torke 1977,

Scavia et al. 1986, Scavia and Laird 1987, Van Mooy et al. 2001). Therefore, the observation of net heterotrophy in the epilimnion in October at station GT3 indicates that autotrophic and heterotrophic activity are uncoupled in the fall and likely triggered by mixing of materials from the DCL.

CONCLUSIONS

The predominance of net heterotrophy at station GT3 implies that additional sources of organic carbon are influential to net metabolism within unproductive systems like GTB. However, relative to other systems, such as Chesapeake Bay (where R:P ratios range from 0.211 to 1.05; Smith and Kemp 2001) and the Amazon River (where R:P ratios ranged from 1.5 to 4; Quay et al. 1995), the range in R:P ratios observed in GTB (0.6 - 1.4) is narrow and never deviates far from unity. The narrow range in R:P values observed at station GT3 indicates that gross primary production and community respiration are temporally coupled. Despite this, R:P ratios near unity were only observed in the upper water column during summer stratification. Periods of imbalance between R and P were frequent and occurred during isothermal periods, the onset of stratification, destratification, and in the hypolimnion (Figure 2 - 3 and 8). While community structure dynamics may influence R (Havskum et al. 2003) resulting in net autotrophy in late spring and early summer, metabolism of noncontemporaneous and allochthonous organic carbon results in a shift away from balance towards net heterotrophy. The occurrence of net heterotrophy during the unstratified periods and throughout the year in the hypolimnion, indicates that non-contemporaneous and allochthonous organic carbon are metabolized. In fact, the persistence of net heterotrophy during the unstratified periods and in the hypolimnion may largely be responsible for the predominance of net heterotrophy observed in GTB. When the average values for O_{2sat} , $\delta^{18}O-O_2$, and R:P ratios are calculated separately for the upper water column (epilimnion + metalimnion)

and the hypolimnion during the stratified periods, the epilimnetic R:P ratios converge towards unity (Figure 10). Community respiration is therefore predominately supported by autochthonous production in the upper water column during stratification. The coincidence of periods of imbalance with disruptions to thermostratification and balance during thermostratification implicates the strong influence exerted on metabolism by the restriction of nutrient and organic matter distribution during thermostratification.

In summary, the deviation of R:P ratios from unity that are observed at station GT3 are likely the result of the temporal and spatial discontinuity between non-contemporaneous and autochthonous inputs thereby resulting in an imbalance between the autotrophic and heterotrophic communities. Similar trends in the temporal and spatial balance between R:P are evident in Lake Superior (Russ et al. 2004) and suggest that the presence of deep waters and isothermal conditions likely contribute to the predominance of net heterotrophy in large temperate lacustrine ecosystems. The occurrence of net autotrophy during periods of thermostratification (Russ et al. 2004) supports the observation in this study that autochthonous products largely support metabolism in unproductive systems and additional sources of organic carbon result in a shift towards net heterotrophy. As a result, large unproductive temperate lakes may alternate between periods of net autotrophy and net heterotrophy over the course of a single year.

Sample Date	Depth	Temperature	[O ₂]	Fraction O ₂	δ ¹⁸ Ο	R:P ratio
(2000)	(m)	(°C)	(µM)	Saturation	(‰ , wrt air)	
24-Apr	5	3.35	393.24	0.94	0.9	1.2
24-Apr	15	3.35	431.47	1.04	*1.0	*1.9
24-Apr	25	3.35	405.78	0.97	1.3	1.3
24-Apr	50	3.35	379.14	0.91	0.9	1.3
24-Apr	80	3.33	388.23	0.93	1.1	1.3
2-May	5	4.52	397.94	0.99	0.6	1.1
2-May	15	4.12	394.50	0.97	0.7	1.2
2-May	25	4.09	396.38	0.97	1.1	1.2
9-Jun	5	12.09	339.97	1.01	-0.4	1.0
9-Jun	10	10.59	364.10	1.05	-1.0	0.8
9-Jun	30	6.35	373.50	0.97	-0.4	1.1
9-Jun	50	5.06	374.44	0.94	0.4	1.2
25-Jul	5	19.20	279.19	0.97	-0.5	1.1
25-Jul	15	15.30	313.34	1.00	-1.1	1.0
25-Jul	25	11.07	333.71	0.97	-0.3	1.1
25-Jul	50	5.87	362.85	0.93	0.0	1.1
25-Jul	100	4.80	354.70	0.89	1.5	1.4
3-Oct	5	14.51	294.85	0.93	0.2	1.2
3-Oct	15	14.48	294 .54	0.93	0.1	1.2
3-Oct	25	14.35	297.99	0.93	0.2	1.2
3-Oct	50	7.58	319.61	0.86	1.7	1.4
3-Oct	100	5.98	336.84	0.87	1.5	1.4
29-Nov	5	8.05	344.67	0.93	1.0	1.3
29-Nov	15	8.05	312.71	0.85	0.8	1.3
29-Nov	25	7.97	314.91	0.85	1.0	1.3
29-Nov	50	7.60	305.51	0.82	0.9	1.3
29-Nov	100	7.50	312.71	0.84	1.3	1.3

Table 1: Summary of measurements collected at station GT3, 2000.

*Associated data omitted from analysis due to error in measurement of δ^{18} O-O₂.

Sample Date	Depth	Temperature	[O ₂]	Fraction O ₂	δ ¹⁸ Ο	R:P ratio
(2001)	(m)	(°C)	(µM)	Saturation	(‰ , wrt air)	
19-Apr	5	2.12	397.32	0.92	1.1	1.3
19-Apr	15	2.14	407.97	0.95	1.0	1.2
19-Apr	25	2.15	410.79	0.96	1.0	1.2
19-Apr	50	2.16	408.91	0.95	1.3	1.3
19-Apr	100	2.18	408.91	0.95	1.1	1.3
23-May	5	6.61	396.38	1.04	0.2	0.6
23-May	15	5.60	398.26	1.01	0.1	0.9
23-May	25	4.88	397. 94	1.00	0.0	1.0
23-May	50	4.23	391.05	0.96	0.3	1.1
23-May	100	3.83	403.58	0.98	0.8	1.1
21-Jun	5	12.88	344.05	1.04	-0.3	0.7
21-Jun	15	9.90	360.34	1.02	-0.9	0.9
21-Jun	25	9.08	377.58	1.05	-0.9	0.8
21-Jun	50	5.66	385.41	0.98	-0.5	1.0
21-Jun	100	4.04	377.58	0.92	0.8	1.2
22-Aug	5	21.00	271.04	0.97	-1.5	1.0
22-Aug	15	19.63	260.07	0.91	0.1	1.2
22-Aug	25	8.10	352.51	0.96	-0.8	1.1
22-Aug	50	5.53	362.85	0.92	0.7	1.2
22-Aug	100	4.89	376.32	0.94	1.1	1.3
2-Oct	5	16.01	297.67	0.97	*-2.5	*1.0
2-Oct	15	12.84	288.27	0.87	-0.2	1.2
2-Oct	25	10.29	301.12	0.86	0.2	1.2
2-Oct	50	8.30	280.75	0.76	0.7	1.3
2-Oct	100	5.75	325.87	0.83	1.2	1.3

Table 2: Summary of measurements collected at station GT3, 2001.

*Associated data omitted from analysis due to error in measurement of $\delta^{18}\mbox{O-O}_2$.







Figure 2: Temperature (°C, bold line) and Fluorescence (RFU, thin line) as a function of depth (m) and sampling date in 2000.



Figure 3: Temperature (°C, bold line) and Fluorescence (RFU, thin line) as a function of depth (m) and sampling date in 2001.



Traverse Bay in (a) April - June 2000, (b) July and October - November 2000, (c) April - June Figure 4. Fraction of O₂ saturation (O_{2sat}) as a function of depth at station GT3 in Grand 2001, and (d) August and October 2001.



(a) April - June 2000, (b) July and October - November 2000, (c) April - June 2001, and Figure 5. δ^{18} O-O₂ as a function of depth at station GT3 in Grand Traverse Bay in (d) August and October 2001.



Figure 6. R:P ratios as a function of depth at station GT3 in Grand Traverse Bay in (a) April - June 2000, (b) July and October - November 2000, (c) April - June 2001, and (d) August and October 2001.



Figure 7. (a) Fraction of O₂ saturation (O_{2sat}), (b) δ^{18} O-O₂, and (c) R:P ratios as a function of depth (m) and sampling date at station GT3 in Grand Traverse Bay in 2000 and 2001. The bold horizontal line represents (a) 100% O₂ saturation, (b) air-water gas exchange (δ^{18} O = 0.7 ‰), and (c) community respiration equal to gross photosynthesis (R:P = 1).



◇Apr-00 ◆Apr-01 □May-00 ■May-01 ∆Jun-00 ▲Jun-01 + Jui-00 XAug-01 0 Oct-00 ● Oct-01 X Nov-00

is indicated by the bold horizontal line. The equilibrium locus represents the initial conditions of an aquatic system at equilibrium with the atmosphere and when biological activity is negligible. Quadrants I and III indicate O_2 input upper 30 m at station GT3. The bold vertical line represents 100 % saturation. Air-water gas exchange (0.7 ‰) plotted and data representing R:P ratios greater than, less than, and approximately equal to one are encircled to and utilization, II suggests O₂ utilization, and IV represents O₂ input. (a.) All data points for the upper 30 m are Figure 8. δ^{18} O-O₂ (‰, wrt air) as a function of the fraction of O₂ saturation (O_{2sat}) and sampling date for the more clearly display seasonal trends. (b.) Mean δ^{18} O-O $_2$ and O $_{2sat}$ values for the upper 30 m are plotted for each month for 2000 (open symbols and dashed lines) and 2001 (solid symbols with solid lines)



Figure 9. Fraction of O_2 saturation (O_{2sat}) as a function of $\delta^{18}O - O_2$ (‰, wrt air). Open squares are data for Lake Kinneret published by Luz et al. (2002), open triangles are data from Amazon floodplain lakes published by Quay et al. (1995), and filled circles are from the present study. The bold vertical line represents 100 % saturation. Air-water gas exchange (0.7 ‰) is indicated by the bold horizontal line. Quadrants I and III indicate O_2 input and utilization, II suggests O_2 utilizationand IV represents O_2 input. The majority of data for each study are encircled for ease of identification.



Figure 10. The progression of thermal stratification with depth over time. The bottom of the thermocline (epi + meta) is indicated by a dotted line. Two vertical dashed lines boxes indicate the start and end of thermostratification (mid-May - Oct/Nov). Values depicted for O_{2sat} , δ^{18} O-O₂, and R:P ratios were averaged for the upper water column and the hypolimnion during the stratified period.

LITERATURE CITED

- Auer, M., Canale, R., and Freedman, P. 1976. The limnology of Grand Traverse Bay, Lake Michigan. Michigan Sea Grant Program No. 47.
- Barbiero, R. P, and Tuchman, M.L. 2001a. Results from the U.S. EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: I. introduction and phytoplankton results. J. Great Lakes Res. 27: 134-154.
- Barbiero, R. P, and M.L. Tuchman. 2001b. Results from the U.S. EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: II. deep chlorophyll maxima. J. Great Lakes Res. 27: 155-166.
- Bender, M., and Grande, K. 1987. Production, respiration, and the isotope geochemistry of O₂ in the upper water column. Global Biogeochem. Cycles 1: 49-59.
- Benson, B.B., and Krause, D. 1984. The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. Limnol. and Oceanogr. 29: 620-632.
- Biddanda, B.A., and Cotner, J.B. 2002. Love handles in aquatic ecosystems: the role of dissolved organic carbon drawdown, resuspended sediments, and terrigenous inputs in the carbon balance of Lake Michigan. Ecosystems 5: 431-445.
- Biddanda, B.A., and Cotner, J.B. 2003. Enhancements of dissolved organic matter bioavailability by sunlight and its role in the carbon cycle of Lakes Superior and Michigan. J. Great Lakes Res. 29: 228-241.
- Brooks, A.S., and Torke, B.G. 1977. Vertical and seasonal distribution of chlorophyll a in Lake Michigan. J. Fish. Res. Board. Can. 34: 2280-2287.
- Carignan, R., Planas, D., and Vis, C. 2000. Planktonic production and respiration in oligotrophic Shield lakes. Limnol. and Oceanogr. 45: 189-199.
- Carpenter, J.H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141-143.
- Cole, J.J., Pace, M.L., Carpenter, S.R., and Kitchell, J.F. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. and Oceanogr. 45: 1718-1730.

- Conley, D.J., Quigley, M.A., and Schelske, C.L. 1998. Silica and phosphorus flux from sediments: importance of internal recycling in Lake Michigan. Can. J. Fish. Aquat. Sci. 45: 1030-1035.
- Cotner, J.B., and Biddanda, B.A. 2002. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems 5: 105-121.
- Cotner, J.B., Johengen, T.H., and Biddanda, B.A. 2000. Intense winter heterotrophic production stimulated by benthic resuspension. Limnol. and Oceanogr. 45: 1672-1676.
- Coveney, M.F., and Wetzel, R.G. 1995. Biomass, production, and specific growth rate of bacterioplankton and coupling to phytoplankton in an oligotrophic lake. Limnol. Oceanogr. 40: 1187-1200.
- del Giorgio, P., and Peters, R. 1993. Balance between phytoplankton production and plankton respiration in lakes. Can. J. Fish. Aquat. Sci. 50:282-289.
- del Giorgio, P., and Peters, R. 1994. Patterns in planktonic P:R ratios in lakes: Influence of lake trophy and dissolved organic carbon. Limnol. Oceaogr. 39: 772-787.
- del Giorgio, P.A., Cole, J.J., and Cimbleris, A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature 385: 148-151.
- Dubowski, Y., Erez, J., and Stiller, M. 2002. Isotopic paleolimnology of Lake Kinneret. Limnol. Oceanogr. 48: 68-78.
- Eadie, B.J., Chambers, R.L., Gardner, W.S., and Bell, G.L. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. 10:307-321.
- Emerson, S., Quay, P., Stump, C., Wilbur, D., and Knox, M. 1991. O₂, Ar, N₂, and ²²²Rn in waters of the subarctic ocean: net biological O₂ production. Global Biogeochemical Cycles 5: 49-69.
- Emerson, S., Stump, C., Wilbur, D., and Quay, P. 1999. Accurate measurement of O_2 , N_2 , and Ar gases in water and the solubility of N_2 . Marine Chemistry 64: 337-347.
- Fahnenstiel, G.L., and Scavia, D. 1987. Dynamics of Lake Michigan phytoplankton: primary production and growth. Can. J. Fish. Aquat. Sci. 44: 499-508.

- Garcia, H.E., and Gordon, L.I. 1992. Oxygen solubility in seawater: better fitting equations. Limnol. Oceanogr. 37: 1307-1312.
- Gardner, W.S., Chandler, J.F., and Laird, G.A. 1989. Organic nitrogen mineralization and substrate limitation of bacteria in Lake Michigan. Limnol. Oceanogr. 34: 478-485.
- Guy R.D., Berry, J.A., Fogel, M.L., and Hoering, T.C. 1989. Differential fractionation of oxygen isotopes by cyanide-resistant and cyanide-sensitive respiration in plants. Planta 177: 483-491.
- Guy, R.D., Fogel, M.L., and Berry, J.A. 1993. Photosynthetic fractionation of the stable isotopes of oxygen and carbon. Plant. Physiol. 101:37-47.
- Hanson, P.C., Bade, D.L., Carpenter, D.L., and Kratz, T.K. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. 48: 1112-1119.
- Havskum, H., Thingstad, T.F., Scharek, R., Peters, F., Berdalet, E., Sala, M.M., Alcaraz, M., Bangsholt, J.C., Zweifel, U.L., Hagstrom, A., Perez, M., and Dolan, J.R. 2003. Silicate and labile DOC interfere in structuring the microbial food web via alga-bacterial competition for mineral nutrients: results of a mesocosm experiment. Limnol. Oceanogr. 48: 129-140.
- Hicks, R.E., and Owen, C.J. 1991. Bacterioplankton density and activity in benthic nephloid layers in Lake Michigan and Lake Superior. Can. J. Fish. Aquat. Sci. 48: 923-932.
- Kiddon, J., Bender, M.L., Orchardo, J., Caron, D.A., Goldman, J.C., and Dennett, M. 1993. Isotopic fractionation of oxygen by respiring marine organisms, Global Biogeochemical Cycles 7: 679-694.
- Knox , M., Quay, P.D., and Wilbur, D. 1992. Kinetic isotopic fractionation during air-water gas transfer of O₂, N₂, CH₄, and H₂. J. Geophysical Research. 97:20,335-20,343.
- Kroopnick P.M. 1975. Respiration, photosynthesis, and oxygen isotope fractionation in oceanic surface water. Limnol. Oceanogr. 20: 988-992.
- Kroopnick, P.M., and Craig, H.C. 1972. Atmospheric oxygen: Isotopic composition and solubility fractionation. Science. 175: 54-55.
- Lane, G.A., and Dole, M. 1956. Fractionation of oxygen isotopes during respiration. Science 123: 574-576.

- Lauff, G.H. 1957. Some aspects of the physical limnology of Grand Traverse Bay. Great Lakes Research Institute No. 2.
- Luz, B., Barkan, E., Sagi, Y., and Yacobi, Y.Z. 2002. Evaluation of community respiratory mechanisms with oxygen isotopes: A case study in Lake Kinneret. Limnol. Oceanogr. 47: 33-42.
- McCusker, E.M., Ostrom, P.H., Ostrom, N.E., Jeremiason, J.D., and Baker, J.E. 1999. Seasonal variation in biogeochemical cycling of seston in Grand Traverse Bay, Lake Michigan. Organic Geochemistry. 30:1543-1557.
- Moll, R.A., and Stoermer, E.F. 1982. A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. Arch. Hydrobiol. 94: 425-440.
- Mortonson, J.A. 1977. The vertical distribution of chlorophyll a and nutrients at a deep station in Lake Michigan. M.Sc. thesis. University of Wisconsin Milwaukee, Milwaukee.
- Odum, W.E., and Prentki, R.T. 1978. Verh. Internal. Vercin. Limnol. 20: 574-580.
- Pomeroy, L.R., and Deibel, D. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland Coastal waters. Science 233: 359-361.
- Praire, Y.T., Bird, D.F., and Cole, J.J. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnol. Oceanogr. 47: 316-321.
- Quay, P., Wilbur, D., Richey, J., Devol, A., Benner, R., and Forsberg, B.R. 1995. The ¹⁸O: ¹⁶O of dissolved oxygen in rivers and lakes in the Amazon Basin: determining the ratio of respiration to photosynthesis rates in freshwaters. Limnol. Oceanogr. 40: 718-729.
- Quay, P., Emerson, S., Wilbur, D., Stump, C., and Knox, M. 1993. The δ^{18} O dissolved O₂ in the surface waters of the subarctic Pacific: a tracer of biological productivity. J. Geophys. Res. 98: 8447-8458.
- Roberts, B., Russ, M., and Ostrom, N. 2000. Rapid and precise determination of the δ^{18} O of dissolved and gaseous dioxygen via gas chromatography isotope ratio mass spectrometry. Environ. Sci. Technol. 34: 2337-2341.
- Russ, M.E., Ostrom, N.E., Gandhi, H., Ostrom, P.H., and Urban, N.R. 2004. Temporal and spatial variations in R:P ratios in Lake Superior, an oligotrophic freshwater environment. In press.

- Scavia, D., and Laird, G.A. 1987. Bacterioplankton in Lake Michigan: dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. 32: 1017-1033.
- Scavia, D., Laird, G.A., and Fahnenstiel, G.L. 1986. Production of planktonic bacteria in Lake Michigan. Limnol. Oceanogr. 31: 612-626.
- Schneider A.R., Eadie, B.J., and Baker, J.E. 2002. Episodic particle transport events controlling PAH and PCB cycling in Grand Traverse Bay, Lake Michigan. Environmental Science and Technology 36: 1181-1190.
- Smith, E.B. 1973. Wind driven and seiche forced water motion in Grand Traverse Bay, Michigan. Ph.D. thesis, University of Michigan, Ann Arbor.
- Smith, E.M., and Kemp, W.M. 2001. Size structure and the production/respiration balance in a coastal plankton community. Limnol. Oceanogr. 46: 473-485.
- Stevens, C.L.R., Shultz, D., van Baalen, C., and Parker, P.L. 1975. Oxygen isotope fractionation during photosynthesis in blue-green and a green alga. Plant Physiology. 56: 126-129.
- Stoermer, E., Schelske, C., Santiago, M., and Feldt, L. 1972. Spring phytoplankton abundance and productivity in Grand Traverse Bay, Lake Michigan, 1970. Internat. Assoc. Great Lakes Res. Proc. 15th Conf. Great Lakes Res. 181-191.
- Tarapchak, S., and Stoermer, E. 1976. Environmental status of the Lake Michigan region, Vol. 4. Argonne National Laboratory.
- Van Mooy, B., MacGregor, B., Hollander, D., Nealson, K., and Stahl, D. 2001. Evidence for tight coupling between active bacteria and particulate organic carbon during seasonal stratification of Lake Michigan. Limnol. Oceanogr. 46: 1202-1208.

