Natural Resources and Environmental Issues

Volume 15 *Saline Lakes Around the World: Unique Systems with Unique Values*

Article 28

1-1-2009

Diel variability and community metabolism in African soda lakes

John M. Melack
Bren School of Environmental Science and Management, University of California, Santa Barbara

Diel Variability and Community Metabolism in African Soda Lakes

John M. Melack[1]
[1]Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106, USA
E-mail: melack@bren.ucsb.edu

ABSTRACT

Information theory based indices of predictability were used to quantify seasonal differences in diel variability of dissolved oxygen and temperature in Lakes Elmenteita and Sonachi. Predictability of patterns in diel variability was high in both lakes for water temperatures and dissolved oxygen. Community metabolism was measured in Lake Elmenteita, a shallow, Kenyan soda lake based on a series of vertical profiles of dissolved oxygen and temperature measured about monthly over several days for 13 periods from February 1973 to May 1974. Variations in areal oxygen content at successive intervals throughout each day and night were corrected for air-water oxygen exchange to calculate net free water oxygen change. Maximal rates of increase usually occurred in late morning or early afternoon and ranged from 0.3 to 2.1 g O_2 m^{-2} h^{-1}. Rates of change were summed to determine night-time respiration and gross photosynthesis (day-time sum plus night-time respiration); gross photosynthesis ranged from 1.5 to 18.2 g O_2 m^{-2} d^{-1}.

INTRODUCTION

In tropical lakes where diel changes often exceed seasonal changes in physicochemical conditions, planktonic organisms must tolerate the full range of conditions since their generation time is longer than one day. However, the diel variability itself varies, and the predictability of the periodicity in the diel cycles is likely to have ecological relevance. Indeed, patterns of temporal fluctuation are of long-standing and broad interest in ecology and limnology (Colwell 1974; Talling & Lemoalle 1998). While time series analysis, such as spectral or wavelet analysis, are powerful techniques (Platt & Denman 1975; Keitt & Fischer 2006), insufficient data often preclude their application to ecological systems. Alternatively, the information theory based statistics derived by Colwell (1974) provide a suitable approach to measure the predictability of diel cycles in lakes.

Evidence that inland waters are an important component in the processing of carbon on a global scale has increased interest in the metabolism of lakes (Cole et al. 2007). Since photosynthethic and respiratory activities are indicated by variations in dissolved oxygen and carbon dioxide, measurements of these gases in lakes provide metrics of metabolism. Although recent technological advances have improved capabilities to determine concentrations of these gases, the theoretical basis for calculations of metabolism and studies in a variety of ecosystems date back over 50 years. In particular, pronounced diel variation in thermal stratification and dissolved oxygen has been documented in productive, tropical African lakes (e.g., Talling 1957; Ganf & Horne 1975), and these diel variations permit robust calculations of community metabolism based on free-water changes in dissolved oxygen (e.g., Melack & Kilham 1974; Melack 1982).

Alkaline, saline (soda) lakes in tropical eastern Africa undergo strong diel heating and cooling with related variations in dissolved oxygen. Measurements of diel cycles of temperature and dissolved oxygen over one to several days about monthly for a period spanning 15 months in Lakes Elmenteita and Sonachi permit evaluation of the periodicity in the diel cycles and calculation of community metabolism. These results support Duarte et al. (2008) who suggest saline lakes with pH above 9 tend to be net autotrophic and demonstrate the regularity of diel variations in equatorial saline lakes.

MATERIALS AND METHODS

Lake Elmenteita (0°27'S, 36°15'E) lies at 1776 m above sea level in central Kenya within a 590 km^2 endorheic basin. The lake was ca. 20 km^2 in area and ranged in mean depth from 0.65 to 1.1 m during the period of study from February 1973 to May 1974 (Melack 1976). The alkalinity and pH (ca. 9.9) are high. Electrical conductance varied from 19.1 to 40.2 mS cm^{-1} as the lake experienced evaporative concentration during low rainfall. No aquatic macrophytes grew in the lake, and concentrations of chlorophyll in phytoplankton ranged from 16 to 310 mg m^{-3}. Further limnological information about Lake Elmenteita is provided in Melack (1979a, 1981, 1988), Melack et al. (1983), Tuite (1981) and Kalff (1983). January and February usually have the highest temperatures, least rainfall and highest winds; climate statistics are summarized in Melack (1981, 1988).

Lake Sonachi (0°47'S, 36°16'E) lies in a volcanic crater 1980 m above sea level in central Kenya. During the period study (February 1973 to May 1974) the lake decreased in area from 16.1 ha to 14.7 ha and in maximum depth from 6.5 to 5.5 m. No streams enter or leave the lake. Lake Sonachi was chemically stratified with a mixolimnion varying from 6.6 to 8.4 mS cm^{-1}, a monimolimnion varying from 10.3 to 17 mS cm^{-1} and a chemocline at about 4 m during the period of study. The waters are high in alkalinity and pH (9.6). Chlorophyll concentrations ranged from 29 to 74 mg m^{-3}. Further limnological information is provided in Melack (1981, 1982), Melack et al. (1981) and MacIntyre & Melack (1982) and references cited in those papers.

Measurements were made at a station located off a point in the southeastern end of the Lake Elmenteita and accessed by inflatable boat. In Lake Sonachi measurements were made mid-lake from a floating platform that permitted day and night presence. The study spanned February 1973 to May 1974 with measurements made about monthly over one to three for 13 periods in Lake Elmenteita and 10 periods in Lake Sonachi.

The vertical distribution of dissolved oxygen was measured with a submersible Clark polarographic electrode and Yellow Springs Instruments (YSI) model 51A meter (precision ca. 0.2 mg O_2 l^{-1}). The Miller method (Ellis & Kanamori 1973) was used to calibrate the polarographic electrode. The vertical distribution of temperature was measured with a thermistor and Wheatstone bridge circuit (YSI model 51A meter readable to 0.05°C or a YSI model 46 meter readable to 0.05°C). The thermistors were calibrated against a certified thermometer accurate to 0.01°C. Measurements were made every 0.2 m or 0.5 m in Lake Elmenteita and every 0.5 m in Lake Sonachi. Wind speeds were measured periodically through the day and night with a hand-held anemometer at about 1 m above the water surface, and concurrent observations of wave heights were recorded.

To characterize temporal variability, Colwell's (1974) information theory based statistics were applied to temperature and dissolved oxygen data from Lakes Elmenteita and Sonachi. Before computing the statistics, the data were interpolated linearly to create a matrix with regular times. The values of the statistics depend on the grouping in increments of the temperatures or dissolved oxygen concentrations. In Lake Elmenteita, calculations were done using 1 and 2°C intervals for temperature and 1.5 and 3 mg l^{-1} intervals for dissolved oxygen. In Lake Sonachi, calculations were done using 1, 2 and 3°C intervals and 1.5 and 3 mg l^{-1} intervals. In the time domain, the calculations were done for each contiguous set of data, for aggregates of 2 or 3 periods and for all the periods.

Community metabolism was calculated based on the series of vertical profiles of dissolved oxygen and temperature. Variations in areal oxygen content at successive intervals throughout each day and night were corrected for air-water oxygen exchange to calculate free water oxygen change. Methodological details for the approach applied to Lake Sonachi are provided in Melack (1982), and those applied to Lake Elmenteita are described below.

The air-water exchange of oxygen (F, mg O_2 m^{-2} h^{-1}) was calculated with the expression:

$$F = D/T\ (C_w - C_{sat})$$

Where T is the thickness of the hypothetical stagnant boundary layer (m), D is the diffusion coefficient for oxygen (m^2 h^{-1}) at the approximate salinity and temperature of the lake, C_w is the concentration of oxygen measured in the lake (mg m^{-3}), and C_{sat} is the oxygen concentration in water at saturation (mg m^{-3}). Measurements of T, as a function of wind speed, provided in Peng & Broecker (1980) were used. Though recent formulations of gas exchange as a function of wind speed are available, they do not significantly alter the values used here.

To determine the solubility of oxygen in soda lakes, samples of lake water from four Kenyan soda lakes (Elmenteita, Nakuru, Simbi and Sonachi) with conductances ranging from 7.7 to 34.1 mS cm^{-1} plus standard seawater and distilled water were air-equilibrated at 20°C as recommended by Carpenter (1966). Concentrations of dissolved oxygen were measured using an in-line gas stripper and injected into a gas chromatograph with a helium carrier and silica gel molecular sieve column and detected with thermal conductivity. The distilled water and seawater values were within 0.3% of those in Carpenter (1966). Since the conductance of Lake Elmenteita changed during the course of the study, the relation between oxygen solubility and conductance was used to determine the concentration of dissolved oxygen at equilibrium after adjusting for altitude and temperature.

Procedures for calculation of lake metabolism based on free-water measurements of dissolved oxygen, proposed in the 1950s (Odum 1956; Talling 1957), have been modified based on practical and theoretical perspectives (e.g., Odum & Hoskin 1958; Welch 1968; Bella 1970; Hornberger & Kelly 1974) and, recently, based on the availability of reliable probes that record continuously (Lauster et al. 2006; Staehr & Sand-Jensen 2007; Coloso et al. 2008). The approach applied here is similar that used by Melack & Kilham (1974) and produces results comparable to those published for other tropical African lakes.

The amount of dissolved oxygen per square meter was determined by planimetry of plots of vertical profiles uncorrected for changes in lake volume with depth. The rate of change of areal concentrations per hour was then calculated and corrected for air-water exchange. Net daytime oxygen (NOC_d) change was determined by planimetry of the rate of change plots. Average nighttime respiration (R_n) was determined for each set of diel plots and added to the NOC_d to calculate gross photosynthesis (GP_d) during daylight. The assumption that nighttime respiration can be applied during the day may not be correct, but with no practical alternative, this assumption continues to be routinely made (e.g., Staehr & Sand-Jensen 2007).

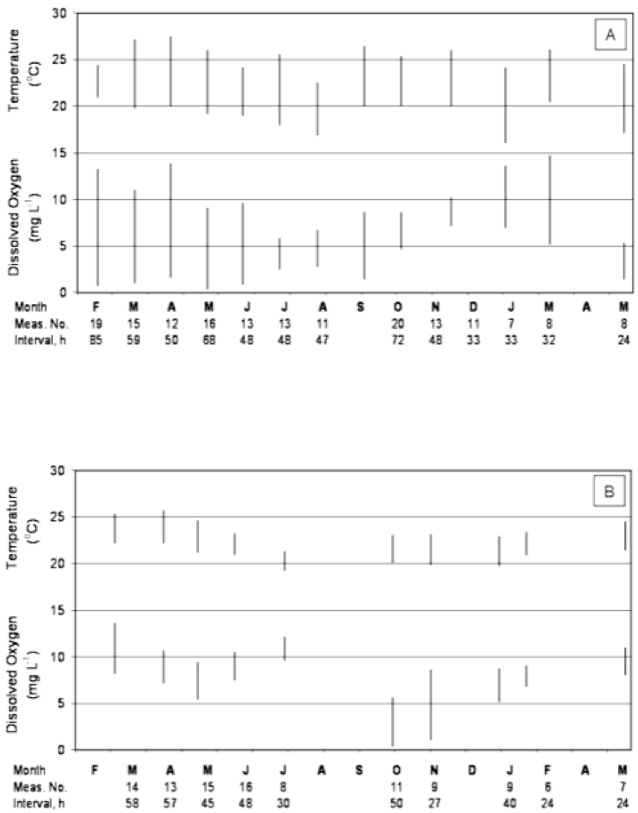


Figure 1–(a) Diel range from maximum to minimum for water temperature and dissolved oxygen at 0.2 m depth in Lake Elmenteita from February 1973 to May 1974. Interval is the length of the period in hours over which measurements (meas. no.) were made. (b) Diel range from maximum to minimum for water temperature and dissolved oxygen at 0.5 m depth in Lake Sonachi from March 1973 to May 1974. Interval is the length of the period in hours over which measurements (meas. no.) were made.

RESULTS AND DISCUSSION

Temporal Variability of Temperature and Dissolved Oxygen

In Lake Elmenteita, diel variations in water temperature and dissolved oxygen were determined from February 1973 to May 1974 during 13 periods that spanned between 24 and 85 hours with between 7 to 20 profiles during each period (Figure 1A). At 0.2 m over all the periods, maximum and minimum temperatures ranged from 27.4°C to 16.1°C, and dissolved oxygen ranged from 14.7 mg l^{-1} to 0.4 mg l^{-1}. The maximum diel differences during a contiguous sequence of days were 8.0°C and 12.5 mg l^{-1}, and minimum differences were 3.4°C and 2.9 mg l^{-1}. The magnitudes and ranges of temperature and dissolved oxygen near the bottom were slightly less than those at 0.2 m; dissolved oxygen near the bottom reached zero or nearly zero during the measurements from February to May 1973.

Vertical stratification of dissolved oxygen in Lake Elmenteita varied on diel and monthly time scales. In mid-February 1973 the lake had a dense suspension of phytoplankton with approximately 300 mg chlorophyll m^{-3} and Secchi disk transparency of 0.12 m (Melack 1979a 1988) and pronounced diel variation in the magnitude and vertical distribution of dissolved oxygen (Figure 2A). In mid-June 1973 diel variation and stratification of dissolved oxygen had lessened in concert with the decline in chlorophyll to 160 mg m^{-3} and increased Secchi disk transparency to 0.2 m (Figure 2B). By late August 1973 dissolved oxygen nearly lacked vertical stratification and had muted diel variation during a period with persistent winds generally between 4 to 8 m s^{-1}, chlorophyll of about 40 mg l^{-1} and Secchi disk transparency of 0.35 m (Figure 2C).

In Lake Sonachi, diel variations in water temperature and dissolved oxygen were determined from March 1973 to May 1974 during 10 periods that spanned between 58 and 24 hours with between 16 to 6 profiles during each period (Figure 1B). At 0.5 m over all the periods, maximum and minimum temperatures ranged from 25.3°C to 19.3°C, and dissolved oxygen ranged from 13.6 mg l^{-1} to 0.4 mg l^{-1}. The maximum diel differences during a contiguous sequence of days were 3.5°C and 7.5 mg l^{-1}, and minimum differences were 1.3°C and 2.2 mg l^{-1}. Diel and monthly variations in vertical profiles of dissolved oxygen in Lake Sonachi are described in Melack (1982). As a consequence of persistent chemical stratification (MacIntyre & Melack 1982), anoxia was perennial below the chemocline at about 4 m and on occasion reached 2 m.

Predictability (P) of diel patterns in temperature and dissolved oxygen has two components: constancy (C) and contingency (M) (Colwell 1974). Predictability ranges from 0 to 1, and C and M contribute varying proportions. P is maximal if the same temperature or dissolved oxygen concentration occurs at the same time every day and minimal if the values are equally probable at any time. Constancy is complete if the state is the same at all times for all days. Contingency is complete if the state is different at each time, but the pattern is the same on every day. Hence, a periodic diel cycle would have high predictability because of high contingency. As an example of the range of values of P, Colwell (1974) analyzed 10 years of monthly precipitation data for four locations. Uaupes, located in the humid rainforests of Brazil, had a P value of 0.75, while Miami, Florida, had a P value of 0.46, and Acapulco, Mexico, and Bella Coola, British Columbia, had intermediate values.

Table 1–Predictability of diel variations in water temperature (at 0.2 m and grouped in 1^{o}C intervals) and dissolved oxygen (at 0.2 m and grouped in 1.5 mg O_2 l^{-1} intervals) in Lake Elmenteita for 5 periods in 1973 and 1974. First number is predictability; within parentheses first number is the percent contribution of constancy to predictability and second number is the percent contribution of contingency to predictability; see text for further explanation.

	Temperature	Oxygen
Feburary	0.84 (67,33)	0.66 (25,75)
March-April	0.68 (37,63)	0.58 (20,80)
May-June	0.68 (45,55)	0.67 (31,69)
July-August	0.71 (38,62)	0.83 (67,33)
September-November	0.75 (31,69)	0.48 (63,37)

Table 2–Predictability of diel variations in water temperature (at 0.5 m and grouped in increments of 1^{o}C intervals) and dissolved oxygen (at 0.5 m and grouped in increments of 1.5 mg O_2 l^{-1} intervals) in Lake Sonachi for 4 periods in 1973 and 1974. First number is predictability; within parentheses first number is the percent contribution of constancy to predictability and second number is the percent contribution of contingency to predictability; (see text for further explanation).

	Temperature	Oxygen
March-April	0.74 (50,50)	0.71 (68,32)
May-June	0.66 (50,50)	0.72 (74,21)
October-November	0.66 (54,46)	0.65 (45,55)
January-February	0.64 (72,28)	0.82 (64,36)

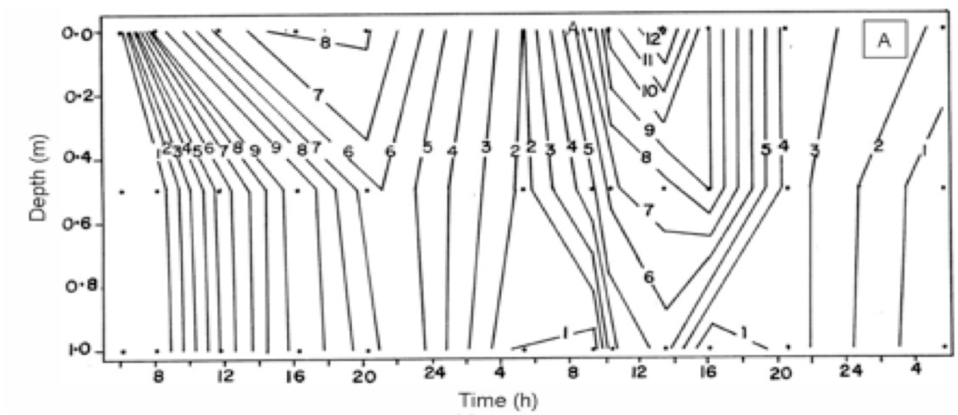
To evaluate the P, C and M of the diel periodicities of temperature and dissolved oxygen, data from 0.2 m grouped in increments of 1^{o}C and 1.5 mg l^{-1} intervals in Lake Elmenteita and from 0.5 m grouped in increments of 1^{o}C and 1.5 mg l^{-1} intervals in Lake Sonachi are presented for sets of periods with similar numbers of measurements spanning several diel cycles (Figure 1). These data are representative of the diel patterns in the water column in Lake Elmenteita and in the mixolimnion of Lake Sonachi.

The predictability and the percentage contributions of C and M differ through time for the two parameters and between the two lakes (Tables 1 and 2). In Lake Elmenteita, predictability of the diel patterns of temperature was high and similar (0.68 to 0.84) among the periods; with the exception of February 1973, contingency accounted for a greater proportion of P than constancy. Diel patterns in dissolved oxygen had slightly lower and more variable P than those for temperature; in three of the five periods contingency was more important than constancy. In Lake Sonachi, predictability of the diel patterns of temperature was high and similar (0.64 to 0.74) among the periods. Contingency and constancy accounted for about equal proportions of P except for the January-February period when constancy dominated. Diel patterns in dissolved oxygen also had high and similar P (0.65 to 0.82); in three of the four periods constancy was more important than contingency. As the separate sets of contiguous data are aggregated to include all the periods, the predictabilities decrease to about half the values in Tables 1 and 2. This is an expected result because of the shifting ranges of values evident in Figure 1. Although diel periodicity is present, the temperature or dissolved oxygen values at a particular time of day varies among the periods resulting in lower P.

To evaluate the implications for planktonic organisms of the differences in P, C and M requires experimental studies and comparative investigations from a variety of lakes. Although time series of diel measurements are available for few tropical lakes (e.g., Lake George, Uganda, Ganf & Viner 1973; Lake Calado, Brazil, Melack & Fisher 1983), the current availability of temperature and dissolved oxygen probes and data logging systems should encourage further investigation of temporal patterns in tropical lakes.

Community Metabolism

Diel changes in dissolved oxygen, expressed as g O_2 m^{-2}, for the three periods in Figure 3, illustrate a strong day to night alternation from increase to decrease and the reduction in amplitude associated with the decline in phytoplankton abundance from February to August (see text below). In February, the values ranged from a minimum of 0.5 g O_2 m^{-2} to a maximum of 9.8 g O_2 m^{-2} while in August the values ranged from a minimum of 2.2 g O_2 m^{-2} to a maximum of 5.4 g O_2 m^{-2}.



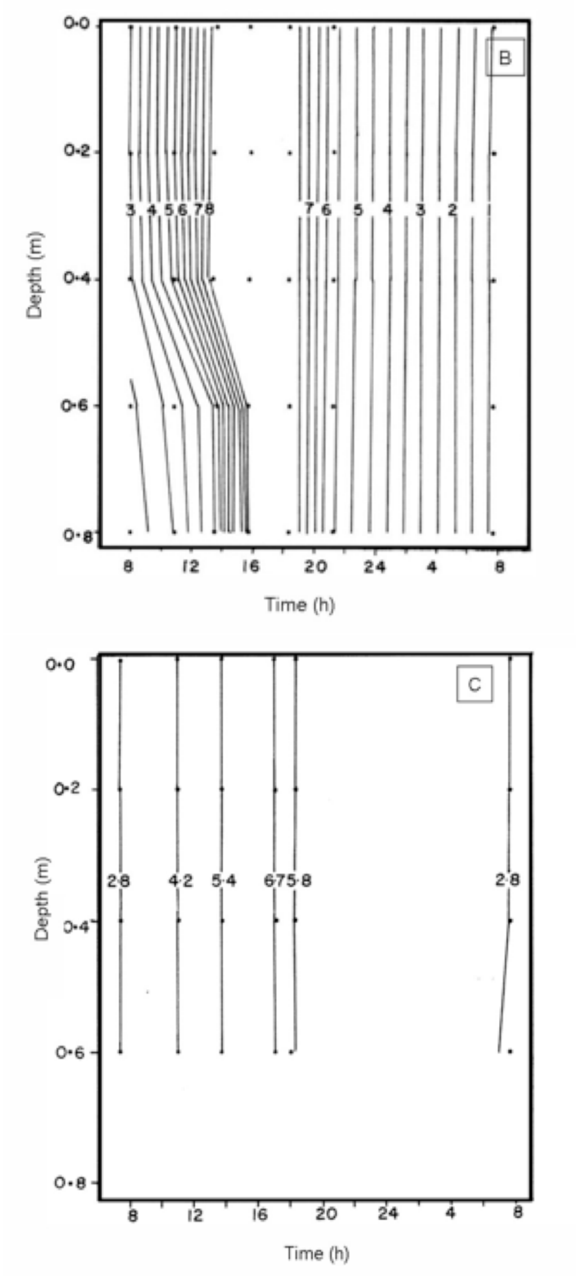


Figure 2–Time-depth diagrams of dissolved oxygen (mg O_2 l^{-1}) in Lake Elmenteita (A) 17 to 19 February 1973, (B) 20 to 21 June 1973 and (C) 24 to 25 August 1973. Dots represent measurement depths and times.

Figure 4 illustrates the typical diel cycle in rate of change of dissolved oxygen, and the area represented by NOC_d and by R_n. Over the course of the study NOC_m varied from 0.3 to 2.1 g O_2 m^{-2} h^{-1}, NOC_d varied from – 0.9 to 10.4 g O_2 m^{-2} 12 h^{-1}, R_n ranged from 0.9 g O_2 m^{-2} 12 h^{-1}, and GP_d varied from 1.5 to 18.2 g O_2 m^{-2} 12 h^{-1} (Table 3). On 7 of the 16 days R_n exceeded NOC_d and on one day NOC_d was negative both of which indicate net heterotrophy. However, on the majority of the days the lake was net autotrophic, which supports Duarte et al. (2008) who suggest saline lakes with pH above 9 tend to be net autotrophic.

Several environmental factors may influence NOC_m , NOC_d and R_n (Staehr & Sand-Jensen 2007), but few were determined during the study and weak correlations were not statistically significant with one exception: chlorophyll in phytoplankton explained 54% of the variance in NOC_d ($P < 0.01$). Chlorophyll explained 23% of the variance of NOC_m but the P value was 0.08. Regressions of insolation and water temperature and chlorophyll in phytoplankton against NOC_m explained in each case only 15% of the variance in NOC_m and P values were greater than 0.20. Nighttime water temperature explained 19% of the variance in R_n and the P value was 0.18.

As a consequence of low rainfall and evaporative concentration during the course of the study in Lake Elmenteita, major biological changes occurred (Melack 1988, 1981). The numerically dominant phytoplankton decreased in abundance precipitously in parallel with large declines in chlorophyll concentration and phytoplankton photosynthesis and increased transparency and benthic algal photosynthesis. Therefore, the variations in community metabolism reflect these changes and a shift in the relative importance of planktonic versus benthic photosynthesis and respiration.

Diel dissolved oxygen variations are influenced by photosynthesis and respiration, other oxidation and reduction reactions, mixing and advection within the lake and air-water gas exchanges. In the shallow, productive, well oxygenated waters of Lake Elmenteita, biological processes are likely to be dominant, although air-water gas exchange and possibly advection will influence the diel oxygen balance. Daytime variations in dissolved oxygen are fairly well characterized based on profiles measured every few hours (Figures 1, 2 and 3).

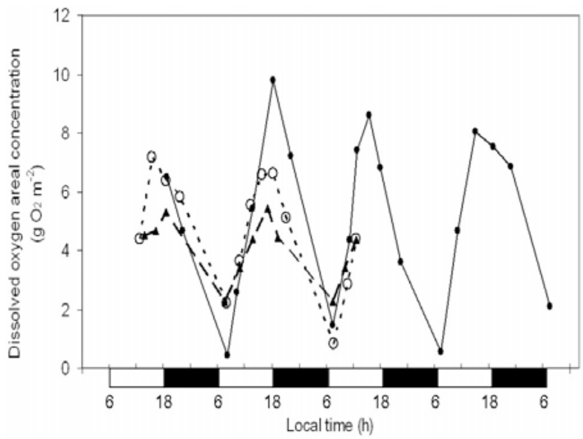


Figure 3–Diel variations in areal dissolved oxygen (g O_2 m^{-2}) in Lake Elmenteita over several days in February (●), June (○) and August (▲) 1973.

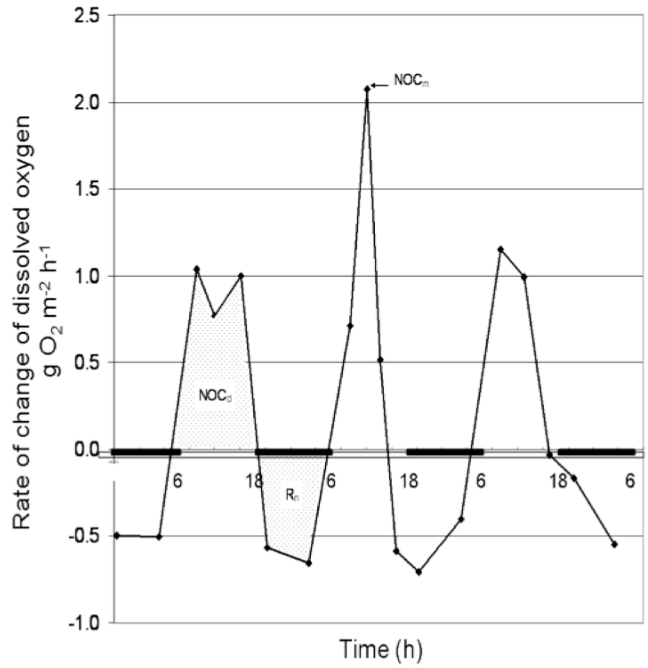


Figure 4–Rate of change of air-water exchange corrected dissolved oxygen in Lake Elmenteita 16 to 20 February 1973. The horizontal solid bar indicates night and the open bar indicates day. The area under the positive rate of change curve and above the open bar represents NOC_d and the highest value is NOC_m. R_n is the area above the negative rate of change line and the solid horizontal bar.

Table 3–Metabolic measurements based on free water, dissolved oxygen measurements in Lake Elmenteita from February 1973 to May 1974. NOC_m is maximal, daytime net change in dissolved oxygen, NOC_d is day-time net dissolved oxygen change, R_n is nighttime respiration and GP_d is the gross photosynthesis during day-time. See Figure 4 and text for further explanation.

Date	NOC_m g O_2 m^{-2} h^{-1}	NOC_d g O_2 m^{-2} $(12\ h)^{-1}$	R_n g O_2 m^{-2} $(12\ h)^{-1}$	GP_d g O_2 m^{-2} $(12\ h)^{-1}$
17-February-73	1.0	9.3	5.4	15.4
18-February-73	2.1	6.5	4.9	13.4
19-February-73	1.2	8.1	4.6	14.2
21-March-73	0.8	2.9	5.6	9.6
20-April-73	1.3	10.4	5.8	18.2
20-May-73	1.6	4.7	6.6	8.3
21-May-73	0.7	3.7	4.4	8.4
20-June-73	0.8	6.9	2.9	10.4
21-July-73	0.3	-0.9	1.9	1.5
24-August-73	0.4	1.1	3.3	4.9
1-October-73	0.5	1.4	4.2	4.7
2-October-73	0.7	3.0	1.2	6.3
1-November-73	1.0	3.2	1.5	4.9
14-December-73	0.5	1.8	0.9	4.9
28-January-74	1.0	-	-	-
7-March-74	1.1	5.5	3.2	10.6
9-May-74	0.3	1.1	1.7	3.3

Measurements of photosynthesis by phytoplankton and benthic algae (Melack 1981, 1988) demonstrate high rates. Air-water gas exchange is related to wind speeds and oxygen saturation in surficial waters. Winds were generally low to moderate (calm to 4 m s^{-1}), but gusts associated with afternoon storms ranged from 5 to 10 m s^{-1}. Surficial waters were up to 9 mg O_2 l^{-1} above or 5.8 mg O_2 l^{-1} below saturation, but mostly were within 1 to 3 mg O_2 l^{-1} of saturation. Synoptic sampling throughout the lake during 9 months revealed uniform Secchi disk transparency and limited variation in abundances of the most important phytoplankton (Melack 1976, 1988); these results suggest advection of water with different characteristics is unlikely.

Table 4–Free water estimates of metabolism in eastern African soda lakes. NOC_m is maximal, day-time net change in dissolved oxygen, and GP_d is the gross photosynthesis. Asterisks denote air-water exchange corrected values. Sources of data are as follows: (1) Melack 1982; (2) Melack & Kilham 1974; (3) Melack 1979b; (4) Talling et al. 1973.

Lake	Country	NOC_m g O_2 m^{-2} h^{-1}	GP_d g O_2 m^{-2} $(12\ h)^{-1}$
Sonachi[1]	Kenya	0.8 to 4.85*	-0.7 to 18.7*
Nakuru[2]	Kenya	2.8, 2	36, 31*
Simbi[3]	Kenya	2.8 to 12	--
Elmenteita	Kenya	0.3 to 2.1*	1.5 to 18.2*
Aranguadi[4]	Ethiopia	3 to 6	43, 57
Kilotes[4]	Ethiopia	0.9 to 4.5	11, 12

When estimates of gross photosynthesis obtained from free water approaches are compared with those from bottled samples, the free water estimates are often higher (cf. Melack 1982). In Lake Elmenteita, sequential deployments of bottled samples were made to obtain measurements of gross photosynthesis by phytoplankton in concert with the free-water profiles of dissolved oxygen (Melack 1976). A subset of these measurements made around mid-day, called GPb, were compared to gross photosynthesis calculated as NOC plus average hourly Rn, called GPh, for approximately the same intervals as the bottle measurements. The ratio GPh:GPb varied from 1 to 2 with an average of 1.7 (n = 9) and indicates that the bottle measurements are likely to underestimate gross photosynthesis.

Free water estimates of community metabolism are available from only five other saline lakes in eastern Africa, and only Lake Sonachi has more than a couple of measurements of daily gross photosynthesis (Table 4). Maximal daytime net dissolved oxygen changes and daily gross photosynthesis in Lake Elmenteita are on the low end of the range reported for these lakes, but high in comparison to many inland waters. The highest values reported for Lakes Aranguadi, Simbi and Nakuru occurred during periods with very abundant *Spirulina platensis* and are near the upper limits found in natural lakes.

ACKNOWLEDGEMENTS

I thank S. MacIntyre for essential contributions in the field, M. Gastil-Buhl for assistance with data analysis, and B. Cole and Soysambu Estates for access to Lake Elmenteita and Ndabibi Ltd. for access to Lake Sonachi. The Office of the President, Republic of Kenya, granted permission for the studies. Financial support was provided by the U.S. National Science Foundation and a James B. Duke Fellowship.

REFERENCES

Bella, D.A. 1970. Dissolved oxygen variations in stratified lakes. Journal of Sanitary Engineering Division, Proceedings American Society of Civil Engineering 96: 1129–1146.

Carpenter, J.H. 1966. New measurements of oxygen solubility in pure and natural water. Limnology and Oceanography 11: 264–277.

Cole, J.J., Y.T. Praire, N.F. Caraco, W.H. McDowell, L.J. Tranvik, R.R. Striegl, C.M. Duarte, P. Kortelainen, J.A. Downing, J. Middleburg & J.M. Melack. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 173–189.

Coloso, J.J., J.J. Cole, P.C. Hanson & M.L. Pace. 2008. Depth-integrated, continuous estimates of metabolism in a clear-water lake. Canadian Journal of Fisheries and Aquatic Science 65: 712–722.

Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55: 1148–1153.

Duarte, C.M., Y.T. Praire, C. Montes, J.J. Cole, R. Striegl, J. Melack & J. Downing. 2008. CO_2 emissions from saline lakes: A global estimate of a surprisingly large flux. Journal of Geophysical Research-Biogeosciences G04041, doi:10.1029/2007/JG000637.

Ellis, J. & S. Kanamori. 1973. An evaluation of the Miller method for dissolved oxygen analysis. Limnology and Oceanography 18: 1002–1005.

Ganf, G.G. & A.J. Horne. 1975. Diurnal stratification, photosynthesis and nitrogen fixation in a shallow, equatorial lake (Lake George, Uganda). Freshwater Biology 5: 13–39.

Ganf, G.G. & A.B. Viner. 1973. Ecological stability in a shallow equatorial lake (Lake George, Uganda). Proceedings of Royal Society London B 184: 321–346.

Hornberger, G.M. & M.G. Kelly. 1974. A new method for estimating productivity in standing waters using free oxygen measurements. Water Resources Bulletin 10: 265– 271.

Kalff, J. 1983. Phosphorus limitation in some tropical African lakes. Hydrobiologia 100: 101–112.

Keitt, T.H. & J. Fischer. 2006. Detection of scale-specific community dynamics using wavelets. Ecology 87: 2895–2904.

Lauster, G.H., P.C. Hanson & T.K. Kratz. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Science 63: 1130–1141

MacIntyre, S. & J.M. Melack. 1982. Meromixis in an equatorial African soda lake. Limnology and Oceanography 27: 595–609.

Melack, J.M. 1976. Limnology and Dynamics of Phytoplankton in Equatorial African Lakes. Ph.D. thesis. Duke University. 453 p.

Melack, J.M. 1979a. Temporal variability of phytoplankton in tropical lakes. Oecologia 44: 1–7.

Melack, J.M. 1979b. Photosynthesis and growth of *Spirulina platensis* (Cyanophyta) in an equatorial lake (Lake Simbi, Kenya). Limnology and Oceanography 24: 753–760.

Melack, J.M. 1981. Photosynthetic activity of phytoplankton in tropical African soda lakes. Hydrobiologia 81: 71–85.

Melack, J.M. 1982. Photosynthetic activity and respiration in an equatorial African soda lake. Freshwater Biology 12: 381–400.

Melack, J.M. 1988. Primary producer dynamics associated with evaporative concentration in a shallow, equatorial soda lake (Lake Elmenteita, Kenya). Hydrobiologia 158: 1–14.

Melack, J.M. & T.R. Fisher. 1983. Diel oxygen variations and their ecological implication in Amazon floodplain lakes. Archiv für Hydrobiologie 98: 422–442.

Melack, J.M. & P. Kilham. 1974. Photosynthetic rates of phytoplankton in East African alkaline, saline lakes. Limnology and Oceanography 19: 743–755.

Melack, J.M., P. Kilham & T.R. Fisher. 1981. Responses of phytoplankton to experimental fertilization with ammonium and phosphate in an African soda lake. Oecologia 52: 321–326.

Odum, H.T. 1956. Primary production in flowing waters. Limnology and Oceanography 1: 102–117.

Odum, H.T. & C.M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publications of Institute of Marine Science Texas 5: 16–46.

Peng, T.H. & W. Broecker. 1980. Gas exchange rates for three closed-basin lakes. Limnology and Oceanography 25: 789–796.

Platt, T. & K.L. Denman. 1975. Spectral analysis in ecology. Annual Review of Ecology and Systematics 6: 189–210.

Staehr, P.A. & K. Sand-Jensen. 2007. Temporal dynamics and regulation of lake metabolism. Limnology and Oceanography 52: 108–120.

Talling, J.F. 1957. Diurnal changes of stratification and photosynthesis in some tropical African waters. Proceedings of Royal Society London B 147: 57–83.

Talling, J.F. & J. Lemoalle. 1998. Ecological Dynamics of Tropical Inland Waters. Cambridge University Press, Cambridge.

Talling, J.F., R.B. Wood, M.V. Prosser & R.M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshwater Biology 3: 53–76.

Tuite, C.H. 1981. Standing crop densities and distribution of *Spirulina* and benthic diatoms in East African alkaline saline lakes. Freshwater Biology 11: 345–360.

Welch, H.E. 1968. Use of modified diurnal curves for the measurement of metabolism in standing water. Limnology and Oceanography 13: 679–687.