Photosynthetic rates of phytoplankton in East African alkaline, saline lakes[1]

John M. Melack and Peter Kilham[2]
Department of Zoology, Duke University, Durham, North Carolina 27706

Abstract

Photosynthetic rates were calculated in six myxophycean-dominated alkaline, saline lakes in Kenya and Tanzania from changes in dissolved O_2 in light and dark bottles and from diurnal variations in dissolved O_2. Rates of gross photosynthesis are exceptionally high for Lake Nakuru, Kenya, by the diurnal free-water technique (e.g. 36 g O_2 m^{-2} day^{-1}). Gross photosynthesis in Lake Nakuru was compared for two consecutive days: on the first day pronounced thermal stratification developed and the dissolved O_2 reached 340% saturation in the upper half meter; on the second day wind-driven turbulence circulated the algae to depths often greater than 2 m in water with Secchi disk visibility of only 15 cm.

Because of analytical difficulties in measuring dissolved O_2 in soda lakes, laboratory experiments were conducted to determine the reliability of the titrimetric (Winkler, Miller), gasometric (Scholander), and polarographic (oxygen probe) methods. The polarographic technique was the most suitable for determinations of dissolved O_2 in the field.

Photosynthesis in East African alkaline, saline (soda) lakes is almost unstudied, but the algae and their photosynthetic activity are of interest for several reasons. First, myxophycean-dominated soda lakes are widespread in the tropics and similar conditions have occurred at other times in lakes which are now fresh. Second, although the lacustrine species diversity is low, the standing crops are high and are eaten by immense flocks of Greater and Lesser Flamingos (Jenkin 1957), suggesting a high productivity. Third, *Spirulina platensis* (Nordst.) Geitl.,[3] frequent in these lakes, is used as a food source by people in Chad (Léonard and Compère 1967).

Our major emphasis here is on the magnitude of phytoplanktonic photosynthesis as measured by changes in dissolved oxygen in six soda lakes in Kenya and Tanzania. Because of difficulties in measuring dissolved oxygen in these alkaline, saline waters, we compared five methods. To describe the biological and physical milieu in which photosynthesis occurs we have included counts of the phytoplankton, extinction coefficients for light at various wavelengths, and concentrations of major ions.

We thank T. J. Harvey, M. C. LaBarbera, D. A. Livingstone and R. E. Hecky for valuable field assistance. R. E. Hecky provided many of the limnological data on the Momela lakes. We are grateful for permission to carry out this study in the national park systems of Tanzania and Kenya. P. M. Olindo, Director of the National Parks of Kenya, permitted us to study Lake Nakuru. D. Vesey-FitzGerald was helpful at Arusha National Park. The manuscript was critically read by G. G. Ganf, R. E. Hecky, D. A. Livingstone, S. S. Kilham, S. MacIntyre, J. R. Richardson, J. F. Talling, and R. B. Wood.

Methods

Photosynthetic rates were calculated by the light and dark bottle technique and from diurnal dissolved oxygen production in situ. Duplicate bottles were filled with water collected from about 10 cm under the surface and suspended at a sequence of depths (Fig. 1) for 4 hr between 1100 and 1600 hours; in Lakes Nakuru and Elmenteita a 2.5-hr incubation was also used.

[1] This work was supported by National Science Foundation Grants GB 8328X and GB 33310 to D. A. Livingstone.

[2] Present address: Zoology Department, The University of Michigan, Ann Arbor 48104.

[3] Fott and Karim (1973) have suggested that the correct identification of *Spirulina platensis* is *Spirulina geitleri* DeToni. Examination of living material from Lake Nakuru, however, does not unambiguously support their reidentification.

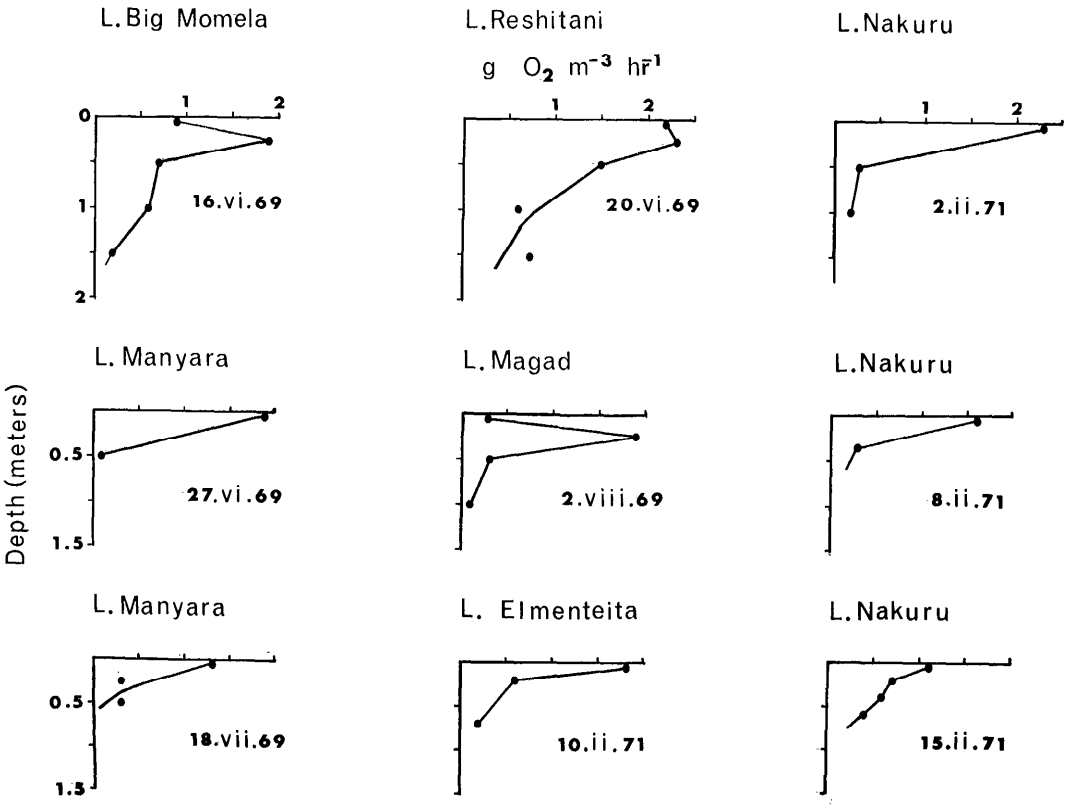

Fig. 1. Vertical distributions of photosynthetic rates (g O_2 m^{-3} hr^{-1}).

Dissolved oxygen in the bottles was measured by the azide modification of the Winkler method, using phenyl arsenine oxide solution to titrate the iodine and dry reagents before the titration (Hach Chem. 1968). The standard deviation of the mean oxygen production of bottles suspended at the same depth was as great as 40% of the mean (i.e. 1 SD was 0.1 to 0.7 mg liter^{-1}), due to severe effervescence during acidification, slight differences in the depth of exposure in the turbid water, and the formation of bubbles owing to the supersaturation of oxygen that developed in the bottles.

The vertical distribution of dissolved oxygen in Lake Nakuru was measured with a YSI meter (model 51A) and polarographic electrode (precision ca. 0.2 mg liter^{-1}). Sampling intervals and depths for both dissolved oxygen and temperature are indicated by the points on Figs. 2 and 3. When the oxygen concentration exceeded the range of the meter, the Miller method (Walker et al. 1970) was used. Oxygen escaping into the air was collected with inverted funnels. Wind velocities were estimated from the roughness of the lake's surface according to the Beaufort scale. In Lake Nakuru a YSI thermistor (No. 401) and Wheatstone bridge circuit were used to follow the diurnal changes in the vertical distribution of temperature, and air temperatures were measured with a mercury thermometer. In the other lakes only surface water temperatures were measured with a mercury thermometer.

Underwater light penetration was estimated with a 20-cm Secchi disk and measured with a sensor containing three cadmium sulfide photoresistors each covered by a set of filters (Kilham and Melack in

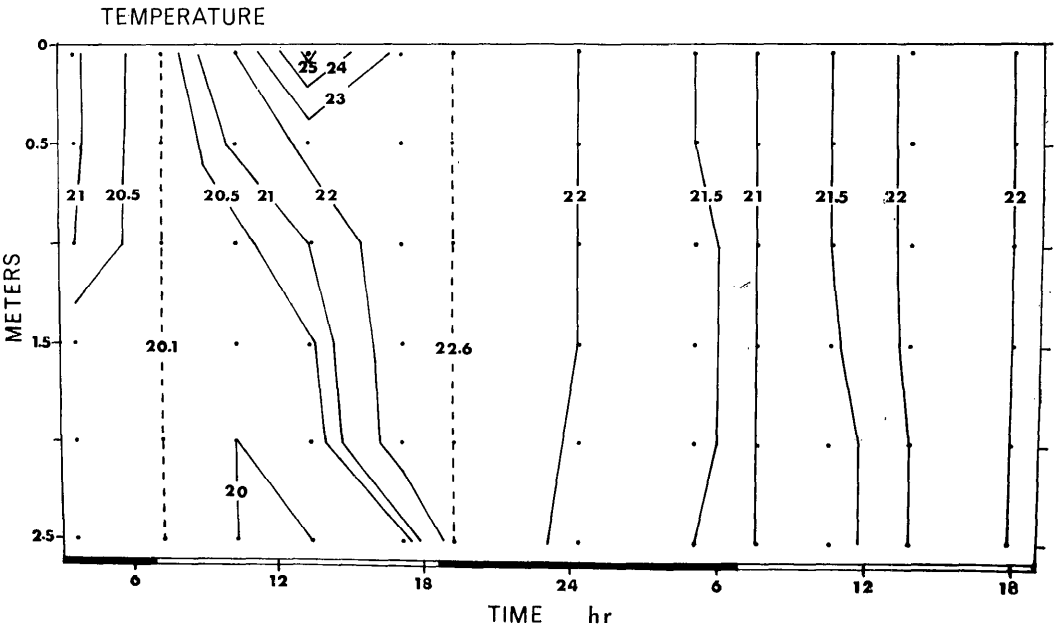

Fig. 2. Time-depth distribution of temperature (°C) in Lake Nakuru (13 to 14 June 1971).

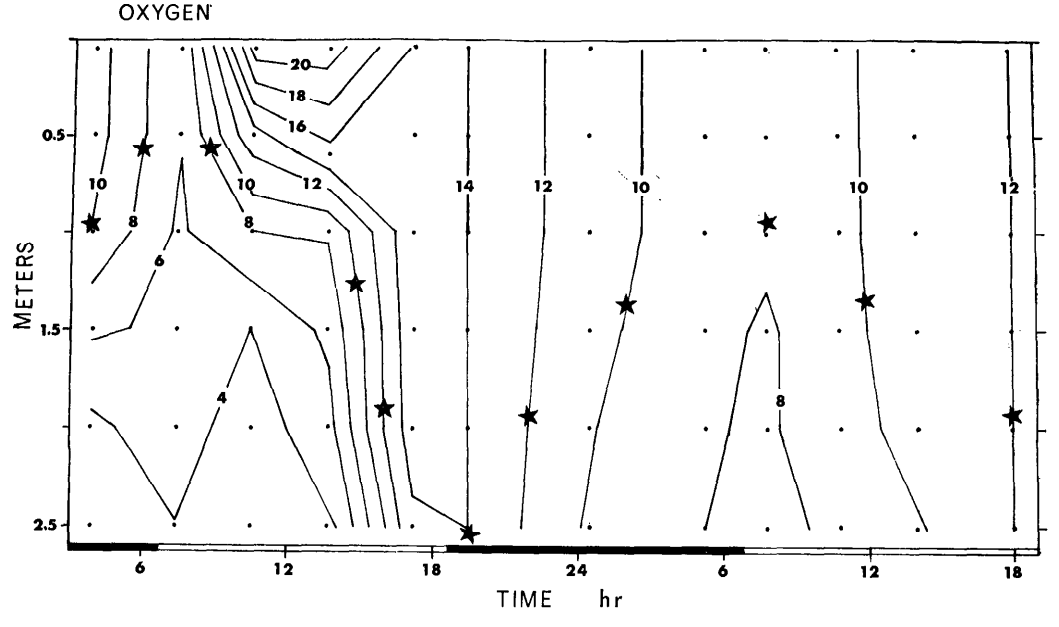

Fig. 3. Time-depth distribution of dissolved oxygen (mg liter^{-1}) in Lake Nakuru (13 to 14 June 1971). The stars indicate the depths above which bubble growth could occur based on the theoretical computations of Ramsey (1962).

Table 1. Location, altitude (H), area (A), maximum depth (z), and origin of each lake.

	Location	H(m)	A(km²)	z (m)	Origin
Nakuru	0° 22'S, 36° 05'E	1758	34* 42†	3.3	tectonic - rift + fault
Elmenteita	0° 27'S, 36° 15'E	1776	18*	1.9	tectonic - rift + fault
Magad	3° 11'S, 35° 32'E	1722	17‡	2	volcanic - caldera
Manyara	3° 35'S, 35° 50'E	960	413‡§	3.7	tectonic - fault scarp
Reshitani	3° 14'S, 36° 54'E	1448	0.2||	29	volcanic - lahar surface
Big Momela	3° 13'S, 36° 54'E	1448	0.9||	31	volcanic - lahar surface

* Geological map of Nakuru area, 1:125,000. (Degree sheet 43, NW quarter; Kenya Government 1966.)
† Nakuru, Kenya, 1:50,000. (Series Y731, sheet 119/3, edition 7-SK; Kenya Government 1970.)
‡ Ngorongoro, Tanzania, 1:125,000. (Quarter degree sheet 53; Geological Survey of Tanzania.)
§ Mbulu, Tanzania, 1:125,000. (Quarter degree sheet 69; Mineral Resources Division, Tanzania.)
|| Hecky 1971.

prep.). The peak sensitivities in air of the filter-photoresistor combinations were 495, 545, and 650 nm (50% bandwidths are about 75, 50, and 75 nm). Because of the high turbidity and concomitant limited depth to which the sensor could be used, the accuracy of the measurements was reduced. The lakes were sounded with a weighted line and their areas were determined by planimetry of appropriate maps (Table 1).

Samples for phytoplankton were collected from about 10 cm below the surface at the same time as the measurements and preserved with Lugol's solution or Formalin. Identifications were based on reference literature listed by Hecky and Kilham (1973). Algae were counted either in a sedimentation chamber with a Unitron inverted microscope (Lund et al. 1958) or in a Sedgwick-Rafter chamber (Serfling 1949) with a Leitz Ortholux microscope.

Table 2. The concentration of dissolved oxygen in air-equilibrated, artificial Lake Nakuru water. T—temperature; σ—1 SD.

Method	T(°C)	O_2 mg liter^{-1}	σ
Scholander	28.0	7.90	0.20
Polarographic	28.0	7.45	0.10*
Miller	28.0	7.91	0.04
Winkler, Carpenter	27.7	7.37	0.02
Winkler, Hach	27.7	7.02	0.32

*Datum from Yellow Springs Instrument Co. (1972).

Phosphate (stannous chloride method) and pH (wide range indicator) were measured colorimetrically in the field using a portable laboratory (Hach Chem. 1968). Analyses of unfiltered, unpreserved water for conductivity, sodium, potassium, calcium, magnesium, sulfate, chloride, alkalinity, and silicon were done at Duke University from 3 to 6 months after collection. Sodium, potassium, calcium, magnesium, and silicon were determined by atomic absorption spectrophotometry (Perkin-Elmer 1964). When necessary, calcium and magnesium were measured by EDTA titration (Am. Public Health Assoc. 1965), chloride with a chloridometer (Lab. Glass and Instr. Co.). Titration with a microburet to the bromcresol green-methyl red end point (Am. Public Health Assoc. 1965) was used to determine total alkalinity. Mackereth's (1963) ion exchange method was used for sulfate. Conductivity was measured on a Philips PR9501 meter. Our chemical methods have been described in greater detail elsewhere (Hecky and Kilham 1973).

We compared titrimetric (Walker et al. 1970; Carpenter 1965; Hach Chem. 1968), gasometric (Scholander et al. 1955), and polarographic (YSI model 51A meter) methods to determine the most suitable one for measuring dissolved oxygen in alkaline,

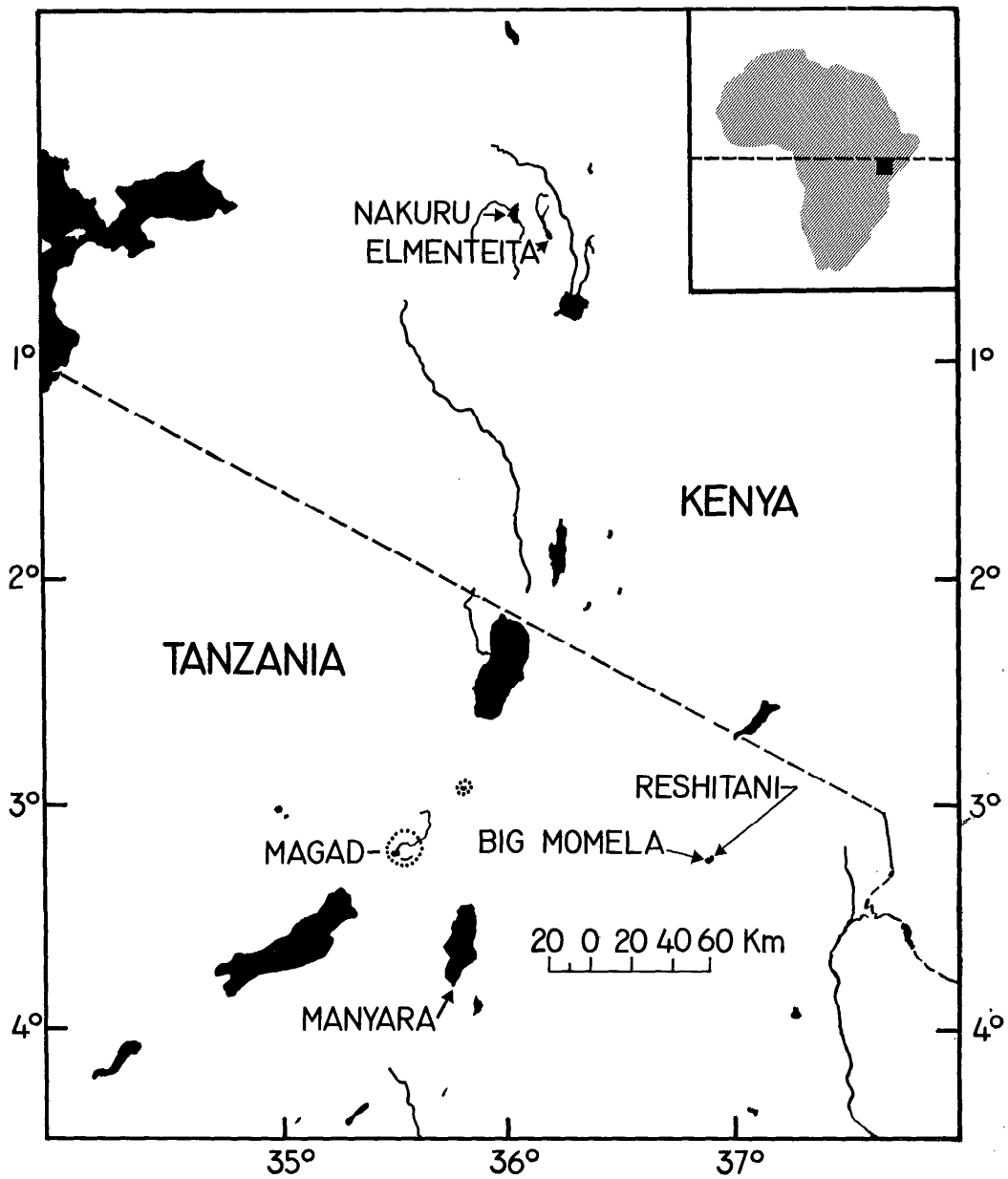

Fig. 4. Map of northern Tanzania and southern Kenya showing the locations of the lakes studied.

saline lakes (Table 2). Titrations were done with a syringe microburet. Each method was repeated three times. The water was of the same ionic strength and composition as water from Lake Nakuru but without dissolved or particulate organic matter and was air-equilibrated by stirring with a magnetic spin bar for at least 10 hr in a temperature controlled water bath (Carpenter 1966).

Based on this comparison and on our experience in the field, we favor the use of a submersible, polarographic electrode for measuring dissolved oxygen in alkaline, sa-

Table 3. Chemical analyses of the lakes. Conductivity (C) is in μmhos cm⁻¹ at 20°C. Alkalinity (A) is $HCO_3^- + CO_3^{2-}$. All analyses are in meq liter⁻¹ except PO_4-P and Si which are in mg liter⁻¹. int—interference. S^+ and S^- are the sum of cations and anions in meq liter⁻¹.

	Cond.	Na	K	Ca	Mg	SO_4	Cl	Alk.	P	Si	pH	S^+	S^-
Nakuru	10,010	144	6	0.00	0.07	1	29	122	4.4	97	10.5	150	158
Elmenteita	11,700	165	7	0.00	0.00	3	56	107	3.0	54	9.4	173	182
Magad	9,540	115	12	0.11	0.00	16	28	84	10.1	26	10.2	127	130
Manyara	8,610	109	0	0.07	0.08	5	33	78	6.5	8.6	9.2	109	117
Reshitani 0m	13,500	183	15	0.19	0.28	6	12	164	int	3.5	10.1	198	201
10m	16,900	237	24	0.27	0.28	5	18	233	int	11.2		261	282
Big Momela 0m	15,000	209	18	0.21	0.42	16	14	168	int	4.0	10.4	227	218
10m	17,580	278	23	0.21	0.46	27	19	239	int	8.4		302	315

line water. It is robust, rapid, reasonably precise, and accurate if calibrated for a particular lake water against the Scholander or Miller methods. If determinations of photosynthetic activity are to be made, the high rate of oxygen evolution typical of soda lakes makes the polarographic technique the method of choice despite its lesser sensitivity.

Description of lakes and their phytoplankton

The locations (Fig. 4), morphometry and modes of origin of the lakes dealt with in this paper are listed in Table 1. All are in basins of internal drainage. The few data describing the climate and drainage areas of Lake Manyara and the two Momela lakes (Big Momela and Reshitani) are reviewed by Greenway and Vesey-FitzGerald (1969) and Hecky (1971). Similar information for the Kenyan Rift Valley lakes is in the *Kenya Atlas* (Kenya Gov. 1970). The large fluctuations in the alkalinity of these lakes during the last 40 years (except for the two Momela lakes which are a special case: Hecky 1971) are an expression of the susceptibility of endorheic lakes to climatic variability. For example, the alkalinity of Lake Nakuru changed from 296 meq liter⁻¹ in 1929 (Jenkin 1936) to 205 in 1931 (Beadle 1932) to 1,440 in 1961 (Talling and Talling 1965) to 122 in 1969 (Table 3). It is difficult to evaluate the effect of these fluctuations on the biota. Fluctuations in salinity undoubtedly contribute to the harshness of these environments and to the low species diversity observed. Over geological time, however, such fluctuations have increased the total number of species that have lived in these lakes as particular species have been favored by various past chemical environments (*see* Hecky and Kilham 1973).

The major ions in these lakes are sodium and bicarbonate + carbonate (Table 3). Algal composition and photosynthesis are likely to be influenced by available quantities of phosphorus, nitrogen, and silica, as well as pH, alkalinity, and high concentrations of dissolved oxygen. The phosphate concentrations are high and should sustain rapid algal growth. Nitrate was not measured because of chloride interference with the field method and the problems associated with preserving the samples for analyses to be done at Duke University. Owing to the weathering of volcanic material in the drainages, the silica concentrations are high, but, at least in Lakes Big Momela and Reshitani, not as high as would be expected (> 120 mg liter⁻¹). This apparent reduction may reflect the sedimentation of silica in diatom frustules, which are plentiful in the surficial sediment (Hecky and Kilham 1973). The high alkalinities may influence the species composition in the lakes. For example, although a strict

Table 4. Underwater extinction of light. Vertical extinction coefficients (ε, ln units m^{-1}) at 650 (R), 545 (G), and 495 (B) nm. S—Secchi disk visibility.

	S(m)	R	G	B	
Nakuru	0.15	10	12	15	2 Feb 71
Elmenteita	0.17	7	9	30	3 Feb 71
Magad	0.10	4	4	4	8 Aug 69
Manyara	-	16	100	80	8 Aug 69
Reshitani	-	4	5	7	25 May 69
Big Momela	0.25	4	6	5	25 May 69

chemical control of the presence of *S. platensis* is unlikely, its blooms are associated with high alkalinity (Iltis 1968). There is also a good correlation between particular ranges in alkalinity and certain diatom assemblages (Hecky and Kilham 1973).

Although the vertical extinction coefficients of light (Table 4) are high in comparison with that of most natural water, such values are typical of lakes with dense algal crops or with suspended silt, and produce very shallow euphotic zones (Ganf 1972; Talling et al. 1973). Referring more specifically to Table 4, the values for Lake Magad are not identical but the uncertainty of the readings does not allow a resolution of the differences. The much lower extinction of red than of green and blue light in Lake Manyara probably resulted from the large amount of suspended silt. Because the sensor could only be used at two depths in Lake Manyara (subsurface and 6 cm) for the green and blue light, the values are approximate and the difference between them is not significant. Low Secchi disk visibilities corroborate the high vertical extinction coefficients and are similar to values reported by Jenkin (1936) for Lakes Nakuru and Elmenteita.

Table 5 lists the abundance of each species of phytoplankton in the countable samples. The absence of *S. platensis* from Lake Elmenteita seems odd, but our counts represent only one sample, and algal periodicity in Kenyan (Lind 1968) and other soda lakes (Iltis 1968) has been documented:

Table 5. Numerical abundance of phytoplankton (units ml^{-1}). Counting technique (C): SR—Sedgwick-Rafter chamber; I—sedimentation chamber used on inverted microscope. P—present but counts not statistically significant. Lake Nakuru count is for 2 February 1971.

	C	Nakuru	Elmenteita	Reshitani	Big Momela
Spirulina platensis (Nordst.) Geitl.*‖	SR	13,350 ± 1,100		3,800 ± 500	9,200 ± 400
Spirulina laxissima G. S. West*	I	19,500 ± 2,300	69,900 ± 4,300	35,300 ± 3,100	P
Chroococcus minutus (Kuetz.) Naegeli†	I	135,700 ± 21,000	18,400 ± 1,100		
Chroococcus sp.†	I		75,100 ± 10,000		P
Arabaenopsis arnoldii Aptekarj.‡	I	6,800 ± 1,550	9,100 ± 1,300		
Nitzschia frustulum (Kutz.) Grun.§	I	2,100 ± 600	1,250 ± 450		
Nitzschia sigma (Kutz.) W. Smith§	I		7,000 ± 800		
Navicula elkab O. Müll.§	I	6,200 ± 900	3,350 ± 500		

*Filaments of three coils. †Cells. ‡Filaments. §Frustules. ‖ All varieties, pooled counts,

Table 6. Photosynthetic activity by phytoplankton. Rates of photosynthesis calculated as g O_2 m^{-3} hr^{-1}, maximum (A); g O_2 m^{-2} hr^{-1} (B); and g O_2 m^{-2} day^{-1} (C).

	A	B	C	
Nakuru	2.3	0.8	8.6	2 Feb 71
	2.1	0.6	6.5	8 Feb 71
	1.1	0.5	5.4	15 Feb 71
Elmenteita	1.8	0.5	5.4	10 Feb 71
Magad	1.9	0.7	7.6	2 Aug 69
Manyara	1.9	0.6	6.5	27 Jun 69
	1.3	0.3	3.2	18 Jul 69
Reshitani	2.3	2.0	20.2	20 Jun 69
Big Momela	1.9	1.3	14.0	16 Jun 69

Jenkin (1936) reported 1,600 filaments ml^{-1} of *S. platensis* in Lake Elmenteita. The complete absence of algae in the collection from Lake Manyara resulted either from an unrepresentative sample or, more likely, from the disintegration of fragile cells. Although the large amount of silt in the sample from Lake Magad made counting impossible, the following species were recognized: *S. platensis, Spirulina laxissima, Anabaenopsis arnoldii, Nitzschia frustulum,* and *Navicula elkab* (*see* Hecky and Kilham 1973 for less abundant diatoms).

Measurements of photosynthetic rates

Figure 1 presents the depth distribution of phytoplanktonic photosynthesis. The maximum rates are high, ranging from 2.3 to 1.1 g O_2 m^{-3} hr^{-1} (Table 6), and the euphotic zones are shallow, usually less than 1 m. The temperature of the water during these measurements was between 21 and 27°C. Because surface water was used, the depth variation was not an expression of varying phytoplankton densities but was the response of uniform algal material to different light intensities. The euphotic zone indicated by these profiles agrees well with the 24-hr compensation depth of 0.6 m estimated by Jenkin (1936) for Lake Nakuru. The lack of surface inhibition in Lakes Nakuru, Elmenteita, and Manyara may have resulted from inadequate resolution of the photosynthetic rates in the upper 20 cm. Even in those profiles exhibiting a subsurface peak, the depth of maximum photosynthesis may have been missed. Talling et al. (1973) used as many as five bottles within the top 20 cm in two Ethiopian soda lakes but did not always find reduced surface rates.

The problems caused by bottling phytoplankton are well known (Vollenweider 1969) and are probably exaggerated in the lakes dealt with here by the dense algal suspensions and the long exposure times. Aggregations of sedimented and floating algae formed within 45 min of bottling. Also, the high dissolved oxygen concentrations may have depressed photosynthesis and affected respiration (Gessner and Pannier 1958). These factors, in combination with the errors in the measurement of dissolved oxygen, certainly make our determinations of photosynthetic rates underestimates.

Calculation by planimetry of the areas enclosed by the depth profiles allows an estimate of the areal photosynthetic activity (Table 6). These values ranged from 0.3 to 2.0 g O_2 m^{-2} hr^{-1} and reflected more the differing depths of the euphotic zones among the lakes, or possible variations in the specific rates of photosynthesis, than differences in the maximum rates of photosynthesis. The hourly rates were converted to daily rates by a factor used by Talling (1965) for other East African lakes. The empirically derived factor of 0.9 was multiplied by the number of hours of sunlight during the day of the experiment and the product multiplied by the hourly rate. Approximately similar insolation on the lakes at the time of the measurements improves the comparability of the calculated daily rates, which ranged from 3.2 to 20.2 g O_2 m^{-2} day^{-1} (Table 6).

The parallel time-depth distributions of temperature and dissolved oxygen in Lake Nakuru (Figs. 2 and 3) were the result of thermal stratification trapping oxygen evolved by the algae near the surface and the subsequent mixing of the whole water column. The importance of both nocturnal cooling and wind as mixing agents is made apparent by comparing the time-depth dia-

grams with the air temperatures and wind velocities (Fig. 5). Winds commonly produce isothermy during the daytime, as on 14 June. The prolonged stratification on 13 June provided an opportunity to compare the influence of mixing depth on gross photosynthesis with 14 June, discussed below. Because diurnal variations in temperature exceed annual variations and because seasonal changes in wind velocity are minor, these 2 days provide examples of the kind of stratification likely to occur at any time of the year.

The diurnal fluctuations in dissolved oxygen, its vertical distribution, and percent saturation (Figs. 3 and 5) are partially an expression of lacustrine metabolism and are vitally important to the organisms. Although oxygen was depleted in the deeper water on 13 June while Lake Nakuru remained stratified, complete deoxygenation was not attained. In fact, the high supersaturation of dissolved oxygen was more likely than oxygen depletion to have had a significant effect on the biota (Owens 1965; Ganf 1972).

The calculation of oxygen production during the day, the so-called gross photosynthesis, based on diurnal changes of dissolved oxygen in situ, has been done in several ways for nonflowing waters (Talling 1957; Odum and Hoskin 1958; Manny and Hall 1969). This plethora of modifications, made because of difficulties in determining the diffusion rates, and variations in respiration and advection, confuses comparison of the calculated values. The principal procedure used here is similar to that of Odum and Hoskin (1958) and only aspects specific to Lake Nakuru are discussed further.

The amount of dissolved oxygen per square meter (Fig. 5D) was calculated after concentrations at each depth were adjusted to account for variations in lake volume with increasing depth and includes the volume of gas collected in the bubble catchers. Two bubble catchers were used (only on 13 June) and the volume of gas collected, assumed to be oxygen, was corrected for water vapor. Only 3.8 g O_2 m^{-2}

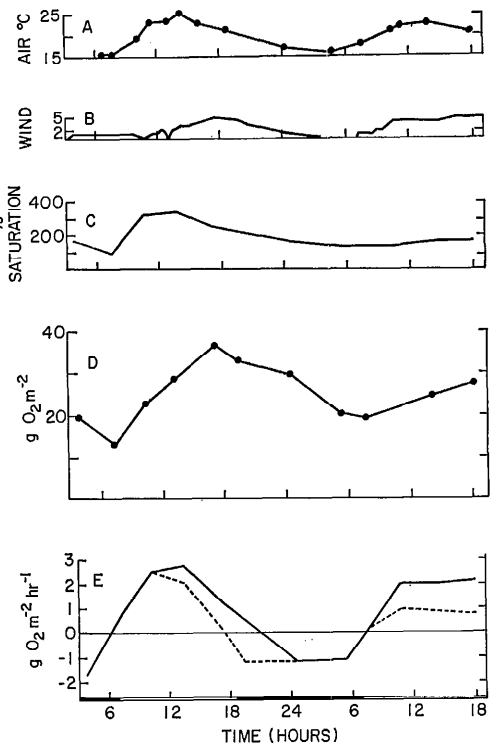

Fig. 5. Diurnal variations of five parameters in Lake Nakuru (13 to 14 June 1971). A. Air temperature measured at sampling station on lake. B. Wind velocity expressed as Beaufort scale numbers. C. Percent saturation of surface dissolved oxygen. D. Areal concentrations of dissolved oxygen. E. Rate of change of areal dissolved oxygen. The dashed line denotes the uncorrected values and the solid line denotes the diffusion corrected values or both values if the same.

were collected by the bubble catchers, which certainly was an underestimate: the bottoms of the catchers were suspended about 10 cm below the surface, thus missing the most productive water, and the devices could not be used when the wind velocity was greater than about 12 km hr^{-1} (Beaufort force 2). To illustrate the importance of oxygen bubbling out of the lake, the depth above which bubble growth could occur was calculated (Ramsey 1962) and plotted on Fig. 3. Inspection of Figs. 3 and 5 shows that during the long intervals when bubbles could form from the greatest depths the wind was too strong to permit collection of the escaping gas.

From the plot of the areal concentrations of dissolved oxygen the rate of change was calculated over 2-hr intervals centered on each sampling time (Fig. 5E). Correcting the rate of change values for diffusion was complicated but necessary because of the variable and often strong winds. A diffusion coefficient (g O_2 m^{-2} hr^{-1}) appropriate for the wind velocity at each sampling time was derived from a linear regression equation, fitted by the least squares method to a scatter diagram of diffusion coefficients versus wind velocities (Odum and Wilson 1962). The use of these data seemed justified because the water depths, surface areas, and salinities of the Texas bays in which the data were gathered were similar to those for Lake Nakuru. The percent saturation of dissolved oxygen, which was also required to compute the diffusion rates, was based on the solubility of oxygen in a dilution of seawater of 6‰ chloride (Carpenter 1966) at the surface temperatures and corrected for the vapor pressure of water and the altitude (Am. Public Health Assoc. 1965). Although the solubility of oxygen in this dilution of seawater is not exactly the same as in Lake Nakuru water, for present purposes the errors are minor. Because the percent saturation values (Fig. 5C) almost always exceeded 100% and reached as high as 340%, oxygen was diffusing out of the lake at an appreciable rate most of the time. The predawn supersaturation on 14 June remains unexplained. The positive rate of change after dark on 13 June, indicating net oxygen production, on the diffusion-corrected line (Fig. 5E) is not reasonable and suggests either that the diffusion rate is in error or that a water mass of higher dissolved oxygen content moved into the sampling area. In Lake Elmenteita nearshore water sometimes contains 20% more oxygen than offshore water by late afternoon.

Gross photosynthesis, calculated by planimetry of the area between sunrise and sunset under the diffusion-corrected rate-of-change curve and above a line drawn from the predawn to the postsunset rate-of-change minima, was 36 g O_2 m^{-2} 12 hr^{-1} (13 June) and 31 g O_2 m^{-2} 11.5 hr^{-1} (14 June). A much simpler method of calculation was used by Talling (1957) and Talling et al. (1973) and because these papers contain the only other values for gross photosynthesis based on oxygen changes in situ in eastern African lakes, Talling's method was applied to the data from Lake Nakuru. The resulting values for oxygen production during daytime were 38 g O_2 m^{-2} 12 hr^{-1} (13 June) and 22 g O_2 m^{-2} 11.5 hr^{-1} (14 June). The great effect of the wind on diffusion was not accounted for by this method of calculation, and, as expected, the value is lower than the previous value for 14 June.

Because of uncertainties of the methods, only large differences can be compared between the estimates of gross photosynthesis derived from free-water changes and those based on changes in bottles. Even with this limitation, in Lake Nakuru the daily rates (g O_2 m^{-2} day^{-1}) derived from diurnal variations in dissolved oxygen averaged almost five times higher than the data from bottles. The diffusion-corrected rates of change in the free water for the same time of day as when the bottles were exposed were 2.75 and 2.0 g O_2 m^{-2} hr^{-1}, rates about four times greater than those determined with bottled phytoplankton. Although exceptions do occur, generally free-water estimates of gross photosynthesis exceed those made with bottles, and this is particularly true for dense algal suspensions (Hoskin 1957; Verduin et al. 1959; Talling et al. 1973). For Lake Nakuru, assuming minor seasonal variation, the disparity probably arose because photosynthesis was suppressed and dissolved oxygen was underestimated in the bottles, and perhaps because diffusion was improperly calculated when the winds were strong. The free-water values are based on natural conditions for the phytoplankton and are probably more accurate.

Discussion

In lakes not enriched by human enterprises, gross photosynthetic rates of 30 g O_2 m^{-2} day^{-1} (ca. 11 g C m^{-2} day^{-1}) or

greater are seldom encountered. Although comparisons among the estimates of lacustrine productivity are confused by methodological differences (*see* Vollenweider 1969), a few examples of exceptionally high values and an approximation of the world mean will help in judging the data presented here. The mean gross primary productivity for the streams and lakes of the world derived by Whittaker and Likens (1972) is about 1.6 g O_2 m^{-2} day^{-1}. Talling et al. (1973) reported the gross photosynthesis as 43 and 57 g O_2 m^{-2} day^{-1} for Lake Aranguadi, an Ethiopian soda lake, based on diurnal changes in dissolved oxygen in situ. Using the same method Odum and Wilson (1962) reported one record of 30 g O_2 m^{-2} day^{-1} for slightly hypersaline Lower Laguna Madre, a bay on the Texas coast. Two extreme examples determined from oxygen evolution and ^{14}C uptake by bottled phytoplankton are respectively 56.9 g O_2 m^{-2} day^{-1} for Amaravathy Reservoir, Madras, India (Sreenivasan 1965), and 17.5 g C m^{-2} day^{-1} for Red Rock Tarn in Australia (Hammer *cited by* Walker 1973). The primary data, however, are either unpublished or difficult to evaluate. Additional references to high rates of photosynthesis are given by Talling et al. (1973) and examples from other plant communities by Westlake (1963).

Although photosynthesis is sensitive to fluctuating light, most ecological studies of photosynthesis are based on measurements of bottled samples suspended at a static sequence of depths. This experimental setup does not indicate possible effects from mixing or increasing oxygen tension. In the dense algal crops of soda lakes, vertical movement of only 5–20 cm can cause a large change in light intensity and spectral composition. Because wind-driven turbulence is frequent, cells are subjected to different light conditions for varying lengths of time. A quantitative expression for these conditions suitable to the situation in Lake Nakuru is discussed below: for more complicated situations a more involved expression would be necessary. For Lake Nakuru, this expression is the depth of mixing (z_m) divided by the depth of the euphotic zone (z_{eu}). The depth of the euphotic zone is considered to be the depth reached by 1% of the incident light. It can be computed using the formula $z_{eu} = 3.7/\epsilon_{min}$ (ϵ_{min} is the minimum vertical extinction coefficient) which Talling et al. (1973) found appropriate for African soda lakes. The mean depth of the lake or the depth of a thermocline can be used for the mixing depth. Previous workers who considered this ratio usually related it to the so-called critical depth and the growth of phytoplankton (Sverdrup 1953; Murphy 1962), although Talling (1971) dealt with some of its broader implications. Fortunately, the differences in stratification in Lake Nakuru—one day (13 June) with pronounced stratification throughout most of the daylight ($z_m : z_{eu} = 2.7$) and the other (14 June) with mixing to the bottom almost all day ($z_m : z_{eu} = 6.2$)—were ideal for observing the influence of mixing depth on photosynthesis. The similarity of the gross photosynthesis on these days, 36 g O_2 m^{-2} day^{-1} on 13 June and 31 on 14 June, was surprising: a greater decrease on 14 June was expected. Reasons for these results may include an enhancement of photosynthesis in the fluctuating light caused by the greater turbulence of 14 June, a larger number of phytoplankters exposed to the light on 14 June, or possibly suppression of photosynthesis on 13 June owing to containment of the algae in a region of high light and high dissolved oxygen.

Here we have provided some of the basic data needed to formulate testable hypotheses concerning the way in which biological, physical, and geochemical factors interact to control the productivity of tropical soda lakes. The basic questions: why are these lakes so productive? and perhaps, why are they not more productive? remain in part unanswered and as intriguing as ever.

References

American Public Health Association. 1965. Standard methods for the examination of water, sewage and industrial wastes, 12th ed.

BEADLE, L. C. 1932. Scientific results of the Cambridge Expedition to the East African lakes, 1930–31. 4. The water of some East African lakes in relation to their fauna and flora. J. Linn. Soc. (Zool.) **38**: 157–211.

CARPENTER, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. **10**: 141–143.

———. 1966. New measurements of oxygen solubility in pure and natural water. Limnol. Oceanogr. **11**: 264–277.

FOTT, B., AND A. G. A. KARIM. 1973. *Spirulina* plankton community in a lake in Jebel Marra, Sudan. Arch. Protistenk. **115**: 408–418.

GANF, G. G. 1972. The regulation of net primary production in Lake George, Uganda, East Africa, p. 693–708. *In* Z. Kajak and A. Hillbricht-Ilkowska [eds.], Productivity problems of freshwater. Pol. Sci. Publ.

GESSNER, F., AND F. PANNIER. 1958. Influence of oxygen tension on respiration of phytoplankton. Limnol. Oceanogr. **3**: 478–480.

GREENWAY, P. J., AND D. F. VESEY-FITZGERALD. 1969. The vegetation of Lake Manyara National Park. J. Ecol. **57**: 127–149.

HACH CHEMICAL CO. 1968. Hach DR-EL portable engineers laboratory methods manual, 7th ed. Ames, Iowa.

HECKY, R. E. 1971. The paleolimnology of the alkaline, saline lakes on the Mt. Meru lahar. Ph.D. thesis, Duke Univ. 209 p.

———, AND P. KILHAM. 1973. Diatoms in alkaline, saline lakes: ecology and geochemical implications. Limnol. Oceanogr. **18**: 53–71.

HOSKIN, C. M. 1957. Oxygen metabolism studies on some North Carolina streams and ponds. M.S. thesis, Duke Univ. 43 p.

ILTIS, A. 1968. Tolerance de salinité de *Spirulina platensis* (Gom.) Geitl. (Cyanophyta) dans les mares natroneés de Kanem. Cah. O.R.S.T.O.M. Ser. Hydrobiol. **2**: 119–125.

JENKIN, P. M. 1936. Reports on the Percy Sladen Expedition to some Rift Valley lakes in Kenya in 1929. 7. Summary of the ecological results with special reference to the alkaline lakes. Ann. Mag. Nat. Hist. Ser. 10 **18**: 133–181.

———. 1957. The filter-feeding and food of flamingoes (*Phoenicopteri*). Phil. Trans. R. Soc. Lond. Ser. B **240**: 401–493.

KENYA GOVERNMENT. 1970. National atlas of Kenya. Survey of Kenya. 103 p.

LÉONARD, J., AND P. COMPÈRE. 1967. *Spirulina platensis* (Gom.) Geitl., algue bleue de grande valeur alimentaire par sa richesse en proteines. Bull. Jard. Bot. Natl. Belg. 37(1), Suppl. 23 p.

LIND, E. M. 1968. Notes on the distribution of phytoplankton of some Kenya waters. Brit. Phycol. Bull. **3**: 481–493.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia **11**: 143–170.

MACKERETH, F. J. H. 1963. Some methods of water analysis for limnologists. Sci. Publ. Freshwater Biol. Assoc. 21. 71 p.

MANNY, B. A., AND C. A. S. HALL. 1969. Diurnal changes in stratification and dissolved oxygen in the surface waters of Lake Michigan. Proc. 12th Conf. Great Lakes Res. (Int. Assoc. Great Lakes Res.) **1969**: 622–634.

MURPHY, G. I. 1962. Effect of mixing depth and turbidity on the productivity of freshwater impoundments. Trans. Am. Fish. Soc. **91**: 69–76.

ODUM, H. T., AND C. M. HOSKIN. 1958. Comparative studies on the metabolism of marine waters. Publ. Inst. Mar. Sci. Texas **5**: 16–46.

———, AND R. F. WILSON. 1962. Further studies on respiration and metabolism of Texas bays, 1958–1960. Publ. Inst. Mar. Sci. Texas **8**: 23–55.

OWENS, M. 1965. Some factors involved in the use of dissolved oxygen distribution in streams to determine productivity. Mem. Ist. Ital. Idrobiol. **18**(suppl.): 209–224.

PERKIN-ELMER. 1964. Analytical methods for atomic absorption spectrophotometry. Perkin-Elmer, Norwalk, Conn.

RAMSEY, W. L. 1962. Bubble growth from dissolved oxygen near the sea surface. Limnol. Oceanogr. **7**: 1–7.

SCHOLANDER, P. F., L. VAN DAM, C. L. CLAFF, AND J. W. KANWISHER. 1955. Microgasometric determination of dissolved oxygen and nitrogen. Biol. Bull. **109**: 328–334.

SERFLING, R. E. 1949. Quantitative estimation of plankton from small samples of Sedgwick-Rafter cell mounts of concentrated samples. Trans. Am. Microsc. Soc. **61**: 217–220.

SREENIVASAN, A. 1965. An instance of unusual oxygen production in a tropical impoundment. J. Mar. Biol. Assoc. (India) **7**: 469–471.

SVERDRUP, H. W. 1953. On conditions for the vernal blooming of phytoplankton. J. Cons., Cons. Int. Explor. Mer **18**: 287–295.

TALLING, J. F. 1957. Diurnal changes of stratification and photosynthesis in some tropical African waters. Proc. R. Soc. Lond. Ser. B **147**: 57–83.

———. 1965. The photosynthetic activity of phytoplankton in East African lakes. Int. Rev. Gesamten Hydrobiol. **50**: 1–32.

———. 1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. Int. Ver. Theor. Angew. Limnol. 19, p. 214–243.

———, AND I. B. TALLING. 1965. The chemical composition of African lake waters. Int. Rev. Gesamten Hydrobiol. **50**: 421–463.

———, R. B. Wood, M. V. Prosser, and R. M. Baxter. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshwater Biol. **3**: 53–76.

Verduin, J., E. E. Whitwer, and B. C. Cowell. 1959. Maximal photosynthesis in nature. Science **130**: 268–269.

Vollenweider, R. A. [Ed.] 1969. A manual on methods for measuring primary production in aquatic environments. IBP Handbook 12.

Walker, K. F. 1973. Studies on a saline lake ecosystem. Aust. J. Mar. Freshwater Res. **24**: 21–71.

———, W. D. Williams, and U. T. Hammer. 1970. The Miller method for oxygen determination applied to saline lakes. Limnol. Oceanogr. **15**: 814–816.

Westlake, D. F. 1963. Comparisons of plant productivity. Biol. Rev. (Camb.) **38**: 385–425.

Whittaker, R. H., and G. E. Likens. 1972. Carbon in the biota, p. 281–302. *In* C. M. Woodwell and E. V. Pecan [eds.], Carbon in the biosphere. AEC Symp. Ser. 30 (CONF-720510).

Yellow Springs Instrument Co. 1972. Instructions for YSI model 51A dissolved oxygen meter. Yellow Springs, Ohio.

Submitted: 17 May 1973
Accepted: 29 April 1974