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Dissolved oxygen and thermal regimes of a Ugandan crater lake

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Abstract

This paper quantifies the temporal pattern of thermal stratification and deoxygenation in Lake Nkuruba, a small (3 ha), deep (maximum depth = 38 m) crater lake in western Uganda. Dissolved oxygen penetrated to an average depth of 9 m and a maximum depth of 15 m below which the lake was permanently anoxic over the 2 years of study. Although surface oxygen levels were correlated with both surface water temperature and rainfall, seasonal cycles of dissolved oxygen were not well-defined and may have been obscured by the high frequency of short-term fluctuations and by inter-annual variations caused by shifts in rainfall.

Surface water temperature averaged 23.3±0.7 °C (S.D.) and varied directly with air temperature. Both diurnal changes and top-bottom temperature differentials were small averaging 1.7±0.7 °C and 1.6±0.8 °C, respectively. Thermal stability ranged from 101.3 to 499.9 g-cm cm^{-2} and was positively related to surface water temperature suggesting that this small protected lake responds rapidly to short-term meteorological changes. Because contribution to the annual heat exchange cycle was confined to upper waters, the lake's annual heat budget was low, 1,073.8 cal cm^{-2} yr^{-1}. However, net primary productivity was relatively high averaging 1.3 g C m^{-2} d^{-1}.

The region where Lake Nkuruba is situated experienced a very strong earthquake (6.2 on the Richter scale) on 4 February, 1994. Subsequently, water levels dropped markedly in the lake, falling 3.14 m over a 5-month period.

Introduction

Hypoxia is widespread in tropical freshwaters particularly in systems characterized by low light and reduced mixing such as heavily vegetated swamps (Carter & Beadle, 1930; Chapman et al., 1998), flooded forests (Kramer et al., 1978), stagnant pools (Chapman & Kramer, 1991), floodplain lakes and ponds (Welcomme, 1979), and deep waters of some lakes (Wetzel, 1975; Beadle, 1981). In shallow wetlands, pools, and streams, dissolved oxygen tends to vary with seasonal changes in rainfall (Chapman & Kramer, 1991; Chapman et al., 1998). However, in deeper lakes, climatic conditions favor prolonged stratification, and several deep lakes in East and Central Africa seem to be permanently anoxic (Beadle, 1963, 1966; Melack, 1978; Kizito et al., 1993). It has been argued that the major determinants of circulation and hence production in tropical lakes are seasonality of wind, rainfall, and humidity rather than rising temperature and illumination in the spring as we see in temperate lakes (Beadle, 1966; Wood et al., 1976). Consequently, small sheltered lakes that are deep relative to their surface area are more likely to be permanently stratified and less productive than shallow lakes with high exposure (Beadle, 1966, 1981). Volcanic crater lakes with steep-sided walls and lakes formed by the blockage of steep-sided river valleys by volcanic lava flows (volcanic barrier lakes) provide wind-sheltered conditions conducive to long-term stratification (Beadle, 1981).

Volcanic crater lakes are well represented in Africa. Several occur in Uganda (Beadle, 1966; Melack, 1978; Kizito et al., 1993), Ethiopia (Prosser

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et al., 1968), Tanzania (Hecky, 1971; Kilham, 1971), Kenya (Melack, 1979; MacIntyre & Melack, 1982), and Cameroon (Kling, 1988). In Uganda, volcanism associated with rifting has been a particularly rich source of lakes. In the Kigezi district of Uganda, lakes have been formed almost exclusively by lava damming river valleys (volcanic barrier lakes), while in the rift valley and adjacent uplands of western Uganda, crater explosions have created large numbers of small, round, maar lakes (volcanic crater lakes, Beadle, 1981; Livingstone & Melack, 1984). In the foothills of the Ruwenzori Mountains in Uganda there are more than 80 crater lakes, sitting at an altitude of 925 m to 1520 m with very steep walls. Most of the lakes are less than 100 ha in surface area, and several cover only a few hectares (Melack, 1978; Kizito et al., 1993). Maximum depth varies from 0.25 m to $>$180 m (Melack, 1978; Kizito et al., 1993; Chapman & Chapman unpubl. data). Based on the concentration of dissolved salts in the surface waters, Melack (1978) divided the lakes into a saline group (conductivity $>$15000 μS cm^{-1}) and a dilute group (conductivity $<$1000 μS cm^{-1}).

In his survey of 16 crater lakes in western Uganda, Melack (1978) found that all lakes over 5 m were characterized by an anoxic hypolimnion; however, the depth to anoxia varied widely among lakes. It is likely that complete mixing in the deeper crater lakes is rare; however, there are few data available that document seasonal and longer-term variation in the incidence of vertical mixing in these lakes.

This paper quantifies temporal patterns of thermal stratification and deoxygenation in Lake Nkuruba, a small crater lake in western Uganda. We first describe the vertical distribution of dissolved oxygen over a 2-year period relative to seasonal patterns of rainfall and water temperature. We then quantify spatial variation in dissolved oxygen concentration by examining vertical patterns of dissolved oxygen among six sites over a 1-year period. Diurnal variation in the vertical distribution of oxygen is used to examine patterns of net productivity over a 1-year period relative to changes in the depth of the hypolimnion and rainfall. Thermal profiles are described and used to quantify the heat content and thermal stability of the lake. On 4 February, 1994, 20 months after we had initiated this study the region experienced a severe earthquake. We use data collected for 4 months subsequent to the event to describe the impact of the earthquake on the limnology of Lake Nkuruba.

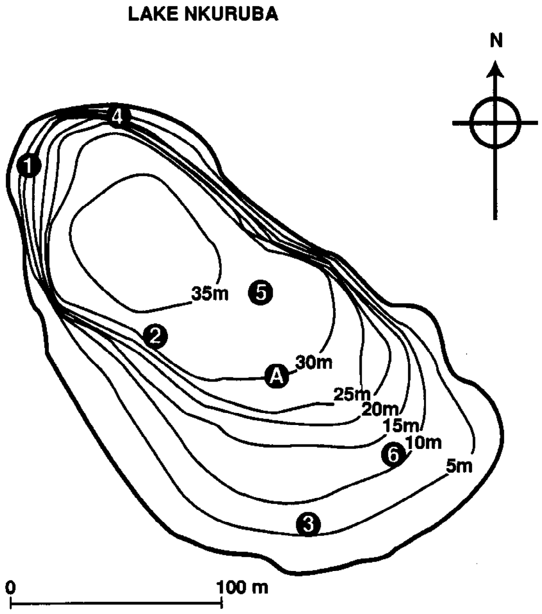

Figure 1. Bathymetric map of Lake Nkuruba, Uganda (5-m contours) depicting the six sampling sites for the examination of spatial variation in dissolved oxygen and water temperature (Sites 1 to 6) and the site for the measurement of diurnal profiles (A).

Methods

Study site

Lake Nkuruba (0° 32′ N and 30° 19′ E) is situated at the northern end of the Kasenda cluster of approximately 40 crater lakes in western Uganda (Melack, 1978). It is a freshwater lake 3 ha in area with a mean depth of 16 m, a maximum depth of 38 m, and a volume of 481,000 m^3 (Figure 1). On the northern two thirds of the lake, the shoreline drops off precipitously, while the south end forms a shallower plate with a gradual slope to the central deep core of the crater (Figure 1). Aquatic macrophytes are absent. There is no superficial inflow or outflow, but groundwater exchange has been proposed to account for relatively small changes in water levels despite marked wet and dry seasons (Kizito et al., 1993). The crater rim averages about 48 m above the water surface. The crater walls are forested to the crater rim; adjacent areas are largely agricultural land with small isolated patches of forest in the crater valleys. Conductivity averages 325 μS cm^{-1} at the surface and 445 μS cm^{-1} at 25 m of depth suggesting some mixing of electrolytes (n=22 measurements over 12 months; Chapman, unpublished data). However, Kizito et al. (1993) found the lake to be anoxic below 6.5 to 8 m in depth.

Chlorophyll concentrations (4 μg l^{-1} to 10–12 μg l^{-1}) correspond to mesotrophic levels in temperate lakes, although total phosphorus concentrations in surface waters are relatively high (40 μg l^{-1}, Kizito et al., 1993, Kizito & Nauwerck, 1996).

The lake harbors two introduced species of tilapia (*Tilapia zillii* and *Oreochromis leucostictus*) and an introduced poeciliid, *Poecilia reticulata*. Zooplankton is dominated by copepods and several species of rotifers, and phytoplankton is dominated by a few widespread small blue-green and green algae (Kizito et al., 1993; Kizito, 1995; Kizito & Nauwerck, 1996).

Mean annual rainfall measured at the Makerere University Biological Field Station located 12 km from Lake Nkuruba (1977–1996) has averaged 1678 mm (range 1205 to 2139 mm), with distinct wet and dry seasons which are bimodal in distribution. May through August and December through February tend to be drier than other months, with the May–August dry period of a longer duration than the second dry season. Mean daily minimum temperature is 15.5 °C and mean daily maximum temperature is 23.7 °C (1990–1996, Chapman & Chapman, 1997).

Sampling protocols

Lake morphometry was determined by extending polypropylene ropes across the lake at 13 locations. Water depth was measured at 5-m intervals along each transect using an echosounder, and the boundaries of the lake were estimated from an aerial photograph. Five-meter depth isoclines were constructed from the transect data.

To quantify seasonal and spatial variation in dissolved oxygen concentration and water temperature, duplicate profiles were taken at six sites in Lake Nkuruba, weekly over a 2-year period (July 1992–July 1994, Sites 1–6, Figure 1). To ensure repeat sampling of the same locations, ropes marked off at 5-m intervals were stretched across the lake from known endpoints and used to anchor the boat at specific stations. The order of sampling stations was determined randomly to minimize any systematic bias associated with diel increase in dissolved oxygen, although diel change was small. Sampling was initiated at approximately 0830 h and was generally completed within 5.5 h. Dissolved oxygen (mg/L) and water temperature (°C) were measured with a YSI Model 51B or a YSI Model 50 meter, and meters were calibrated for dissolved oxygen each sampling day.

Estimates of an index net productivity were derived from diel samples of dissolved oxygen profiles. Following Cole (1983), we assume that the increase in oxygen over the day reflects net primary productivity. Duplicate profiles were taken in the center of the lake (Site A, Figure 1) at 0800 h, 1200 h, and 1600 h. Because of the steep crater rim and small size of the lake, there is little direct sunlight before 0800 h or after 1600 h.

Water transparency was measured bi-monthly using a 20 cm Secchi disk between March 1993 and July 1994 in the center of the lake. Values represent the average of two estimates. Water levels were measured weekly between July 1992 and July 1994.

Analyses

Isopleths of dissolved oxygen and water temperature were calculated from arithmatic means of the six stations for each meter of depth between 0 and 30 m. Simple linear regressions were used to quantify the relationships between depth to anoxia and three independent variables (surface oxygen concentration (upper 20 cm), surface water temperature, and rainfall), and the relationship between surface oxygen concentration and two independent variables (surface water temperature and rain). A multiple regression analysis was not possible because both the condition index and the variance decomposition matrix indicated significant collinearities incurred by the correlated predictor variables which can seriously destabilize the regression coefficients (Belsley et al., 1980). We used the regression model of depth to anoxia over the ratio of maximum diameter of the lake and minimum crater height provided by Melack (1978) to compare the depth to anoxia in Lake Nkuruba to other crater lakes.

Spatial variation in dissolved oxygen was examined for July 1992–July 1993 by calculating the mean value of dissolved oxygen for each of the six sites at 0, 1, 2, 3, 4, 5, and 6 m of depth. The nonparametric Friedman test with multiple comparisons was used to test for significant differences among sites in mean dissolved oxygen.

Net primary productivity (g O_2 m^{-2} day^{-1}) was estimated by integrating the area under the curve for the relationship between maximum diurnal change in dissolved oxygen versus depth (Cole, 1983). This is really an index of net productivity since dissolved oxygen concentration also depends on exchange at the air-water interface. However, in Lake Nkuruba, error associated with diffusion of oxygen across the air-water boundary is potentially small because of low levels of wind-induced turbulence. Multiple regression analysis was used to examine the relative importance of depth to anoxia and rain in explaining variation in productivity over the 1 year of study. Partial correlation analyses determined the relationship between productivity and one independent variable when the linear effects of the other variable were removed.

The annual heat budget for Lake Nkuruba, representing the difference between the minimum and maximum heat contents of the lake during the course of a year, was calculated using formulae provided by Hutchinson (1957). In Lake Nkuruba, the position of the metalimnion is difficult to estimate because of the gradual change in water temperature. In addition, the metalimnion bears little or no correspondence to the depth or thickness of the oxycline. Thermal stability, the amount of energy required to mix a thermally stratified column of water to isothermy (Viner, 1984), was calculated following Idso (1973) and Cole (1983) and expressed as g-cm/cm^2. Stability was estimated bi-weekly between January 1993 and December 1993. Linear regression was used to examine the importance of surface water temperature in accounting for variance in thermal stability. Kling (1988) provided a review of thermal stability values for a series of temperate and tropical lakes and found maximum lake depth to be the best predictor of thermal stability. We used the regression derived from the data set in Kling (1988) to compare the average thermal stability in Lake Nkuruba to other temperate and tropical lakes.

Simple linear regressions were used to look for relationships between water level (which dropped markedly subsequent to the earthquake) and several limnological characters including: dissolved oxygen at the surface, depth to anoxia, water transparency, and productivity.

Results

Rainfall data show a bimodal pattern typical of this equatorial region; peak rainfall occurred between September and December of 1992 when 986 mm of rain fell over a 12-week period (Figure 2a). Maximum and minimum air temperature over the 24-month study period averaged 24.1±2.7 °C (S.D., range = 18.9 to 30.2 °C) and 14.3±1.2 (S.D., range = 12.0 to 18.0 °C), respectively; however, the pattern was unusual, with lower average air-temperature in the first 9 months of the study (July, 1992–March, 1993) than during the remainder of the sampling period.

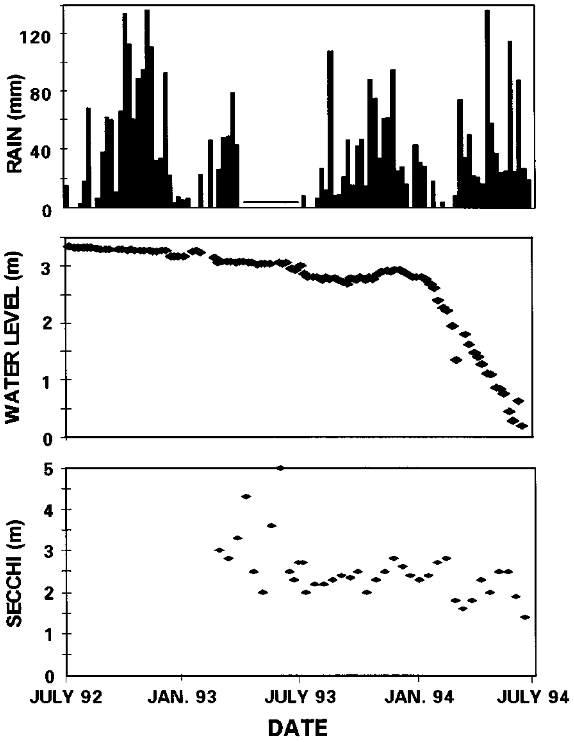

Figure 2. Temporal variation in (A) rainfall (mm, measured at the Makerere University Biological Field Station, 12 km from Lake Nkuruba), horizontal bar represents a period during which rainfall data are not available (B) water level change (m) of Lake Nkuruba, and (C) water transparency (Secchi disk, m) of Lake Nkuruba.

Surface levels of dissolved oxygen concentration averaged 6.6±1.3 mg l^{-1} (S.D.) and ranged from 3.1 to 9.1 mg l^{-1}. Surface oxygen saturation values averaged 75.5±0.2% and ranged from 35 to 106%. Dissolved oxygen penetrated to a maximum depth of 15 m, below which the lake was permanently anoxic over the 2 years of study (Figure 3a). The average depth to anoxia (0 mg l^{-1}) was approximately 9 m; however, the depth of the oxycline showed considerable short-term and long-term fluctuations. Epilimnetic mixing from above prevented the anoxic boundary from rising higher than 6–7 m below the water surface (Figure 3a). Depth to anoxia was negatively related to surface oxygen concentration (r^2 = 0.088, P = 0.005) reflecting periods of mixing which bring cool, hypoxic waters to the upper layers. Depth to anoxia was not significantly related to rainfall (P = 0.847); however, higher rainfall did relate to lower surface oxygen concentration (r^2 = 0.145, $P < 0.001$)

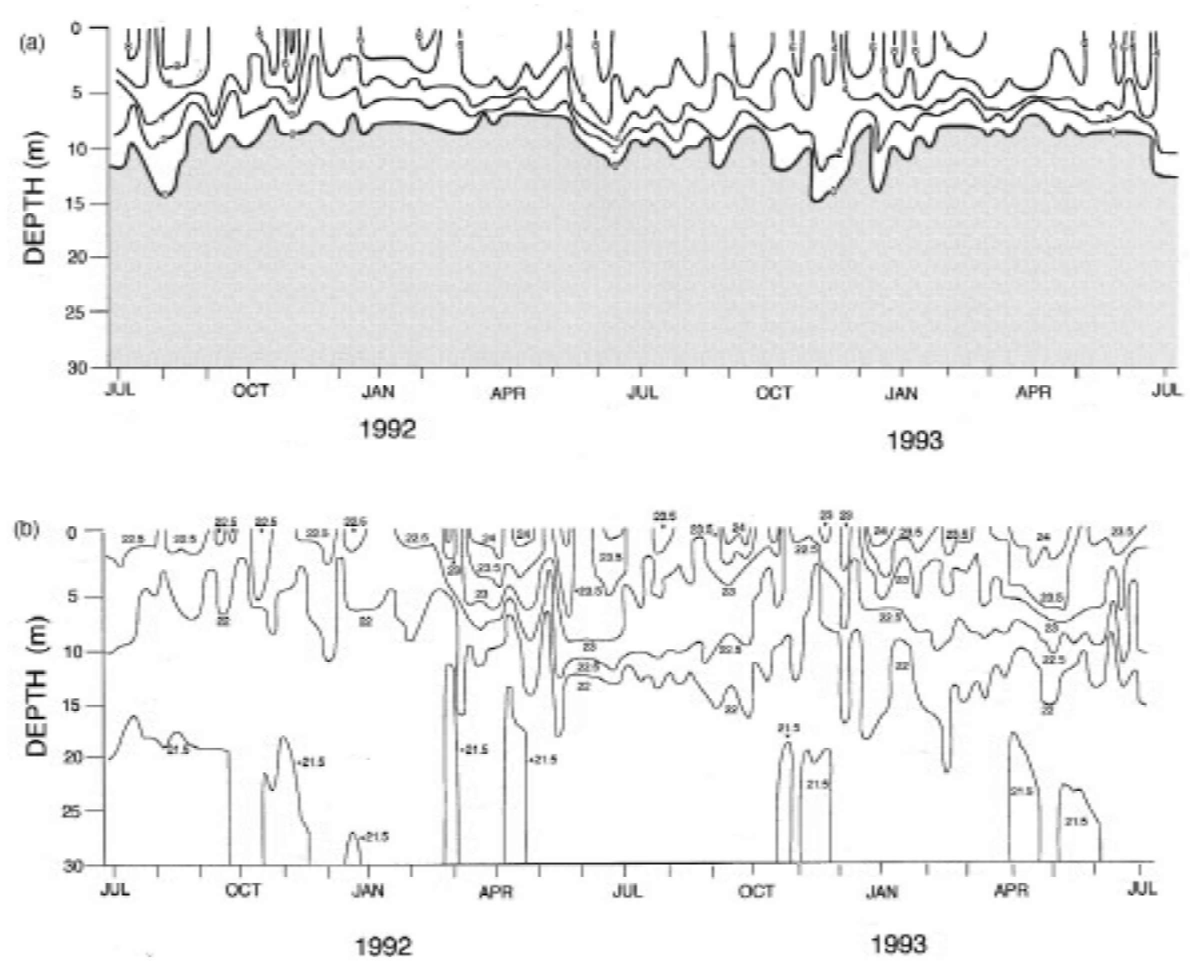

Figure 3. Isopleths of (A) dissolved oxygen concentration at 2 mg/L intervals and (B) isotherms of water temperature at 0.5 °C intervals for Lake Nkuruba, Uganda (July 1992 to July 1994, surface to 30 m of depth). The shaded section of the dissolved oxygen figure represents the distribution of anoxic water.

indicating that some peak rainy periods are characterized by mixing. Surface oxygen concentration was positively related to surface water temperature (r^2 = 0.071, P = 0.008), and depth to anoxia was negatively related to surface water temperature (r^2 = 0.081, P = 0.008), suggesting that mixing may also occur as a result of evaporative cooling of the surface water. The low amount of variance in surface oxygen and depth to anoxia explained by either rainfall or temperature indicates that other factors may account for the irregular patterns observed.

Dissolved oxygen concentration profiles exhibited significant spatial variation (Friedman's test, χ^2 = 27.7, $P < 0.001$). Sites 1 and 4 exhibited the lowest oxygen levels over the range of depths examined (Friedman's test, multiple comparisons, $P<0.05$, Figure 4). Sites 1 and 4 are located in the northern end of Lake Nkuruba (Figure 1) where shading is more pronounced than other areas due to the precipitous nature of the crater rim and the narrow shape of the northern region of the lake.

Surface water temperature averaged 23.3±0.7 °C (S.D.) and ranged from 22.0 to 24.7 °C, varying directly with air temperature (r^2=0.45, $P<0.001$, Figure 3b). Diurnal changes were small averaging only 1.6±0.8 °C (range=0.5 to 3.3 °C) reflecting the high degree of shading imposed by the crater walls. Top-bottom temperature differentials were also small averaging 1.7±0.7 °C and ranging between 0.5 and 3.3 °C (Figure 3b). Water temperatures were lower between July 1992 and March 1993 than during the remain-

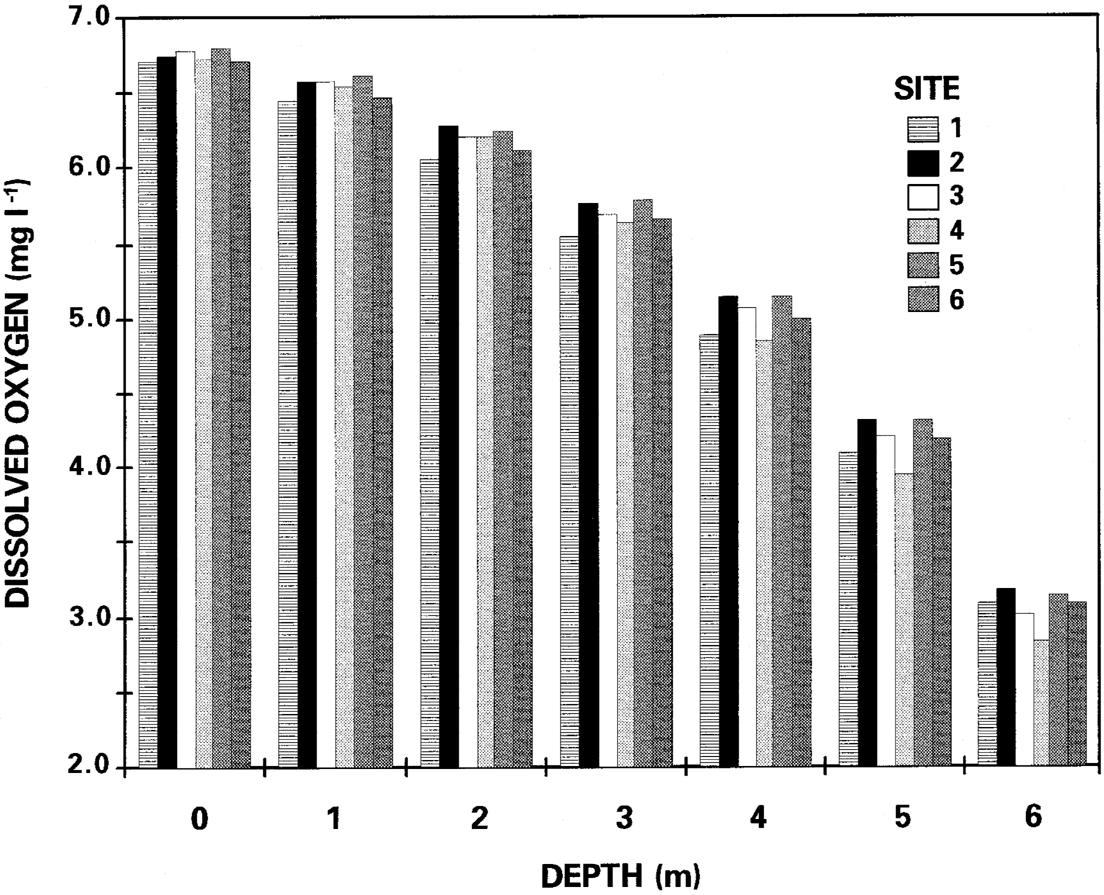

Figure 4. Mean level of dissolved oxygen concentration (July 1992 to July 1993) at 0, 1, 2, 3, 4, 5, and 6 m of depth for six systematically selected sites in Lake Nkuruba, Uganda. Site numbers refer to sites indicated on Figure 1.

der of the study; however, thermal stratification was maintained throughout the 24-month study period.

Lake Nkuruba showed considerable short- and long-term fluctuations in thermal stability averaging 330.3±129.1 g-cm cm^{-2}, but ranging from 101.3 to 499.9 g-cm cm^{-2}. Increases in thermal stability and surface water temperature occurred almost concurrently (r^2=0.87, P<0.001, Figure 5) suggesting that this small protected lake responds rapidly to short-term meteorological changes. Changes in the stability of the lake occurred in response to variation in the heat content of the shallow epilimnetic waters, rather than to the way that heat was distributed throughout the water column. Because contribution to the annual heat exchange cycle in Lake Nkuruba was confined to upper waters, the lake's annual heat budget was low, 1,173.8 cal cm^{-2} yr^{-1} for 1993 (Figure 6).

We used diurnal shifts in oxygen profiles to calculate an estimate of net productivity for the period of

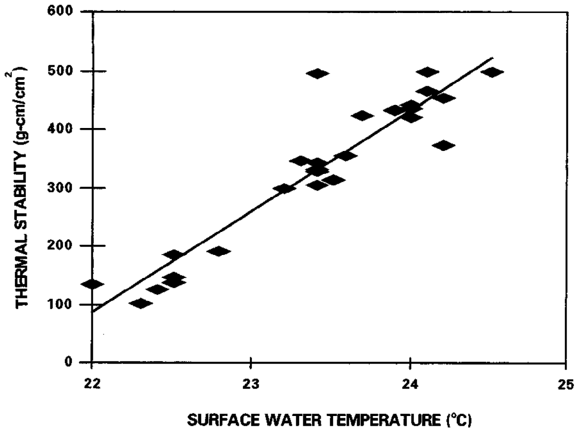

Figure 5. Relationship between thermal stability (g-cm/cm^2) and surface water temperature (°C) for Lake Nkuruba, Uganda (January to December 1993, r^2=0.87, P<0.001).

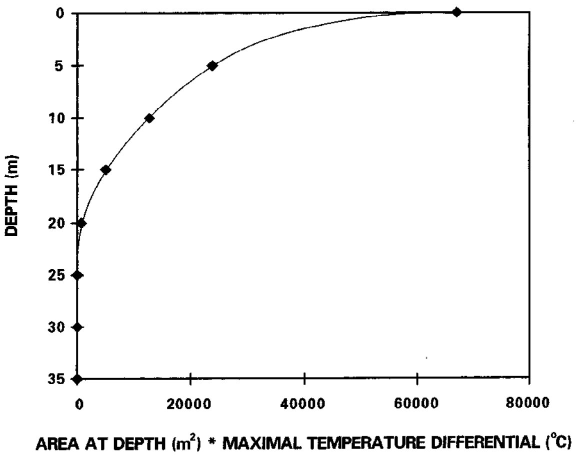

Figure 6. Relationship between water depth and maximum change in heat content per volume for each depth stratum for Lake Nkuruba, Uganda (January to December 1993).

Table 1. The relationship between net productivity (g O_2 $m^{-2}d^{-1}$) in Lake Nkuruba, Uganda and two independent variables: rain and depth to anoxia. Data were collected between January and December, 1993

Total r^2	*P* value	Factor	Partial correlation coefficient	*P* value
0.403	0.006	Rain	0.529	0.007
		Depth to anoxia	−0.487	0.012

January 1993 to December 1993. Data for individual strata were integrated to provide estimates of productivity per square meter of lake surface. Productivity averaged 3.4±2.8 g O_2 m^{-2} d^{-1} (1.3 g Cm^{-2} d^{-1}) and ranged from 0.0 to 8.4 g O_2 m^{-2} d^{-1}. A multiple regression with rain and depth to anoxia as independent variables explained 39% of the variance in net productivity (Table 1). Productivity was positively correlated with rainfall when the linear effects of depth to anoxia were removed. In addition, net productivity was negatively correlated with depth to anoxia when the linear effects of rain were removed (Table 1).

Water transparency, measured bi-weekly between March 1993 and July 1994 averaged 2.5±0.7 m (S.D.) and ranged between 1.4 and 5.0 m. Although water transparency showed short-term fluctuations, there was a general decrease over the period of study (Figure 2c).

The region of Uganda where Lake Nkuruba is situated experienced a very strong earthquake (6.2 on the Richter scale) on 4 February, 1994 with the epicenter located very close to Lake Nkuruba. The event was 14 km below the earth's surface and was felt as far as Kampala, the capital city of Uganda, located ∼250 km from the epicenter. Subsequent to the severe earthquake, water levels dropped markedly in Lake Nkuruba falling 3.14 m over a 5-month period (Figure 2b). During the post-earthquake period large bubbles were continuously released from certain locations in the lake.

This decline in water level did not relate to any significant change in surface oxygen (r^2=0.019, P=0.174), depth to anoxia (r^2=0.006, P=0.444), or productivity (r^2=0.085, P=0.167). However, water transparency was positively related to water level (r^2=0.119, P=0.006).

Discussion

Dissolved oxygen: spatial and temporal dynamics

Over the 2 years of our study, the average depth to anoxia in Lake Nkuruba was approximately 9 m; however, the depth of the oxycline showed considerable short-term and long-term fluctuations. There seems to be a frequent exchange of oxygen between the upper edge of the anoxic zone and the water above it as evidenced by variation in the depth to which oxygen penetrated (6–15 m), and because epilimnetic mixing from above prevents the anoxic layer from rising higher than 6–7 m from the water surface. Although surface oxygen levels were correlated with both surface water temperature and rainfall, seasonal cycles of dissolved oxygen in Lake Nkuruba were not well-defined and may have been obscured by the short-term fluctuations and by inter-annual variations caused by shifts in the onset, magnitude, and duration of the seasonal rains.

Long-term data on small, steep-sided tropical lakes which permit an evaluation of the long-term permanency of anoxic hypolimnia are very limited; however, studies of the Bishoftu crater lakes in Ethiopia and small mountain lakes in East Africa are of sufficient length to provide a consideration of seasonal trends. The comparative study of five crater lakes in Ethiopia (1963–1965) revealed mixing or near mixing of the lakes on an annual basis (Baxter et al., 1965; Prosser et al., 1968; Wood et al., 1976). The deep circulation observed in these lakes was attributed to evaporative cooling and radiative heat loss at night during the sunny dry season which reduced thermal stratification. Variation among the five lakes in the degree of deep circulation seemed to relate to variation in the depth and degree of exposure to wind. Melack (1978) points out that the location of the Ethiopian lakes (1900 m and 9 °N) produces more severe seasonal cooling than in the equatorial lakes of Uganda. Small deep mountain lakes in East Africa have been investigated by Löffler (1964, 1969). In these lakes, seasonal temperature fluctuations are very small, water temperature levels are very low, and circulation is frequent. Most of these lakes are considered as cold-polymictic or oligomictic, showing little sign of stratification or only temporary stratification.

Although the hypolimnion was continuously anoxic in Lake Nkuruba over the 2 years of study, the vertical distribution of ions and the conductivity gradients in this lake suggest some circulation into its deeper waters (Kizito et al., 1993). Beadle (1966) measured oxygen profiles on six occasions over a 12-year period in Lake Nkugute, Uganda and never observed complete mixing. However, Beadle (1966, 1981) reports anecdotal observations of occasional fish kills in Lake Nkugute and other deep volcanic lakes presumably associated with partial mixing of deep, anoxic water to the surface with heavy storms. In Lake Bunyoni, a volcanic barrier lake in Uganda, there was a serious fish kill in 1964 associated with partial mixing after which the commercial fishery (based on stocked species) was abandoned (Beadle, 1981). Beadle (1981) suggests that these deep volcanic crater lakes and barrier lakes may be characterized by a long-term supra-annual mixing cycle with a rare and unpredictable climatic trigger.

There may be other more gradual processes providing some slow mixing in deep, tropical lakes, but not rapidly enough to override oxygen consumption in the deep hypolimnion (Beadle, 1981). In Lake Toba (Indonesia; Ruttner, 1931) and Lake Mainit (Philippines; Lewis, 1973a) circulation seems sufficient to prevent meromixis but not vigorous enough to offset oxygen consumption leading to continuous deep water anoxia (Lewis, 1973b). Talling (1963) proposed a marginal cooling hypothesis to account for slow circulation in Lake Albert. He suggested that cooling of shallow inshore waters reduces their density permitting them to flow down and under the warmer deep water. This process may provide slow circulation while maintaining anoxic conditions in the hypolimnion. However, it is doubtful that marginal cooling is an important factor in the temperature regime of all permanently stratified tropical lakes because many of them have, like Lake Nkuruba, precipitous shorelines descending quickly into deeper waters (Beadle, 1966). In addition, diurnal fluctuations of water temperature in Lake Nkuruba were small, averaging only 1.6 °C, which would limit the potential impact of marginal cooling.

A striking zooplankton phenomenon reported from crater lakes Nkuruba and Nyahirya, and the volcanic barrier lake Nkugute (Uganda) may contribute to a modest level of deep mixing. Copepods (primarily *Thermocyclops* spp.) have been reported from deep down in the oxygen-free section of these lakes (Kizito et al., 1993; Kizito, 1995; Beadle 1963). In Lake Nkugute, Beadle (1963) found *Thermocyclops schuurmanni* extremely close to the bottom with approximately 40 m of oxygen-free water between the plankters and the surface. The egg-bearing females were confined to the upper oxygenated layer which also contained all other stages; however, the deeper anoxic waters contained nauplius larvae and young copepods. Beadle also found the rotifers *Horaella brehmi* and *Keratella tropica* and a ciliate protozoan in the anoxic zone. In Lake Nkuruba, Kizito (1995) found that both adults and younger instars of *Thermocyclops* spp. (*T. macracanthus* and *T. incisus*) and *Mesocyclops aequatorialis* showed abundance peaks in the anoxic hypolimnion near the beginning of his 2-year investigation (March 1992). Later in the study, abundance peaks for most crustacean zooplankton occurred in the well-oxygenated waters (2–6 m of depth) though the plankters were also present in anoxic waters (Kizito, 1995). A similar pattern was observed in Lake Nyahirya (Kizito et al., 1993; Kizito, 1995). Kizito (1995) reported LD_{50} levels of 49 and 27.5 days under anoxia for adults of *M. aequatorialis* and *Tropocyclops tenellus*, respectively, reflecting far reaching adaptation to low oxygen conditions in these two species. Beadle (1963) suggested that the activities of such plankters may contribute to a modest degree of chemical circulation between upper and lower water layers under the conditions of stable stratification observed in lakes such as Nkuruba and Nkugute mitigating the inhibiting effects of stratification. In such a process, nutrients trapped in the anoxic hypolimnion may be brought back into circulation.

Melack (1978) found that 47% of the variation in depth to anoxia in a data set of crater lakes from western Uganda and Australia could be explained by the ratio of the maximum diameter of the lake and minimum height of the crater rim. Only crater lakes with well defined rims and very slight or no chemoclines were used in his analysis. The average depth to anoxia in Lake Nkuruba prior to the beginning of the water level decline (9.7 m) is deeper than predicted by Melack's regression (5.0 m). This may reflect additional factors of stratification such as turbidity and evaporative/radiative cooling. Several of the crater lakes examined by Melack 1978 did not have heavily forested crater rims. The large degree of shading in Lake Nkuruba imposed by the forested rim and the small size of the lake creates very small temperature differentials and cooler waters which may decrease the energy required to induce mixing. Given the post-earthquake water level decline of 3.1 m and assuming stabilization of water level at this stage, the new predicted depth to anoxia would be 5.1 m. The average depth to anoxia after the earthquake declined to 8.6 m. However, given the short- and long-term fluctuations in depth to anoxia that characterize Lake Nkuruba, additional data will be required to evaluate whether the drop in water level affects depth to anoxia.

We found significant differences among sites in the depth profile of oxygen concentration with lower values in the two sites in the northern region of the lake. The narrow width of the lake in this region and the precipitous cliffs minimize sunlight exposure which may account for the pattern observed. Values were highest in the center of the lake (Sites 2 and 5) which may reflect a higher periphyton input in this region relative to the southern plateau of the lake (Chapman & Chapman, personal observations).

Thermal stability and heat content

In Lake Nkuruba, the position of the metalimnion is difficult to estimate because of the gradual change in water temperature. In addition, the metalimnion bears little or no correspondence to the depth or thickness of the oxycline. This pattern is typical of many crater lakes in western Uganda (Melack, 1978; Kizito et al., 1993). We therefore used other thermal characters (thermal stability and heat content) for comparison with other lakes.

Kling (1988) found that maximum depth explained 85% of the variation in thermal stability in a data set of temperate and tropical lakes including 10 volcanic crater lakes in Cameroon. The average thermal stability for Lake Nkuruba (330.3 g-cm/cm^2) falls 56% below the predicted line derived from the data set in Kling (1988). This may be due to other factors which influence thermal regimes such as the high degree of shading in Lake Nkuruba and its low transparency, both of which limit thermal penetration. In Lake Nkuruba thermal stability was strongly correlated with surface water temperature suggesting that this small protected lake responds rapidly to short-term meteorological changes. Bowling and Salonen (1990) found that increases in thermal stability, Birgean wind work, and heat content occurred concurrently in small forested Finnish lakes. Like Lake Nkuruba, changes in stability in these lakes also occurred in response to changes in the heat content of epilimnetic waters, rather than to the distribution of heat throughout the water column.

Because contribution to the annual heat exchange cycle in Lake Nkuruba is confined to upper waters, the lake's annual heat budget is low, 1,073.8 cal cm^{-2} for 1993. This annual budget is lower than all lakes reported by Hutchinson (1957, *n*=75, range = 2,240 to 65,500 cal cm^{-2}), a series of five crater lakes in Western Victoria, Australia (range=5,300 to 19,120 cal cm^{-2}, Timms, 1975, 1976), six of the eight dystrophic Tasmanian lakes examined by Bowling (1990, range = 1,023 to 19,806 cal cm^{-2}), three of the Bishoftu crater lakes of Ethiopia (Wood et al., 1976, range = 3,100 to 5,700 cal cm^{-2}), and a small forested sinkhole lake in Florida (Nordlie, 1972, 4,391 cal cm^{-2} (1964); 3,767 cal cm^{-2} (1965)). In addition to limited surficial heat exchange in Lake Nkuruba, another factor that may contribute to low heat content is direct solar heating which is restricted due to the high turbidity of the water.

Kling (1988) found a strong positive relationship between water transparency and thermocline depth in his review of tropical and temperate lakes and suggested that reduction in resistance to vertical mixing caused by deeper penetration of solar radiation is important in contributing to mixing depths. Bowling (1990) reported lower heat budgets than expected based on the depth and area of polyhumic forested lakes in Tasmania. This anomaly was attributed to the dystrophic and sheltered character of the lakes which permitted only their surface waters to contribute to heat exchange. Values for two of the eight lakes and reservoirs considered by Bowling (1990, Sulphide Pool – 1013 cal cm^{-2} and Morrison Lake – 1023 cal cm^{-1}) closely match values for Lake Nkuruba. It seems that epilimnetic waters in these small sheltered lakes exchange the majority of the heat with the environment while deeper waters have minimal impact (Bowling, 1990). Timms (1975) found that the annual heat budget for two crater lakes in Australia was lower than predicted by the relationship between mean depth and heat budget in other Australian lakes. This was attributed to the fact that deep mixing is limited by the sheltered position of the lakes and the low transparency of the water (Timms, 1975). Small humic forest lakes in Finland (Bowling and Salonen, 1990) show much higher heat budgets than Lake Nkuruba, the small Tasmanian lakes, and the crater lakes from Australia which reflects winter freeze over in the Finnish lakes. Bowling and Salonen (1990) found that the input of latent heat of fusion of the ice contributed at least 50% of the annual heat budgets of the Finnish lakes.

Timms (1975) argued that larger lakes have more variable heat budgets due to relaxation of morphometric control. For example, Lewis (1984) found a high degree of variation in rate of heat uptake and heat content among years in Lake Valencia, Venezuela (350 km^2). However, Bowling and Salonen (1990) found a high degree of interannual variation in small forested Finnish lakes. They surmised that very small lakes may be too small for morphometric control to be effective, because the low volume is insufficient to facilitate thermal buffering. We were not able to calculate heat budgets for more than 1 year in Lake Nkuruba, but given the high degree of short- and long-term fluctuations in thermal stability, it seems reasonable to expect similarly high inter-annual variation in heat content.

Productivity

Beadle (1981) argued that the major determinant of circulation and hence production in tropical lakes is wind rather than seasonal fluctuations of illumination and atmospheric temperature. He therefore concluded that small sheltered lakes, deep relative to their area would be in tropical regions the least productive. However, our estimates of net primary productivity for Lake Nkuruba (averaging 1.3 g C m^{-2} d^{-1}) are relatively high and would correspond to eutrophic levels of temperate lakes. In Lake Nkuruba nutrients trapped in the anoxic hypolimnion may be brought back into circulation via the feeding activities of the zooplankton or periodic climatic events which produce productivity spikes. Productivity was positively correlated with rainfall when the linear effects of depth to anoxia were removed which may reflect the importance of allochthonous nutrient input during rain events. Although the slopes of the crater rim of Nkuruba are forested, adjacent lands on the crater rim have largely been converted to agricultural land which may contribute to nutrient loading with rain events. In addition, productivity was negatively correlated with depth to anoxia when the linear effects of rain were removed which may reflect high rates of respiration during periods of high productivity.

Earthquake

Subsequent to the severe earthquake in February of 1994, water levels dropped markedly in Lake Nkuruba falling 3.14 m. We believe the lava tube under the crater may have been fractured during the earthquake permitting some slow drainage below the crater. Water level also declined slowly prior to the earthquake, which may relate to annual variation in rainfall. The annual rainfall in 1993 was the lowest of any year since 1986.

Water transparency generally decreased as water level decreased between March 1993 and July 1994, and this may have been associated to some degree with the earthquake. However, the decrease in water transparency was modest, and the lowest three values recorded subsequent to the earthquake (1.4 m, 1.6 m, 1.8 m) were within the range recorded by Kizito & Nauwerck (1996) for Lake Nkuruba between March and July of 1992.

Summary

With the exception of montaine lakes, small, equatorial crater lakes, which are deep relative to the area are likely to be characterized by low heat content, low thermal stability, and anoxic hypolimnia. Patterns of long-term mixing in these lakes are unclear because they seem susceptible to episodic climatic events which may be supra-annual in nature. We need long-term data on these systems to clarify the importance of unpredictable, rare mixing events associated with major disturbance relative to other more gradual mixing processes in accounting for the absence of meromixis in these lakes.

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