Plant Ecology and Evolution 143 (3): 365–377, 2010
doi:10.5091/plecevo.2010.420

PLANT ECOLOGY EVOLUTION

REGULAR PAPER

Observations on the limnology and phytoplankton community of crater Lake Kyaninga (Uganda), with special attention to its diatom flora

Christine Cocquyt[1,2,*], Pierre-Denis Plisnier[3], Vanessa Gelorini[2], Bob Rumes[2] & Dirk Verschuren[2]

[1]National Botanic Garden of Belgium, Domein van Bouchout, BE-1860 Meise, Belgium
[2]Ghent University, Limnology Unit, K.L. Ledeganckstraat 35, BE-9000 Gent, Belgium
[3]Royal Museum for Central Africa, Leuvensesteenweg 13, BE-3080 Tervuren, Belgium
*Author for correspondence: christine.cocquyt@br.fgov.be

Background and aims – With a depth of at least 220 m, Lake Kyaninga is the deepest known maar crater lake in western Uganda. We studied its limnology and phytoplankton community to determine how the frequency and depth of water-column mixing influences nutrient cycling and seasonality in this aquatic ecosystem.
Methods – Water-column temperature was measured continuously during a full annual cycle between August 2007 and August 2008. Other physical and chemical variables as well as diatom and other phytoplankton communities were investigated on three occasions, namely during the dry season in August of 2007 and 2008, and during the main wet season in April 2009.
Key results and conclusions – The water column of Lake Kyaninga is permanently stratified (meromictic) below ~ 100 m depth. Above this depth, mixing frequency varies from daily (down to 8–12 m depth) over at least once per year (down to 39–47 m depth), to once in several years or decades (between 39–47 and ~ 100 m depth). Nutrient and chlorophyll concentrations as well as phytoplankton data classify the lake as low in aquatic productivity (oligotrophic). Its pelagic, open-water phytoplankton community is dominated by Cyanobacteria (blue-green algae) and Chlorophyta (green algae). Bacillariophyta (diatoms) contribute only a minor part of total phytoplankton biomass in both wet and dry seasons, and are characterized by an assemblage of small *Nitzschia* species. Epiphytic and epipelic diatoms are relatively few, because steep rocky crater slopes limit the littoral zone even though water-column transparency is high. The composition of recently deposited diatom assemblages preserved in offshore surface sediments gives a good, annually integrated representation of the present-day pelagic diatom community. The documented species richness of the diatom flora of Lake Kyaninga is moderate with about 150 taxa. Only ~ 17% of these are biogeographically restricted to tropical Africa; and most of these belong to the genus *Nitzschia*.

Keywords – Africa, crater lakes, diatoms, lake dynamics, phytoplankton, Uganda.

INTRODUCTION

Lake Kyaninga (00°41.85'N 30°17.86'E) is a relatively large (24 ha) and very deep (> 220 m) maar crater lake situated at 1530 m above sea level on the shoulder of the Edward-George extension of the western branch of the East African Rift System, in western Uganda. The local equatorial climate is tropical sub-humid (Fort Portal mean annual rainfall 1903–1980 = 1484 mm) with little seasonal variation in monthly temperature (T_{min}: 11.7–13.7°C; T_{max}: 24.5–26.8°C), and two wet seasons (March–May and late August to November) and two drier seasons (December–February and June to mid-August; fig. 1) associated with the twice-annual migration of the Intertropical Convergence Zone (ITCZ) over the area. The crater catchment of 42 ha is enclosed by a crater rim reaching up to 77 m above the present-day lake surface. The lake consists of a deep northern basin (> 220 m) and a shallower southern basin (58 m), both with mostly very steep sloping shores. Lake Kyaninga is one of 48 fresh crater lakes in western Uganda studied in the framework of the comprehensive research programme CLANIMAE (Climatic and Anthropogenic Impacts on African Ecosystems), which investigates the relationship between the limnological environment of these crater lakes and their vulnerability to water-quality loss caused by anthropogenic disturbance of their catchment vegetation and soils. Study lakes were selected along gradients

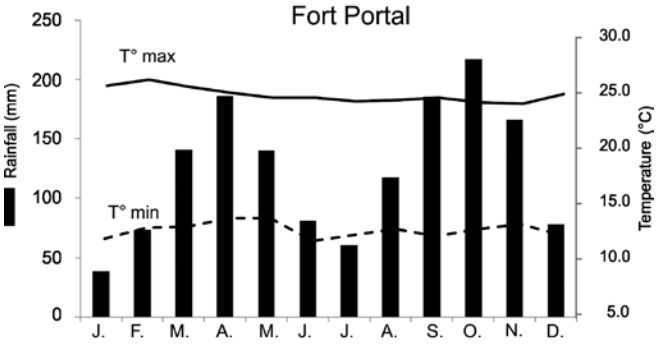

Figure 1 – Monthly rainfall (mm), and monthly average maximum (daytime) and minimum (nighttime) air temperature at Fort Portal, 7 km south of Lake Kyaninga.

from low to high primary productivity (oligotrophic to hypertrophic) and from virtually non-existent to intense human activity within their crater catchments. One aim is to develop a multivariate statistical transfer function for reconstruction of past changes in lake productivity based on the species composition of fossil diatom assemblages preserved in the bottom sediments of African lakes. Lake Kyaninga is among a subset of study sites where besides the diatom flora the entire phytoplankton community was examined during both dry and wet seasons, and where a direct comparison was made between the present-day diatom flora and its representation in recently deposited diatom assemblages preserved in the lake's sedimentary record.

MATERIAL AND METHODS

Physical and chemical limnology

Lake Kyaninga was visited three times between August 2007 and April 2009 to measure depth profiles of temperature (T in °C), pH, dissolved oxygen (DO in mg/l) and conductivity (K, specific conductivity in µS/cm at 25°C) through the water column. Measurements were obtained either continuously (with a Seabird®19 CTD profiler in August 2007 and April 2009), or at discrete 1-meter intervals (with a Hydrolab Quanta® multi-sensor probe in August 2008). Inter-calibration had previously shown the results from these instruments to be fully interchangeable. When DO content is low (< 0.5 mg/l), the DO sensors on both instruments may take ~ 10' to achieve the correct value even when providing continuous flow with a built-in propeller. Therefore, values dropping below 0.5 mg/l were assumed to reflect anoxic (0.0 mg/l) conditions. On 2 Aug. 2007 we installed a series of Vemco® automatic loggers to record temperature at 3, 15, 30 and 57 m water depth at 2h intervals, and from these data we derive the timing of deep seasonal mixing. The depth of daily, seasonal, and low-frequency water-column mixing was estimated from the mid-point of prominent inflections common to the vertical profiles of T, pH, K and DO.

Water transparency (SD, in cm) was measured with a standard white Secchi disc of 20 cm diameter. The depth of the euphotic zone (Z_{eu}, where light is 1% of that just below the water surface) was estimated as 1.9 times SD (Vollenweider 1974). We estimated water-column stability using the potential energy anomaly (PEA) for fresh water according to Simpson et al. (1982). The probability of nutrient-rich hypolimnetic water re-circulating to the surface is increased when PEA is low. The total stability of the lower water column is enhanced by the density increase due to accumulation of dissolved salts (K= 1585 µS/cm at 200 m), but unknown details of deep-water chemistry do not allow to quantify this additional chemical stability at this time.

For water sampling at depth we used a Hydrobios® Niskin-type bottle of 2 l volume. Water samples were kept cool (4°C) in the field, and nutrients were analysed the same day using a Hach Lange DR2800 spectrophotometer. Total phosphorus (TP, in mg/l) and total nitrogen (TN, in mg/l) concentrations were determined using quartz-cuvette tests following hydrolysis. Dissolved silica (Si, in mg/l) was analysed upon return to Belgium, using inductively-coupled plasma atomic emission spectrometry. Chlorophyll *a* (Chl *a*, in µg/l) concentrations were measured at the surface and at 10, 25 and 160 m depth. For this purpose between 400 and 700 ml of water was filtered using a Nalgene filtration unit and GF5 Macherey Nagel glass fiber filters of 45 mm diameter. The filter was extracted by placing it for 24 hours in a tube containing 5 ml of 90% acetone, at 4°C. The extracted solution was filtered using a syringe with encapsulated filter into a 5-cm spectrophotometric cell. The Chl *a* concentration was calculated from the absorption value at 665 nm with a DRELL 2800 spectrophotometer after zeroing with pure acetone.

Phytoplankton

The present-day living algal community of Lake Kyaninga was sampled by filling a 50 ml bottle, and fixed in situ with an alkaline lugol solution and formalin. These samples were analyzed quantitatively (excluding the picophytoplankton) following Uthermöhl (1931) using an Olympus CKX41 inverted microscope equipped with an Olympus Color View digital camera. We studied six quantitative phytoplankton samples: mid-lake pelagic phytoplankton from near the water surface collected on 2 Aug. 2007 and 18 Aug. 2008, and from near the water surface, 10 and 25 m water depth collected on 15 Apr. 2009; and a near-shore open-water phytoplankton sample also collected on 15 Apr. 2009. Additionally four samples for semi-qualitative diatom analyses (counts and identifications) were collected. Two are pelagic phytoplankton samples from a mid-lake location, collected with a phytoplankton net (mesh 10 µm) on 2 Aug. 2007 and 15 Apr. 2009. The others are a littoral epiphyton sample from submerged *Phragmites mauritianus* Kunth stems, and an epipelon sample scraped from submerged rocks, both collected on 15 Apr. 2009.

The time-integrated diatom assemblage preserved in recently deposited bottom sediments was analyzed in the 0–1, 1–3 and 3–5 cm intervals of two UWITEC gravity cores recovered on 10 Jan. 2007. Both cores were taken in the shallower southern basin, KYANINGA-07-1G at 58 m depth in the deepest part of this basin and KYANINGA-07-2G near the southern shore at 5 m depth; the cores were extruded upright in watertight plastic bags using a fixed-interval sectioning device (Verschuren 1993). The sediment samples were oxidized with peroxide to remove organic material, and embedded in Naphrax® to obtain permanent microscope slides.

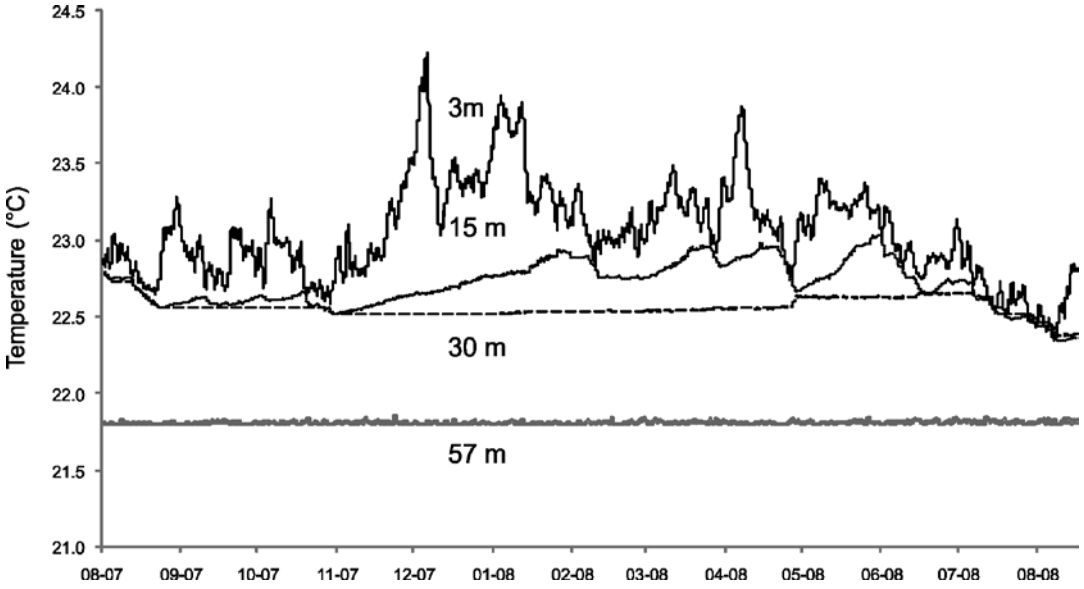

Figure 2 – Temperature measured by 4 temperature loggers every two hours from 2 Aug. 2007 to 18 Aug. 2008 at four depths (3m, 15 m, 30 m and 57 m) in the water column in the south basin of Lake Kyaninga.

Samples and permanent slides are kept at the herbarium of the National Botanic Garden of Belgium (BR). Identification of diatom taxa was performed using an Olympus BX 51 light microscope equipped with differential interference contrast at a magnification of 1000× and an Olympus Color View digital camera. For some problematic taxa, a small fraction of the oxidized suspension was gold-coated with a sputter coater SCD 020 and studied with a JEOL 5800 scanning electron microscope (SEM) operating at 25 KV. Identification of the phytoplankton taxa was done with reference to Compère (1974, 1976), Huber-Pestalozzi (1941, 1955), Huber-Pestalozzi & Fott (1968), Komárek (2008), Komárek & Fott (1983), Komárek & Anagnostidis (1999, 2005), Komárek & Jankovska (2001), Popovský & Pfiester (1990), Starmach (1985), Van Meel (1954) and other works. For diatoms we also referred to Cholnoky (1960, 1964, 1968, 1970a, 1970b), Cocquyt (1998, 2007), Gasse (1986), Hustedt (1949) and Müller (1905). The relative abundance of diatom taxa is expressed in percentages relative to total counts of 500 valves. Statistical data analysis, e.g. Pearson correlation coefficients on relative species abundances, was done using STATISTICA 6.0 software.

RESULTS

Water-column stratification and mixing

The water column of Lake Kyaninga displays both thermal and chemical density stratification (figs 2–4), and the typical multiple–thermocline structure of tropical lakes which reflects the decreasing frequency of water-column mixing with depth (Lewis 1983, 1987). Daytime temperature stratification due to solar heating of the water surface under wind-calm conditions was typically limited to the uppermost 2–4 m (fig. 3A), and very often followed by mixing due to wind-driven evaporative cooling and/or nighttime surface cooling followed by convection (fig. 2). The more or less daily cycle of this surface stratification and de-stratification typically extends to between 9 and 12 m water depth, as can be deduced from the near-constant pH values over at least this depth range on 18 Aug. 2008 and 15 Apr. 2009 (fig. 3D). This frequently mixed uppermost part of the water column is bounded below by a first and principal thermocline (fig. 3A), below which temperature varies only on longer time scales (fig. 2; 15 m). Physical separation of this uppermost water column (epilimnion) from deeper water is indicated by the notably reduced conductivity values in the uppermost 12 m on 15 Apr. 2009 (fig. 3B: 436 µS/cm vs. ~ 460 µS/cm deeper down). This lower surface conductivity is due to dilution of the epilimnion following significant rainfall over the crater catchment in the days (or less likely, weeks) before the profiling. Frequent complete mixing of the epilimnion also maintains high (> 5 mg/l) and often near-constant DO concentrations over this interval (fig. 3C). The DO profile of 15 Apr. 2009 displays a strong subsurface maximum between 9 and 12 m depth, suggesting elevated photosynthetic activity in that zone. This positive heterograde profile (Kalff 2002) may be related to the high water-column transparency on 15 Apr. 2009 compared with that in August of 2007 and 2008 (table 1: SD = 605 cm vs. 390–470 cm), causing the euphotic zone to extend to about 11.5 m rather than 7.4–8.9 m and allowing a sub-surface maximum in photosynthetic activity.

In the course of the annual cycle between August 2007 and August 2008, sustained warming of the epilimnion of Lake Kyaninga occurred only during a ~ two-month period from mid-November to mid-January, i.e. largely coincident with the dry season of December-January. Even then warming was limited to a modest 1.0–1.5°C (fig. 2) with peak surface temperature of 24.3°C reached in early December. Over this period also water below the principal thermocline warmed up gradually, by ~ 0.3°C at 15 m depth (fig. 2). From mid-January, surface cooling followed by convective and/or wind-driven mixing started to gradually erode the principal thermocline until around 10 February it was temporarily annihilated and deeper mixing cooled the upper water column

Table 1 – Limnological data at various depth (m).
Water temperature, pH, conductivity (K_{25}), dissolved oxygen (DO), anoxic depth, potential energy anomaly (P.E.A.), total phosphorous (TP), total nitrogen (TN), silica ($Si0_2$ as Si), alkalinity (as $CaCO_3$), chlorophyll a and Secchi disk transparency at Lake Kyaninga at three periods (< DL = below detection limit).

			2 Aug. 2007	18 Aug. 2008	15 Apr. 2009
temperature	° C	surface	23.10	22.40	24.25
		25 m	22.80	22.30	22.45
		160 m	-	-	21.00
pH		surface	8.20	7.99	8.50
		25 m	8.10	7.74	7.80
		160 m	-	-	6.00
K25	µS/cm	surface	429	462	436
		25 m	429	460	459
		160 m	-	-	1394
DO	mg/l	surface	5.10	6.30	9.10
		25 m	4.70	2.80	0.00
		160 m	-	-	0.00
anoxic depth	m		38	46	25
P.E.A.	J m^{-3}		0.102	0.217	0.835
TP	mg/l	surface	0.07	0.02	< DL
		160 m	-	0.50	0.58
TN	mg/l	surface	-	0.27	0.07
		160 m	-	1.03	1.74
SiO_2	mg/l	surface	12.90	15.60	14.02
		160 m	-	27.89	25.63
alkalinity	mg/l	surface	-	-	220
		10 m	-	236	223
		25 m	-	-	230
		160 m	-	748	753
Chl a	µg/l		5.24	9.27	3.49
Secchi depth	cm		470	390	605

to below 15 m depth (fig. 2). Similar cycles of epilimnetic stratification and de-stratification, and of gradual warming and abrupt cooling below the depth of the principal thermocline, were repeated through the main wet season from March to May. One particularly prominent but short-lived surface-cooling event to 22.7°C at the end of April even caused mixing to below 30 m, but stratification was restored soon after. After mid-June only weak stratification developed, such that when in mid-July, i.e. during peak dry season, the water-surface temperature consistently dropped below 22.6°C, a period of near-continuous deep mixing ensued. Ending on 10 August, this deep mixing set the water-column temperature at 30 m (and at 15 m) depth to 22.3°C, ~ 0.2 °C below its lowest value in the previous 12 months. However, this is still 0.5°C above the constant temperature of 21.8°C at 57 m depth. Our temperature-logger data show no evidence that Lake Kyaninga ever mixed to the bottom of the south basin between 2 Aug. 2007 and 18 Aug. 2008.

The temperature-logger data provide the context which helps to interpret the profiles of temperature and other physical variables measured at the start and end of the logging period, and in April 2009. With the exception of modest temperature stratification at the surface (fig. 3A), values for temperature, DO and pH on 2 Aug. 2007 are homogeneous down to ~ 35 m water depth; for temperature we note the identical value of 22.8°C at 15 and 30 m (fig. 2). This suggests that shortly before logging started an event of deep seasonal mixing occurred, which injected fresh oxygen to a depth of 37 m and created a distinct deep thermocline at 39 m (fig. 3A). Similarly, sustained deep mixing during the July-August 2008 dry season extended to at least 47 m (fig. 3A & C), but by 18 Aug. 2008 a new principal (seasonal) thermocline (and oxycline) had already formed around 9 m depth. The 0.5°C higher temperature of the water column from immediately above the deep (annual) thermocline in August 2007 compared to August 2008 suggests that the July–August dry season of 2007 was warmer, or less windy, than the 2008 dry season. This inference can also be drawn from the observation that water above the deep thermocline in August 2008 has higher conductivity and lower pH, i.e. more similar to values in the lower water column, consistent with the notion that 2008 mixing has entrained water from greater depths. This is confirmed by the greater depth of the deep thermocline in August 2008 (47 m), compared with August 2007 (39 m). The conductivity and pH of this mid-depth water column remained quite stable between August 2008 and April 2009.

During the rain-season profiling in April 2009, three thermoclines occurred within the upper water column of Lake Kyaninga (fig. 3A): one around 45 m that formed following the deepest mixing of the most recent dry season, a modest secondary thermocline at 21 m, and the principal thermocline at 12 m depth that separates the epilimnion from the deeper water column. Comparable to evidence for intermittent mixing in the logger data of the previous year, the secondary thermocline likely represents one or more occasional events of deeper mixing which occurred earlier during the March-to-May rain season, or at least after the main mixing phase of the previous dry season. Their effect on DO concentration within this depth zone is evident in fig. 3C. Below 20 m the water column was anoxic, because its supplies had not been replenished for up to eight months and had by then been exhausted by bacterial respiration. The DO gradient between 20 and 12 m is created by the shifting balance between the rate of oxygen consumption in the lower water column and the frequency of oxygen replenishment by down-welling of epilimnetic water.

The variable thermal structure of the upper 40 m of the Lake Kyaninga water column during our three surveys (fig. 3A) is translated in strikingly variable PEA values: upper-water thermal stability was four times stronger during the rain-season survey in April 2009 than in August 2008 and eight times stronger than in August 2007 (table 1).

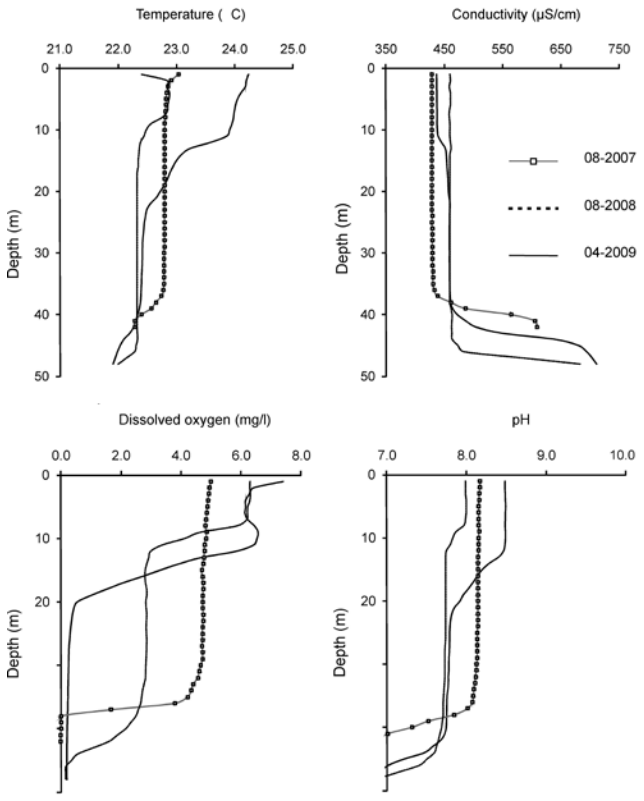

Figure 3 – Upper water-column (0 to 50 m) profiles of: A, temperature (°C); B, specific conductivity (µS/cm); C, dissolved oxygen (mg/l); D, pH. Measurements were made on 2 Aug. 2007, 18 Aug. 2008 and 15 Apr. 2009 at Lake Kyaninga.

During all three surveys a sharp increase in conductivity, from ~ 450 to 750 µS/cm, was observed between 40 and 47 m depth. Water temperature below this level drops below 22°C (see also fig. 2) and decreases further to a minimum of 20.8°C near 120 m depth (fig. 4). Below 75 m also conductivity further increases with depth, to cross 1000 µS/cm at ~ 120 m, reach a stable level of 1400 µS/cm between 160 and 185 m, and then rise again to ~ 1600 µS/cm at 200 m depth. Successful mixing of this deep water column requires downwelling water to overcome both the greater density due to low temperature (at 120 m, ~ 1.5°C below the present-day annual minimum of 22.3°C) and the greater density due to the higher concentration of dissolved substances. For example, the alkalinity of water at 160 m is 3.4 times higher than at the surface (table 1). Based on the entire temperature profile from the deep northern basin (fig. 4) we surmise that such very deep mixing occurs occasionally down to ~ 80 m (reflected in a modest thermocline at that depth), exceptionally even down to ~ 100 m. The recurrence frequency of these very deep mixing events is hard to estimate. Considering that the total density difference (i.e. due to both temperature and dissolved substances) between 40 and 80 m depth is equivalent to a reduction in surface-water temperature of ~ 3.0°C below the present-day annual minimum, we surmise that the frequency of such very deep mixing events is on the order of decades or even centuries, rather than years. It is certainly not a regular annual phenomenon, as testified by the strong H_2S smell of water brought up from below 50 m. Based on our observations we thus conclude that the water column of Lake Kyaninga is probably meromictic (permanently stratified) below ~ 100 m depth, oligomictic (mixing infrequently) down to 80–100 m, and mixing at least once each year down to between 39 and 47 m. Our logger data indicate that deepest mixing occurs during the main dry season of June to early August (fig. 1), and that intermittent deep mixing also punctuates the wet seasons of March to May and late August to November. During our year of observation, most pronounced lake-surface heating and stratification of the upper water column occurred during the dry season of December to February, notwithstanding low seasonal insolation and the lowest monthly day- and nighttime air temperatures (fig. 1).

Below 140 m water depth we measured a slight temperature increase, to a stable value of 21.0°C at 160–190 m and 21.2°C at 200 m. Corresponding with changes in conductivity and pH (fig. 4), this elevated near-bottom temperature is probably due to geothermally heated groundwater inflow into the lake. Geothermal activity has been reported to exist in the region, as close as 12 km from Lake Kyaninga (Bahati et al. 2005). Formation of bubbles upon recovery of water from 160 m is a probable consequence of its high dissolved CO_2 content. Echo-sounding of the lake's bathymetry also showed plumes of bubbles rising to the surface.

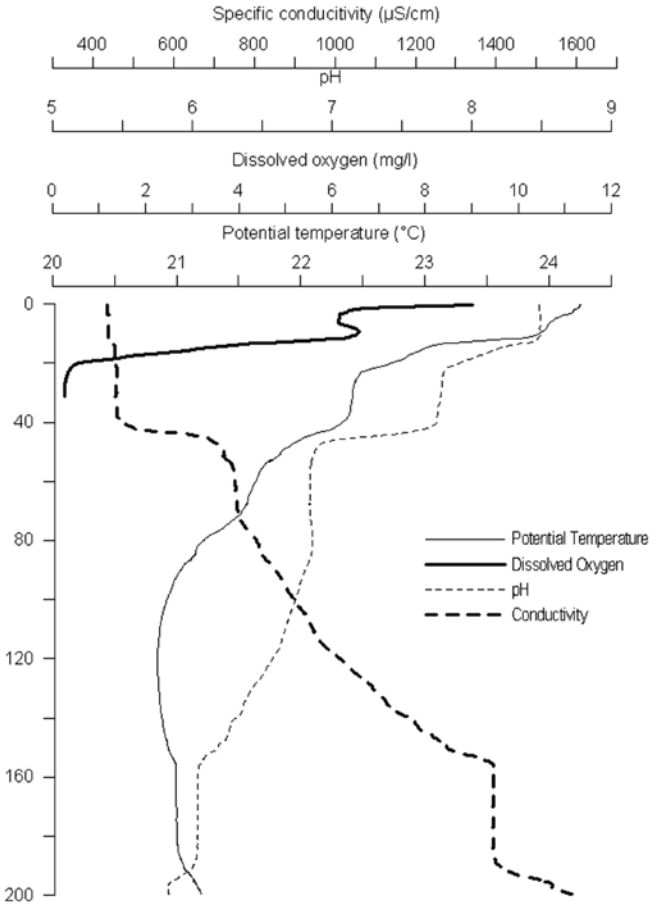

Figure 4 – Profiles (0 to 200 m) of temperature (°C), dissolved oxygen (mg/l), pH and specific conductivity (µS/cm) on 15 Apr. 2009 in the deep basin of Lake Kyaninga.

Table 2 – Phytoplankton abundance.
Expressed in cells/ml and in biomass (µg/l) from 3 differences depths (0, 10 and 25 m) on 15 Apr. 2009 at Lake Kyaninga, as derived from cell counts and biovolume calculations.

	cells/ml			biomass (µg/l)		
depth	0 m	10 m	25 m	0 m	10 m	25 m
Cyanobacteria	10000	11000	48000	8.22	1.125	2.07
Chlorophyta	700	800	2000	2.35	0.72	1.72
Euglenophyta	20	0	0	0.03	0	0
Dinophyta	70	0	0	1.03	0	0
Chrysophyta + Cryptophyta	30	0	300	0.12	0	0.47
Diatoms	50	20	0	0.24	0.15	0

Nutrient data show high TP, TN and Si values in the hypolimnion (table 1), consistent with their long-term accumulation in a stratified water column. The molar TP:TN ratio of the surface water (12.1) is slightly below the Redfield TP:TN ratio of 16 for phytoplankton (Redfield 1958, Teubner & Dokulil 2002), suggesting that algal productivity in Lake Kyaninga is limited by a shortage of nitrogen. Surface-water SiO_2 concentrations do not differ much between mixing and stratified seasons, and molar ratios TP:Si (0.001 to 0.005) and TN:Si (0.01 to 0.03) indicate no limitation of silica for diatom growth (Roberts et al. 2003).

Temporal variation in phytoplankton composition

Chlorophyll *a* measurements indicate that phytoplankton biomass in surface waters of Lake Kyaninga was low (3.49 µg/l) during the rain season in April 2009 and higher during the dry season of 2007 (5.24 µg/l) and particularly 2008 (9.27 µg/l). This is consistent with variation in water-column transparency being inversely proportional to Chl *a* values, and with the surface-water TN and TP concentrations, which are also lowest in April 2009 (table 1). Low algal productivity in April 2009 can be attributed to a shortage of essential nutrients due to their inefficient recycling from algae that decompose after sinking out of the stratified upper water column. Productivity was only modestly higher during deep water-column mixing on 2 Aug. 2007, but substantially higher in the period following deep mixing on 18 Aug. 2008. We propose two alternative explanations for this difference. During mixing events algal cells may spend too much time below the photic zone to allow rapid growth, whereas incipient stratification in the weeks following deep mixing (figs 2 & 3A) creates a stable sub-surface environment where algae can optimally benefit from the newly available nutrient supply. To the extent that our two dry-season surveys are representative, an alternative (or additional) reason for the observation of highest productivity in August 2008 may be the deeper mixing which occurred that year compared to the year before, and hence a greater supply of recycled nutrients being provided.

The depth distribution of pelagic phytoplankton in Lake Kyaninga was quantified only in April 2009, with volumetric cell counts near the surface and at 10 and 25 m water depth (tables 2 & 3). Since 25 m is well below the photic depth at that time (~ 11 m), the high abundance of (mostly small) cyanobacteria at that depth must represent dying cells sinking slowly into the cooler, and thus denser hypolimnion. The by far highest biomass (in µg/l) was observed near the surface; the lowest at 10 m depth. This result argues against the existence of a sub-surface phytoplankton maximum as principal explanation for the heterograde oxygen profile during that time (fig. 3C).

The phytoplankton of Lake Kyaninga is dominated by a Cyanobacteria-Chlorophyta community both in mid-lake and near-shore zones, and at mid-lake both during stratified and mixing seasons (table 3, based on biovolume calculations). Chlorophyta were the most important group during deep annual mixing in 2007, whereas Cyanobacteria dominated during the stratified season in April 2009; a few weeks after deep annual mixing in August 2008 the two groups' percent abun-

Table 3 – Phytoplankton abundance (%).
Relative abundance (%) of the algae groups in the pelagic zone of Lake Kyaninga in August 2007, August 2008 and April 2009, and in the near-shore zone in April 2009, derived from biomass calculations.

Date	2 Aug. 2007	18 Aug. 2008	15 Apr. 2009			
Depth	0 m	0 m	0 m	10 m	25 m	littoral
Cyanobacteria	33.6	30.9	68.7	92.7	48.6	73.7
Chlorophyta	63.7	44.3	19.6	6.0	40.5	18.9
Euglenophyta	0.2	0.0	0.2	0.0	0.0	0.0
Dinophyta	1.5	3.2	8.6	0.0	0.0	2.2
Chrysophyta	0.0	1.1	0.9	0.0	9.6	0.0
Cryptophyta	0.1	0.0	0.0	0.0	1.3	0.5
Diatoms	0.9	20.4	2.0	1.3	0.0	4.0

dance was more similar to each other. Diatoms were a minor component of the phytoplankton community, but contributed 20% to total biovolume in August 2008 when nutrients had just been replenished and the water column had started to stratify. The most important diatom taxa at this time were *Urosolenia* sp., *Nitzschia* spp. and *Cyclotella* spp. (see below). Excluding picocyanobacteria, which are not abundant in our samples, about eighteen taxa of Cyanobacteria were found. The most abundant of these are *Planktolyngbya limnetica* (Lemmerm.) Komárk.-Legn. & Cronberg, *Cylindrospermopsis raciborskii* (Wołosz.) Seenayya & Subbaraju, *Aphanizomenon* sp., *Aphanocapsa* sp. and *Aphanothece* sp. *Merismopedia minima* Beck, *Merismopedia tenuissima* Lemmerm. and *Snowella* cf. *lacustris* (Chodat) Komárk. & Hindák are less abundant, but still significant. The Chlorophyta are represented by about 25 taxa, among which *Tetraedron minimum* (A.Braun) Hansg., *Monoraphidum irregulare* (G.M.Sm.) Komárk.-Legn., *M. komarkovae* Nygaard and *M. circinale* (Nygaard) Nygaard are most abundant, and *Monoraphidium dybowkii* Hindák & Komárk.-Legn., *M. griffithii* (Berk.) Komárk.-Legn., *M. minutum* (Nägeli) Komárk.-Legn., *Chlorella* sp., *Crucigenia tetrapedia* (Kirchn.) W.West & G.S.West, *C. quadrata* C.Morren, *Quadrigula* sp., *Scenedesmus quadricauda* (Turpin) Bréb. and small *Cosmarium* spp. less abundant. The most common Dinophyta, Euglenophyta and Chrysophyta are respectively *Peridinium africanum* Lemmerm., *Euglena pisciformis* var. *minor* Hansg. and *Ochromonas variabilis* Meyer.

Diatoms

In total around 130 diatom taxa were identified in all ten living samples (phytoplankton, periphyton and epipelon) collected in Lake Kyaninga during 2007, 2008 and 2009. Scanning electron microscopic pictures of some of these taxa are given in fig. 5. The percent abundance of the twenty most important taxa, reaching 5% in at least one sample, is listed in table 4. Total diatom species richness in the five surface-sediment samples was about 75 taxa, of which 22 were not observed in the living samples. These additional taxa were all only sporadically observed, except *Sellaphora seminulum* which reaches 33.1% in the 1–3 cm interval of near-shore core 07-2G and *Staurosira construens* which amounts to 19% in the 3–5 cm interval of core 07-1G (table 4), and further *Epithemia sorex* Kutz. (1.6% in the 0–1 cm interval of near-shore core 07-2G) and *Nitzschia mediocris* Hust. (1.4% in the 0–1 cm interval of mid-lake core 07-1G). The diatom species richness of Lake Kyaninga is substantially higher than that found in Lake Kaitabarago, located about 4 km to the west, where in February 2008 only 28 taxa were found in living mid-lake and near-shore phytoplankton samples, and only seventeen taxa were recovered from a comparable volume of surface sediments (Cocquyt & Verschuren 2009).

Of the diatom taxa reported from Lake Kyaninga, only 22 (~ 17%) can be considered to have a tropical-African distribution. Most of these belong to the genus *Nitzschia*: *N. accomodata* Hust., *N. adapta* Hust., *N. bacata* Hust., *N. confinis*, *N. congolensis* Hust., *N. epiphytica* O.Müll., *N. epiphyticoides*, *N. lancettula*, *N. mediocris* Hust., *N. palea* var. *tropica* Hust., *N. spiculum* Hust., *N. tropica* Hust. and *N. vanoyei* Cholnoky. Other Lake Kyaninga taxa with tropical African distribution are *Caloneis aequatorialis* Hust., *Encyonema grossestriatum* (O.Müll.) D.G.Mann, *E. geisslerae* Krammer, *E. neomuelleri* Krammer, *Gomphonema affine* Kütz. var. *rhombicum* E.Reichardt, *Navicula zanonii* Hust., *Rhopalodia gracilis* O.Müll., *R. hirudiniformis*, *R. rhopala* (Ehrenb.) Hust. and [S*ellaphora*] *Navicula platycephala* O.Müll. One taxon, *Navicula zanonii*, has a broader distribution and is also reported from the temperate southern part of the African continent.

The fossil diatom assemblage preserved in recently deposited surface sediments showed reasonably high similarity in three successive depth horizons (0–1 cm, 1–3 cm and 3–5 cm) of deepwater core 07-1G and in two successive horizons (0–1 cm and 1–3 cm) of near-shore core 07-2G (table 5). In the deepwater core this annually integrated community is dominated by *Achnanthidium microcephalum*, *Cyclotella stelligera*, *Nitzschia epiphyticoides*, *N. fonticola* sensu Hustedt, *N. frustulum* and *Pseudostaurosira brevistriata* (table 4). Significant correlation can also be reported between the surface-sediment assemblages at mid-lake and near-shore localities, except for the somewhat deviating 1–3 cm layer of the mid-lake core (table 5).

The diatom assemblage in the uppermost sediment horizon (0–1cm) has a strongly significant similarity with the pelagic living diatom communities collected both in mid-lake and near-shore zones during both the 2007 dry season and the 2009 wet season; similarity is highest with the 2009 wet season community. The six taxa that dominate the sediment samples also rank among the diatom species most abundantly found in the living pelagic phytoplankton. However two common local taxa that are conspicuously missing in the surface-sediment assemblages are *Amphora pediculus* and *Urosolenia* sp. The latter species has very thin valves, dissolving rapidly in the water column. Also notable is that the surface-sediment assemblages at the near-shore locality do not show more affinity with living near-shore, epiphyton and epipelon samples than surface-sediment assemblages at the mid-lake locality. This can be attributed to the limited development of true littoral habitat, and the overall scarcity of epiphytic and epipelic substrate on an areal basis, in this steep-sided crater lake rather than to spatial integration of distinct near-shore and mid-lake diatom communities prior to burial. Not surprisingly, a significant positive correlation also exists between the species composition of epiphyton and epipelon diatom samples and all planktonic samples, with exception of the mid-lake sample of the dry season in 2007. This correlation is highest with the April 2009 wet season sample.

DISCUSSION

Deep seasonal mixing in tropical freshwater lakes occurs when a temporarily favourable combination of relatively low daytime insolation, wind-driven turbulence and evaporative heat loss break down the temperature-related density stratification of the water column (Talling 1969). The deepest annual water-column mixing typically occurs when surface-water temperature is lowest, but given limited seasonal variation in solar insolation (386–439 W/m^2, resp. in June and March; Berger & Loutre 1991) at the Equator, lowest surface-water temperature does not necessarily coincide with the seasonal insolation minimum or lowest near-surface air temperatures.

Table 4 – Relative abundances (%) of the most important diatom taxa, i.e. taxa representing > 5% in at least one sample, across all samples studied.

	living community							surface sediments				
	pelagic 2007	pelagic 2009	pelagic 2009	near-shore 2007	epiphyton (1) 2009	epiphyton (2) 2009	epipleon 2009	0–1cm (1G)	1–3cm (1G)	3–5cm (1G)	0–1cm (2G)	1–3cm (2G)
Achnanthidium exiguum (Grunow) Czarnecki	0.4	0.5	1.0	0.8	0.4	7.1	4.3	0.0	0.0	0.0	0.0	0.0
Achnanthidium microcephalum Kütz.	0.4	3.9	4.2	4.9	3.3	1.0	2.9	13.0	30.2	3.1	0.2	0.2
Amphora pediculus (Kütz.) Grunow	0.0	5.4	8.8	2.9	26.6	27.7	10.6	0.0	0.0	0.4	0.0	0.4
Cyclotella stelligera Cleve & Grunow	11.3	5.9	5.3	1.2	0.2	1.8	3.5	15.1	32.5	12.0	0.0	0.0
Eolimnia minima (Grunow) Lange-Bert.	0.0	0.5	0.6	0.2	0.0	0.6	3.1	2.5	0.0	0.6	6.5	4.4
Epithemia adnata (Kütz.) Breb.	0.8	1.6	1.9	2.1	9.5	1.4	0.2	0.0	0.8	1.4	0.0	0.0
Navicula seminuloides Hust.	0.0	0.5	0.6	0.2	0.0	0.6	3.1	2.5	0.0	0.6	6.5	4.4
Navicula cryptotenella Lange-Bert.	0.4	0.0	0.2	0.6	0.4	6.7	2.9	0.0	0.0	0.2	0.6	0.0
Nitzschia confinis Hust.	5.9	1.6	1.7	0.4	0.0	2.2	1.0	1.5	11.0	0.2	1.6	0.0
Nitzschia epiphyticoides Hust.	0.0	4.7	1.0	8.8	5.5	8.8	3.9	8.5	2.4	2.3	12.4	0.0
Nitzschia fonticola Grunow sensu Hustedt	60.9	13.7	9.9	3.5	7.9	9.2	6.5	13.2	0.0	1.2	14.8	7.6
Nitzschia frustulum (Kütz.) Grunow	0.8	15.2	21.1	4.9	9.5	8.1	16.2	10.1	0.0	19.0	16.9	17.3
Nitzschia lancettula Hust.	0.8	3.4	3.0	5.7	0.5	0.8	3.7	0.6	1.8	0.6	2.2	1.7
Placoneis gastrum (Ehrenb.) Mereschk.	0.0	1.3	1.5	9.2	1.1	1.6	0.8	0.0	0.2	0.0	0.0	0.2
Pseudostaurosira brevistriata (Grunow) D.M.Williams & Round	4.7	5.4	4.0	4.9	0.0	0.4	4.1	14.7	7.7	19.5	22.4	20.1
Rhopalodia gibberula var. *vanheurckii* O.Müll.	0.0	0.5	0.6	3.7	6.0	2.8	7.4	0.6	0.0	1.0	2.4	0.0
Rhopalodia hirudiniformis O.Müll.	0.8	1.0	0.8	2.5	8.2	0.4	0.6	0.0	0.0	0.0	0.0	0.0
Sellaphora seminulum (Grunow) D.G.Mann	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	33.1
Staurosira construens (Ehrenb.) Grunow	4.3	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	19.0	0.0	1.7
Urosolenia sp.	1.2	12.7	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subtotal	92.7	77.8	77.5	57.7	79.1	81.2	74.8	82.3	87.8	81.1	86.5	91.1

Table 5 – Pearson correlation coefficients between the % species compositions of diverse diatom samples from Lake Kyaninga.
Samples are from the living diatom community sampled in 2007 and 2009, and from recently deposited sediments in mid-lake (core KYANINGA-07-1G) and near-shore (core KYANINGA-07-2G) locations of the southern basin. Significant correlations are given in bold ($p < 0.001$).

		living community						surface-sediment assemblage				
		pelagic 2007	pelagic 2009	pelagic 2009	near-shore 2007	epiphyton 2009 (1)	epiphyton 2009 (2)	epipelon 2009	0–1cm (1G)	1–3cm (1G)	3–5cm (1G)	0–1cm (2G)	1–3cm (2G)
living community	pelagic 2007	1.00	**0.56**	**0.40**	0.19	0.22	0.27	0.28	**0.52**	0.15	0.16	**0.47**	0.19
	pelagic 2009		1.00	**0.90**	**0.50**	**0.47**	**0.48**	**0.69**	**0.67**	0.27	**0.49**	**0.64**	**0.37**
	pelagic 2009			1.00	**0.46**	**0.58**	**0.57**	**0.83**	**0.61**	0.24	**0.57**	**0.63**	**0.41**
	near-shore 2007				1.00	**0.46**	**0.40**	**0.54**	**0.49**	0.24	**0.35**	**0.44**	0.23
	epiphyton 2009 (1)					1.00	**0.87**	**0.69**	0.23	0.04	0.16	0.24	0.12
	epiphyton 2009 (2)						1.00	**0.72**	0.27	0.05	0.15	0.27	0.12
	epipelon 2009							1.00	**0.53**	0.18	**0.49**	**0.60**	**0.36**
surface-sediment assemblage	0–1cm (1G)								1.00	**0.69**	**0.65**	**0.71**	**0.40**
	1–3cm (1G)									1.00	**0.36**	0.10	0.07
	3–5 cm (1G)										1.00	**0.64**	**0.47**
	0–1 cm (2G)											1.00	**0.58**
	1–3 cm (2G)												1.00

Rather more important is the annual timing of weather systems moving across the region that cause sustained strong winds, from a direction allowing a long fetch across the lake surface. In East Africa this timing is mostly controlled by the twice-annual migration of the ITCZ to north and south of the Equator, and associated east-west movement of the Congo Air Boundary, the zone of surface air convergence separating Atlantic monsoon (and Congo Basin) influences from Indian Ocean monsoon influences. As a result, in our Fort Portal study region of south-western Uganda the highest monthly day-time (T_{max}) and nighttime (T_{min}) air temperatures (fig. 1) coincide only broadly with the insolation maximum in February–March, and the lowest monthly T_{max} and T_{min} values occur during a secondary insolation minimum in December–January instead of the primary insolation minimum in June (fig. 1). In the year of our continuous temperature monitoring at Lake Kyaninga and most probably also the year before, deepest water-column mixing (to 39–47 m depth) occurred in late July and early August, i.e. during the principal dry season and around the end of the primary insolation minimum. Strikingly, temperature stratification of the water column was strongest during the other dry season, even though this broadly coincides with the secondary insolation minimum. Further, the only other mixing events extending beyond 30 m depth occurred in late October and late April, i.e. in the middle of the two wet seasons. Our present data thus indicate that seasonal variation in the physical limnology of Lake Kyaninga is only modestly tied into the annual succession of climate variables such as air temperature and rainfall; and hence that significant inter-annual variability can be expected to occur in the timing of water-column stratification, mixing, and nutrient supply to the phytoplankton community.

Based on Chl *a* data, Lake Kyaninga had a lower phytoplankton biomass during the rain season of 2009 than during the northern summer dry seasons of 2007 and 2008, as can be expected when algal productivity mainly depends on nutrients regenerated from the hypolimnion during deep-mixing events. Still, phytoplankton biomass measured on 15 Apr. 2009 may have benefited from a secondary event of deep mixing in the weeks before our visit, such as occurred on at least one occasion during the rain season of 2008 (fig. 2). More frequent rain-season measurements of aquatic productivity are clearly needed to obtain a representative value, and from it determine Lake Kyaninga's mean trophic status.

We explained the elevated DO concentration at 10–12 m depth on 15 Apr. 2009 as reflecting an active phytoplankton community deeper in the water column, favoured by the increased transparency associated with limited algal production near the surface. In such circumstances the phytoplankton prefers to reside in sub-surface water to avoid the damaging UV radiation which penetrates relatively deep into the surface water. However the low algal biomass at 10 m depth indicates instead that the heterograde profile may have resulted because very low photosynthetic activity during peak stratification failed to compensate for oxygen consumption by zooplankton and fish concentrated in the 3–8 m depth range.

The marked difference in phytoplankton community between dry and rain seasons and the pronounced accumulation of nutrients below the thermocline during stratification adds to our arguments above that the productivity of Lake Kya-

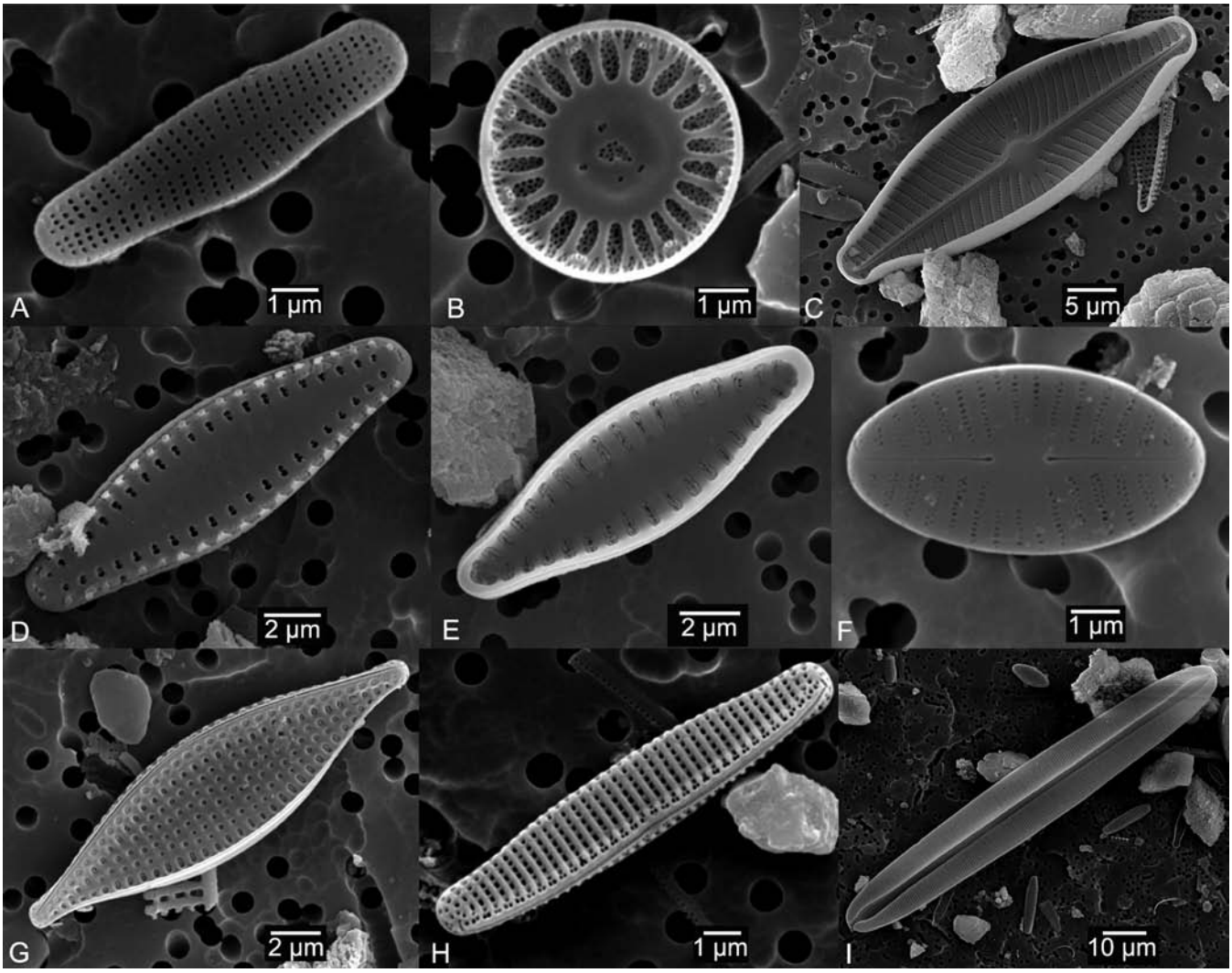

Figure 5 – Scanning electron microscopic photographs of diatom taxa: A, *Achnanthidium microcephalum*; B, *Cyclotella stelligera*; C, *Placoneis gastrum*; D–E, *Pseudostaurosira brevistriata*, external and internal valve view; F, *Navicula seminuloides*; G, *Nitzschia lancettula*; H, *Nitzschia epiphyticoides*; I, *Rhopalodia gracilis*.

ninga must be highly sensitive to variations in the timing and depth of seasonal mixing as controlled by inter-annual climate variability. Slight changes in air temperature and winds may cause significant thermic stability changes allowing variable quantities of hypolimnion water to reach the surface and influence rates of photosynthesis. Though the lake is meromictic, a great part of its lower water column can mix at rare occasions depending of specific climate conditions. Whether seasonal mixing extends to the typical depth of between 39 and 47 m (affecting a hypolimnetic volume of ~ 0.2 km^2 × 27–35 m = ~ 5.4–7.0 × 10^6 m^3) or the more extreme depth of 80 m (affecting a hypolimnetic volume of ~ 0.2 km^2 × 68 m = ~ 13.4 × 10^6 m^3) implies a 100% difference in nutrient supply.

This low-frequency, extreme deep mixing also brings a large quantity of anoxic water to the surface, potentially lowering DO concentration in Lake Kyaninga epilimnetic waters to below the limit tolerated by fish. As an indication of the frequency of extreme deep mixing events (not necessarily to 80 m depth), local fishermen reported fish kills to occur approximately every five years; the most recent fish kill appears to have taken place in 2006. The local population reports that during those periods a strong 'bubble' emerges from Lake Kyaninga, possibly reflecting ebullition and release of gases (CO_2, CH_4) accumulating in the lower water column. Such events may have importance in avoiding excessive build-up of dissolved gases in the lake. Multiple sites of on-land gas emission are reported to occur in the immediate vicinity of Lake Kyaninga, where dead animals such as birds, otters and python snakes have been found. This could be similar to the 'mazukus' phenomenon in the Nyaragongo area near Lake Kivu, D.R.Congo (Vaselli et al. 2004, Smets et al. 2010) where high concentrations of carbon dioxide are released.

Transparency, Chl *a*, TP and TN values classify Lake Kyaninga as oligotrophic (Forsberg & Ryding 1980, Carlson1977, Wetzel 1983). However, when mixing the lake may temporarily reach the lower mesotrophic level. Our preliminary measurements indicate that N seems to be more limiting to algal growth than P, consistent with Talling's (1966) general observation for tropical-African lakes. More measurements would be needed however to confirm this. The in-

creased biomass and percentual contribution of Cyanobacteria during stratification in April 2009 could be explained by their ability to circumvent N depletion by fixing atmospheric nitrogen.

The algal community of Lake Kyaninga also does not seem to fit one of the functional groups of phytoplankton defined by Reynolds et al. (2002), which "group together species with similar morphological and physiological traits and with similar ecologies" (Reynolds et al. 2002). On the one hand, the presence of *Urosolenia* spp. suggests affinity with functional group A, typical for clear lakes. But the lakes typified by functional group A are slightly acidic and often well-mixed, unlike Kyaninga. *Cyclotella comensis* Grunow, the other typical group A representative, is not observed in Lake Kyaninga but possibly replaced by another small *Cyclotella*, namely *C. stelligera*. This group A has nutrient deficiency tolerance but is sensitive to pH rise. On the other hand the presence of *Synechococcus* spp. points to a relationship with functional group Z, typical for a clear, well-mixed habitat with a tolerance for low nutrients and sensitive to light deficiency and grazing. Thus, the classification of Reynolds et al. (2002) is evidently problematic here, and may not be applicable to African lakes in general. Richardson (1968) proposed a diatom-based typology specifically for East and Central African lakes. This typology does not seem to be applicable here either, since the lake set used to calibrate it does not include any of the crater lakes located in the Edward-George extension of the East African Rift Valley, but only high-elevation in the Ruwenzori Mountains. Lake Kyaninga has a diatom assemblage dominated by small *Nitzschia* species, such as *N. fonticola* sensu Hustedt, *N.* aff. *frustulum* and *N. confinis*. In contrast, *Nitzschia* dominated lakes in Richardson's (1968) classification, such as Lake Tanganyika, are represented by large *Nitzschia* species such as *N. lacustris* Hust. With ~ 130 recorded taxa diatom species diversity in Lake Kyaninga is much higher than in Lake Kaitabarago (Cocquyt & Verschuren 2009), but rather moderate, compared to some other crater lakes in the area (CLANIMAE, unpubl. data). Literature data (e.g. Gasse 1986) on some Ugandan crater lakes typically involve single samples and are therefore not truly comparable. A maximal number of 32 species was reported for lakes Bisina (eastern Uganda) and Mwamba, a crater lake in the Kasenda area south of Fort Portal (treated as 'Rwenzori region' in Gasse, 1986).

The correlations between the composition of the actual planktonic diatom community and the sub-fossil diatom assemblage preserved in offshore surface sediments (upper 5 cm) reveals good representation of the annual pelagic diatom community of Lake Kyaninga in recent years (table 5). The lack of correlation between the 1–3 cm layer and living samples taken in 2007 and in 2009 suggests substantial inter-annual variability in the pelagic diatom community. Although the match between the 2007 and 2009 planktonic samples themselves is significant, the rather low Pearson values further reflect seasonal variability within the diatom community. Indeed, in April 2009 the pelagic diatom community was dominated by *Nitzschia frustulum* (small morphotype), *N. fonticola* sensu Hustedt, *Urosolenia* sp., *Cyclotella stelligera* and *Amphora pediculus* while in August 2007 *Nitzschia fonticola* sensu Hustedt and *Cyclotella stelligera* were the most important taxa. *Pseudostaurosira brevistriata* was co-dominant in both seasons (table 5).

In comparison with Lake Kaitabarago (Cocquyt & Verschuren 2009) the living diatom community of Lake Kyaninga is less well reflected in its surface-sediment assemblages. Where the Pearson's correlation between the percent abundances of living and recently buried taxa exceeded 0.90 in Lake Kaitabarago, for Lake Kyaninga the highest value is 0.67. We suggest that this difference can be explained by the much larger surface area of Lake Kyaninga (24 ha) vs. Kaitabarago (1.8 ha). Although the maximal height of the crater rim (77 m) is greater than for Lake Kaitabarago (46 m), Lake Kyaninga is more exposed to the wind than the strongly sheltered Lake Kaitabarago. By implication, seasonality in the diatom community may also be less pronounced in Lake Kaitabarago, but more research is needed. The small difference between the near-shore and offshore pelagic phytoplankton community of Lake Kyaninga is due to the mostly very steep crater slope below the waterline, causing the littoral euphotic zone to be highly restricted.

In summary, our present data indicate that the deepest known crater lake in western Uganda is permanently stratified below ~100 m depth, and mixes at least once per year to between 39 and 47 m depth when lake-surface temperatures are lowest. Based on our observations deep mixing is most likely to occur in July or early August towards the end of the dry season coinciding with the period of minimum solar insolation. Most strongly pronounced stratification occurs during the other dry season of December–January, despite its coincidence with lowest monthly day- and nighttime air temperatures. Near-daily mixing of the upper water column (epilimnion) extends to 8–12 m depth, and the photic zone to between 7.5 and 11.5 m. This high transparency is due to low phytoplankton biomass and production: nutrient and chlorophyll concentrations as well as phytoplankton composition classify Lake Kyaninga as oligotrophic, except that it may briefly reach mesotrophy after deep mixing has regenerated deep-water nutrient supplies to the surface. Its open-water phytoplankton community is dominated by Cyanobacteria and Chlorophyta. Bacillariophyta (diatoms) contribute only a minor part of total phytoplankton biomass in both wet and dry seasons, and are characterized by an assemblage of *Urosolenia* and small *Nitzschia* species. Steep rocky crater slopes limit the littoral zone even though water-column transparency is high. We report about 130 diatom taxa in the living community and recent surface-sediment assemblages, of which ~ 17% (most of them *Nitzschia* spp.) are biogeographically restricted to tropical Africa.

ACKNOWLEDGMENTS

This study was conducted in the framework of the CLANIMAE (Climatic and Anthropogenic Impacts on African Ecosystems) project SD/BD/03A, financed by the Science and Sustainable Development programme of the Belgian Science Policy (BelSPO). The fieldwork was conducted with permission of the Uganda National Council of Science and Technology (Uganda NCST research clearance NS 162) and the Uganda Wildlife Authority (permit UWA/TBDP/RES/50). The "Fondation pour favoriser la recherche scientifique en

Afrique" funded the field campaign of the first author. The authors are grateful to Johnson Bwambale and Maureen Fagot for field assistance, Myriam de Haan (NBGB) for technical assistance with scanning electron microscopy, Laurence Monin (RMCA) for laboratory assistance, and Harold Hughes and Nourdine Dahkani (RMCA) for dissolved Si determination using ICP-AES.

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Paper based on results presented during the Symposium "Diatom Taxonomy in the 21st Century" (Meise 2009). Manuscript received on 19 Jan. 2010; accepted in revised version 30 Sep. 2010.

Communicating Editor: Bart Van de Vijver.