The Future of Tropical Water Resources: Using Palaeolimnology to Inform Sustainable Management.

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Abstract
Lakes are an important resource. They provide vital ecosystem services and employment for many communities worldwide. Maintaining lakes as ecosystem providers without damaging the lake ecosystems themselves, against a background of increasing human use of landscapes and climate change, requires careful and informed management. Key to such management is an understanding of how lakes will respond to ongoing and future changes in their catchments. Long-term monitoring, through regular measurements of lake chemistry for example, can help provide this understanding but such data are rare, particularly for tropical lakes. Using a palaeolimnological approach can provide an alternative to long term monitoring. This paper compares the information that monitoring data and lake sediment records can bring to an understanding of lake change in western Uganda. Water chemistry data show a general pattern to lakes with higher Chlorophyll-a and TP values over the last 15 years, although not all lakes follow this pattern. Sediment cores from Lakes Kamunzuka and Nyungu both show changes in diatom flora through the latter half of the twentieth century and increases in dry mass accumulation rate between c. 1980 and 2000. This study highlights the importance of a co-ordinated monitoring approach to provide the data needed to benchmark management decisions. The importance of understanding each lake on its own merits, from a monitoring or palaeolimnological perspective is also highlighted. Combined, these approaches provide an approach to inform management decisions to sustain lake ecosystems in a healthy state, for the benefit of all users.
Keywords: Uganda, lakes, water chemistry, sediment cores, diatoms.

1. Introduction

In parts of western Uganda where potable water supplies via groundwater pumps are sparse, clusters of crater lakes supply valuable freshwater resources to rural communities, in addition to providing opportunities for aquaculture, tourism, and wider ecosystem services (Saulnier-Talbot et al., 2014). Like water bodies globally, the lakes are subject to multiple stressors, including the impacts of climate change (e.g. changes in precipitation, increases in temperature) and human activity within the lake and its catchment (e.g. changing land use, introduction of fish) (Ormerod et al., 2010). In western Uganda these stressors are amplified in the context of a growing population alongside low levels of water infrastructure.

Globally, lakes have experienced increased phytoplankton blooms, and therefore a decline in water quality since the 1980s (Ho et al., 2019). There is particular concern over the sensitivity of tropical African lakes to climate change and anthropogenic pressures; climatic warming and enhanced sediment and nutrient flux to lakes has already led to an increased frequency of algal blooms and eutrophication in eastern African lakes in recent decades (Ndebele-Murisa et al., 2010; Odada et al., 2020). This is likely to have significant negative impacts upon livelihoods that are reliant on lakes, such as aquaculture, which is threatened by a reduction in fish abundance and diversity (Ndebele-Murisa et al., 2010) and an increased frequency of fish kill events associated with declining water quality (Odada et al., 2010).

The future water quality of the crater lakes is uncertain. This is due, in part, to the understudied nature of tropical lakes in general, when compared to other regions of the world (Escobar et al., 2020) and the limitations with monitoring of remote systems. As with many other regions of the world, the lack of long-term monitoring of the lakes limits understanding of the drivers and dynamics of water quality in this part of Uganda.

Implementing sustainable management of tropical lakes to ensure their long-term sustainability as a water resource and critical ecosystem service is important in the delivery of UN Sustainable Development Goals (SDGs) 6 (clean water and sanitation), 13 (climate action), and 2 (zero hunger), which have been identified as priority SDGs requiring action in eastern Africa (Gill et al., 2019). Furthermore, ensuring equitable access to water resources is a key step in achieving gender parity (SDG 5) in sub-Saharan Africa (UN Water, 2006).

In order to inform sustainable management of lake systems, and to predict and mitigate their responses to future stressors, there is a need to understand how lakes respond to different drivers over multiple timescales. Ideally, this would include the use of, for example, continuous water chemistry data collected over a "long" time frame (e.g. pre- and post-impact). However, in many parts of the world, these data do not exist. In the crater lake region of western Uganda water chemistry data have been collected sporadically over the course of the 20^{th} Century. The earliest measurements from the area were that of lake depth and conductivity, taken during the Cambridge Expeditions in 1931 (Beadle, 1932). A number of field campaigns to the region followed in the 1960s, 70s and 90s, and the number of water quality parameters measured increased and included: Secchi depth (an indicator of turbidity), dissolved oxygen, chlorophyll-a (Chl-a), and nutrient (total phosphorus and total nitrogen) concentrations of the lake waters (Beadle, 1932; Talling and Talling, 1965; Kilham, 1971; Melack, 1978; Kizito et al., 1993; Chapman, 1998; Crisman, 2001). In almost all cases, these datasets were collected during the dry season (December-February or June-July) and comprise a single sample, offering only a snapshot in time, and resulting in a patchy and incomplete time series. The collection of lake data and water samples from across the crater lake region has persisted into the 21^{st} Century, with the most recent datasets collected in 2019.

In the absence of long-term water quality monitoring and associated datasets, it is possible to make use of a palaeolimnological approach, to understand long-term changes in the lake systems. Palaeolimnology uses the sediments that accumulate at the bottom of lakes to infer how lakes have changed in the past and the drivers of these changes (Dalton et al., 2009). These natural archives can extend back many hundreds of years (Battarbee, 2000; Birks and Birks, 2006; Fritz, 2008). A number of palaeolimnological studies from the western Uganda crater lake region exist in published literature (Rumes et al., 2005; Ssemmanda et al., 2005; Eggermont et al., 2006; Russell et al., 2007; Bessems et al., 2008; Russell et al., 2009; Rumes et al., 2011; Ryves et al., 2011; Mills and Ryves, 2012; Colombaroli et al., 2014; Gelorini et al., 2014; Mills et al., 2014; Mills et al., 2018) and have been used to understand changes in climate and environment over the last 2,000 years.

This paper presents a collation of water chemistry data collected from crater lakes in Uganda to investigate trends in water quality change over the past two decades. Sediment core records from two lakes which have been subject to contrasting levels of human disturbance are presented in this paper to demonstrate how palaeolimnology can infer long-term changes in water quality. The paper discusses how palaeolimnological records can be used as a benchmark for lake conditions, in the absence of lake monitoring data, and as a tool to inform their sustainable management.

2. Materials and methods

2.1 Study sites

Volcanic crater lakes associated with the East African Rift System (EARS) occur in clusters in the west and southwest of Uganda (Melack, 1978). The lakes are associated with the Toro-Ankole volcanic field and are thought to have formed as a result of volcanic activity (maars or phreatomagmatic craters), possibly as recently as 6,000 years ago (Temple, 1971). The lakes lie within 4 distinct groups: the Kasenda, Fort Portal, Katwe-Kikorongo, and Bunyaruguru clusters (Figure 1). The northern lakes of the Fort Portal and Kasenda clusters are located at high altitude (1520 and 1,220-1,400 m.a.s.l.) whereas the Katwe-Kikorongo cluster to the south lies on the rift valley floor (895-925 m.a.s.l), and the southernmost cluster (Bunyaruguru) extends into the southern uplands (975-1,250 m.a.s.l).

Uganda experiences a tropical climate with a bimodal rainfall pattern during March-May and October-December (Nicholson, 1996; Nicholson, 2000). Rainfall earlier in the year (March-May) tends to be longer, heavier, and more reliable than that from October to December (Nicholson, 2017). The crater lakes located at higher altitudes receive c. 1,300-1,600 mm yr^{-1} of rainfall, whereas those located on the rift valley floor receive c. 750-1,000 mm yr^{-1} (Uganda Government Department of Land and

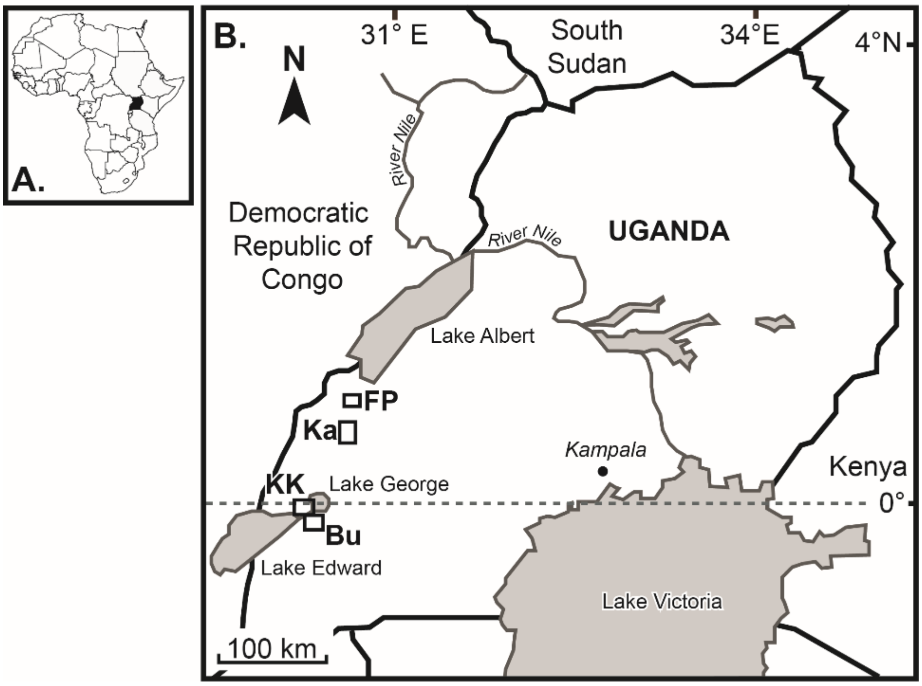

Figure 1. Map of study area showing (a) the position of Uganda in eastern Africa, and (b) a map of Uganda identifying the location of the crater lake clusters in the western part of the country as described by Melack (1978): Fort Portal (FP), Kasenda (Ka), Katwe-Kikorongo (KK), and Bunyaruguru (Bu).

Table 1. Location and sampling information for the lakes and data used in the water chemistry analyses (NP = National Park, CFR = Central Forest Reserve)

Lake	Code	Cluster	Longitude	Latitude	Depth (m)	Protected?
Kyaninga	Kyan	Fort Portal	30°17’46.6”E	0°42’8.11”N	57	
Saaka	Saak	Fort Portal	30°14’34.4”E	0°41’19.2”N	7.8	
Kanyanmukali	Kan	Kasenda	29°20’9.23”E	0°24’01.4”N	10.8	
Kasenda	Kas	Kasenda	30°17’19.6”E	0°26’5.01”N	13.5	
Katanda	Kand	Kasenda	30°15’42.6”E	0°29’0.67”N	145	
Kifuruka	Kif	Kasenda	30°17’9.87”E	0°29’33.2”N	5.3	
Kyerbwato	Kyer	Kasenda	30°19’20.8”E	0°26’14.8”N	12.7	Kibale NP
Lugembe	Lug	Kasenda	30°16’48.9”E	0°27’10.0”N	18.6	
Murusi	Mur	Kasenda	30°17’29.3”E	0°25’47.1”N	57	
Nkuruba	Nkur	Kasenda	30°18’1.53”E	0°31’10.8”N	34.8	
Myamswiga	Niga	Kasenda	30°17’4.99”E	0°30’35.0”N	75	
Wandakara	Wand	Kasenda	30°16’10.1”E	0°25’11.3”N	12.1	
Chibwera	Chi	Bunyaruguru	30°8’20.25”E	0°9’0.04”S	11.7	
Kamunzuka	Kam	Bunyaruguru	30°9’19.96”E	0°15’33.6”S	61	Kasyoha-Kitomi CFR
Kamweru	Kwer	Bunyaruguru	30°7’28.49”E	0°15’20.6”S	45	
Katinda	Kat	Bunyaruguru	30°6’15.82”E	0°13’2.38”S	17	
Kyasanduka	Kyas	Bunyaruguru	30°2’57.06”E	0°17’16.0”S	2	Queen Elizabeth NP
Mirambi	Mir	Bunyaruguru	30°9'21.14"E	0°10'26.08"S	2.6	
Nkugute	Mkug	Bunyaruguru	30°5’54.73”E	0°19’14.8”S	58	
Nyamogusingiri	Nyam	Bunyaruguru	30°1’36.29”E	0°18’55.3”S	4.4	Queen Elizabeth NP
Nyungu	Nyun	Bunyaruguru	30°6’0.00”E	0°15’27.1”S	27	

Surveys, 1962). The mean annual temperature in the region is 22.4°C, varying by c. 2°C throughout the year (based on average monthly temperatures 1901-2016; World Bank Group, 2020).

The lakes span a range of ecotones and vegetation types, from the moist evergreen forests of the rift valley shoulders to the grass savannah of the equatorial rift valley floors (Uganda Government Department of Land and Surveys, 1962; Kizito et al., 1993; Gelorini et al., 2011). Human activities have unevenly impacted the vegetation and land cover of the region including the crater lake catchments; outside of the National Parks and Central Forest Reserves natural forest and shrub has been cleared, and many of the lake catchments contain small-scale subsistence agricultural plots and plantations (Ssemmanda et al., 2005; Gelorini et al., 2011). Lakes located within the National Parks and Central Forest Reserves have catchments that have remained relatively undisturbed by clearance.

The surface waters of 80 crater lakes have been sampled for analysis over the last 20 years (see Introduction), and span both freshwater (70 lakes) and saline lakes (10 lakes). For the purposes of this study, the focus is only on freshwater systems (those with a conductivity of <1,500 µS cm^{-1}) and those that have a minimum of two data points in time in each of the key water chemistry parameters that can be used to understand changes in water quality (conductivity, total phosphorus (TP), total nitrogen (TN) and Chlorophyll-a (Chl-a)). The final list of 21 lakes that were used in this paper are given in Table 1.

Sediment cores were collected from two crater lakes in the Bunyaruguru crater lake cluster with contrasting lake catchments (Figure 2). Lake Nyungu (0°15’22.9” S, 30°05’42.5” E) is a 27 m deep lake, with a catchment that has been heavily modified by human activity; nearly all of the natural vegetation has been replaced by banana plantations. The lake is used for fishing, with large nets permanently in place, and as a source of drinking water for local communities. In contrast, Lake Kamunzuka (0°15’49.8” S, 30°09’18.5” E; 60 m deep) is located within the Kasyoha-Kitomi Central Forest Reserve (CFR), and as result of this protected status the vegetation within the lake catchment is largely natural/secondary forest. The lake is used as a water resource and for fishing, and human activity such as clearance for small scale agriculture is evident just beyond the boundaries of the CFR.

2.2 Water chemistry analysis

The water chemistry data used here are a combination of recently collected samples (2019) that were processed at the University of Nottingham, and a collated series of older data from published datasets (Rumes et al., 2011, Mills and Ryves, 2012, and Nankabirwa et al., 2019).

Water chemistry parameters were all measured on surface water samples (at a depth of c. 0.5 m below the water surface) and include: conductivity (µS cm^{-1}), pH, temperature (°C), dissolved oxygen (mg l^{-1}), Secchi depth (cm), total nitrogen (TN, mg l^{-1}), total phosphorus (TP, mg l^{-1}), and chlorophyll-a (Chl-a, mg l^{-1}). In previously published studies conductivity, pH, temperature, and dissolved oxygen concentrations were measured *in situ* using a Quanta Hydrolab multi-parameter water quality probe. The same parameters were measured in 2019 using a YSI EXO 1 multiparameter sonde water chemistry probe. Water transparency was measured using a Secchi disk.

Methodologies for the analysis of TN, TP, and Chl-a differed between studies, with datasets from Mills and Rumes using the same analytical laboratories and methods (see Rumes et al, 2011; Mills and Ryves, 2012). Data from Nankabirwa et al (2019) used a different approach, with samples for all three analyses processed using a Hach Lange DR800 Spectrophotometer. The analytical methods for the samples collected by Hunt (2019) are summarised below.

The total nitrogen content of each unfiltered water sample was digested using an oxidising reagent, then reduced by shaking with ammonium chloride and spongy cadmium pellets and measured against a blank calibration standard at 543 nm, following the methodology of Jones (1984). Total phosphorus content of each unfiltered water sample was determined using the methodology of Mackereth et al. (1978); samples were oxidised with an acid persulphate solution and measured using colorimetric spectrophotometry against a blank calibration standard at 885 nm.

Measurement of the concentration of Chl-a in lake water samples were obtained using the residue left on 0.7 µm glass fibre filter after water was filtered in the field. On return the University of Nottingham, the dry filter papers were soaked in an extraction solution and the absorbance of light by the samples measured at 665 nm, 645 nm, 630 nm and 750 nm using a spectrophotometer, and calculated following the method of Richards and Thompson (1952).

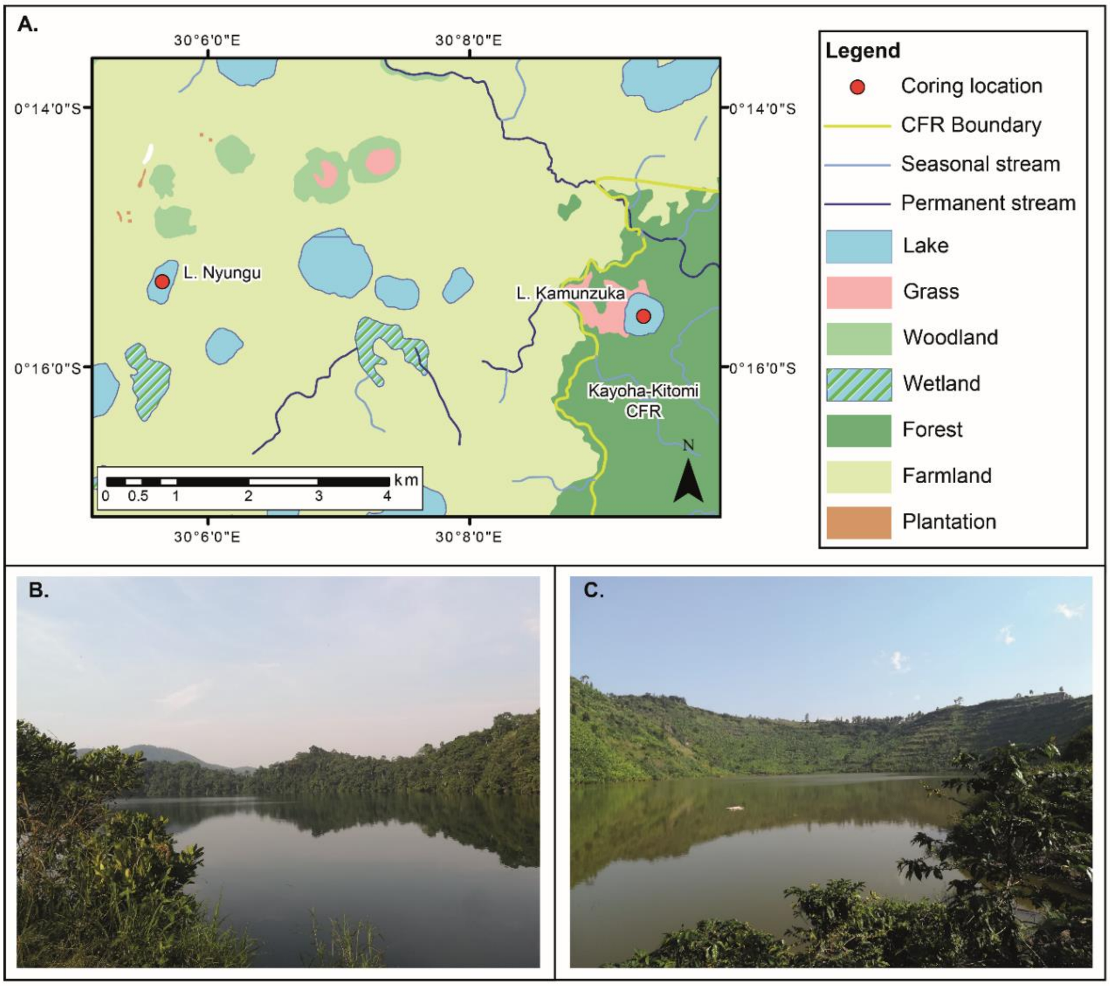

Figure 2. A small-scale map of part of the Bunyaruguru crater lake cluster showing (a) the locations of lakes Kamunzuka and Nyungu, the two lakes where sediment cores were retrieved. The colours on the map represent the land use types. Two photos show the dominant catchment vegetation in (b) Kamunzuka (woodland) and (c) Nyungu (farmland - though as seen in the picture, the majority of the catchment is dominated by banana plantation).

2.3 Sediment records

2.3.1 Core collection and Lead-210 dating

Sediment cores were collected in 2007 from the deepest parts of Lakes Nyungu and Kamunzuka (25.2 m and 62.0 m, respectively) using a HON Kajak gravity corer. The sediment cores were extruded and sectioned at 0.5 cm intervals These samples were stored in a cool box before being transported back to Loughborough University, where they were stored in a dark refrigerator (4°C) prior to analysis.

Five subsamples from each core were analysed for ^{210}Pb, ^{226}Ra, and ^{137}Cs by direct gamma assay using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al. 1986) at the Liverpool University Environmental Radioactivity Laboratory. Lead-210 dates for each core were calculated using the constant rate of supply model (CRS; Appleby and Oldfield, 1978; Appleby, 2001) and compared with the stratigraphic date of 1963, as determined by the ^{137}Cs record, to obtain radiometric dates for the cores.

2.3.2 Loss-on-ignition (organic and carbonate content) and DMAR

The methodology of Dean (1974) was used to estimate the organic and carbonate content of the sediment cores. Sub-samples of a known dry weight were placed in a furnace at 550°C for 2 hours. The at 925 °C for 4 hours. The reweighed sample allowed an estimate of the carbonate content. The results from the LOI and ^{210}Pb dating were used to calculate the dry mass accumulation rate (Appleby and

Oldfield, 1978).

2.3.3 Diatom and ordination analyses

Diatoms were analysed from the Kamunzuka and Nyungu cores at 2 cm and 0.5 cm resolution respectively. Diatom samples were prepared using the method of Renberg (1990). Sub-samples of sediment were digested using 30% w/v hydrogen peroxide and placed in a water bath at 90°C for 4 hours. Following digestion, a few drops of 10% hydrochloric acid were added to remove any carbonates. The samples were washed with distilled water and left to settle for 24 hours. The supernatant was decanted, and the washing process repeated 4 times. Samples were placed onto coverslips and mounted onto microscope slides using Naphrax. At least 300 valves per sample were counted in parallel transects under oil-immersion phase-contrast light microscopy at x1000 magnification on a Leica DMRE research microscope. A variety of general (Krammer and Lange-Bertalot, 1986-1991) and regional floras (Gasse, 1986; Cocquyt, 1998) were used, and valves identified to species level where possible. Stratigraphic diatom assemblage data were plotted using C2 (Juggins, 2003).

Ordination analysis was undertaken on the diatom assemblage data from both lakes. Based on the generated gradient lengths from an initial Detrended Correspondence Analysis (DCA), it was determined that a Principal Components Analysis (PCA) would be undertaken on the samples from Kamunzuka, and a DCA applied to Nyungu. Analyses were completed using Canoco 4.5 (Ter Braak and Šmilauer, 2002).

3. Results

3.1 Modern water chemistry results

The total phosphorus (TP) concentration in surface waters across all lakes in all years ranges from 0 mg l^{-1} (Lake Kamunzuka, 2007) to 1.6 mg l^{-1} (Lake Kanyanmukali, 2015); with a median value of 0.08 mg l^{-1}. Sixteen of the 21 lakes presented all show an increase in TP from 2007 to 2019. Whilst little is known of the phosphorus dynamics of these smaller tropical lakes, published research from eastern Africa suggests that very high phosphorus values (1 mg l^{-1}) are usually common in saline lakes, and values >0.15 mg l^{-1} are usual in shallow, productive lakes (Talling and Talling, 1965). In this dataset, 2 lakes (Mirambi and Murusi) have values similar to those observed in hyper-saline systems, and the majority of lakes (14) have values that are close to, or exceed >0.15 mg l^{-1}; yet only 2 of these lakes are shallow systems (Kyasanduka at 2 m deep, and Nyamogusingiri at 4.4 m deep). Therefore, the higher TP (>0.15 mg l^{-1}) values in some of the deeper, freshwater lakes are likely attributable to human activity in the catchment, and internal cycling of the phosphorus (Talling and Talling, 1965). Total nitrogen (TN) has more variability than TP values, with the lowest value of 0.07 mg l^{-1} (Lake Kamunzuka, 2007) and a maximum value of 6.33 mg l^{-1} (Lake Kyasanduka, 2019). Across the 21 lakes, Chl-a varies from 0.69 μg l-1 (Lake Kamunzuka, 2007) to 203 μg l-1 (Lake Kyasanduka, 2007). The majority of lakes sampled across all years have Chl-a concentrations >10 μg l^{-1}.

The water chemistry data (Table 2) were analysed using unconstrained ordination to understand the underlying trends in the data, and the relationship between lakes through time. The analyses focused on three time periods where there were (almost) complete datasets across the 21 lakes: 2007, 2015, and 2019. Principal Components Analysis (PCA) was undertaken using Canoco 4.5; all water chemistry data were log-transformed prior to analysis. The PCA of the water chemistry data was undertaken as four separate datasets (Figure 3), three of which focussed on datasets from the Bunyaruguru and Kasenda clusters (Figure 3a-c) comparing different years, and then a PCA that analysed all lakes together (Figure 3d). Fort Portal lakes were not analysed separately as there were only 2 systems that passed the initial dataset screening.

While there are some minor differences between the four ordination sub-sets, in all cases Chlorophyll-a and/or TP appear to be strongly correlated to PCA axes 1 and 2, which suggests that these parameters are major drivers of the lake systems. In the four datasets, axis 1 accounts for 44% (Bunyaruguru: 2007 vs 2015) to 60% (All Clusters: 2007 vs 2015) of all variance observed in the datasets; and in all cases, the first 2 PCA axes explain around 80% of the variance in the data. Furthermore, in all four ordinations - regardless of comparative time frame (e.g. 2007 vs 2015, 2007 vs 2019) or lake cluster, there is a split observed in the lake samples, with more recent samples associated with higher Chlorophyll-a and TP values.

Table 2. Lake water chemistry data used in the PCA analyses. Cond = conductivity (µS cm^{-1}), Secchi = Secchi depth (cm, indicator of turbidity), TP = total phosphorus (mg l^{-1}), TN = total nitrogen (mg l^{-1}), and Chl-a = Chlorophyll-a (µg l^{-1}). The datasets available are from 2007 (Rumes et al., 2011), 2015 (Nankabirwa et al., 2019) and 2019 (collected by Hunt, and methodologies described in this paper). Shaded cells = missing data / no data collected.

Lake	**2007 [Rumes]**					**2015 [Nankabirwa]**					**2019 [Hunt]**				
	Cond	**Secchi**	**TP**	**TN**	**Chl-a**	**Cond**	**Secchi**	**TP**	**TN**	**Chl-a**	**Cond**	**Secchi**	**TP**	**TN**	**Chl-a**
Kyaninga	420	585.0	0.01	0.10	0.81	408	410.7	0.03	0.50	2.63					
Saaka	612	45.0	0.08			655	48.5	0.15	1.80	90.45					
Kanyamukali	920	65.0	0.42	0.44	7.16	992	90.0	1.6	1.05	14.85					
Kasenda	312	83.0	0.04			322	91.5	0.07	0.70	32.27	235	105.0		0.76	15.15
Katanda	419	200.0	0.04	0.77	25.43	428	200.0	0.03	0.50	6.80					
Kifuruka	411	82.0	0.08			356	38.5	0.12	3.90	70.9					
Kyerbwato	411	165.0	0.02	0.23	1.72	400	216.0	0.13	0.50	6.50					
Lugembe	407	135.0	0.05	0.53	5.69	453	54.5	0.08	1.10	25.95					
Murusi		140.0	0.02	0.31	3.75							100.0	1.26	0.76	4.22
Nkuruba	370	101.0	0.04	0.66	26.31						315	137.0	0.39	0.79	4.32
Nyamswiga	330	110.0				370	87.0	0.16	0.50	18.95					
Wandakara	1125	70.0	0.06	0.75	11.35	1239	40.5	0.15	3.00	97.65	1172		0.57	1.60	
Chibwera	457	135.0	0.05	0.30	6.74	455	89.0	0.1	0.70	25.46					
Kamunzuka	58	770	0	0.07	0.69						56	250.0	0.14		2.45
Kamweru	170	55.0	0.07	0.66	13.85	166	101.0	0.06	0.85	29.9					
Katinda	743	53.0	0.04	0		772	29.5	0.15	3.57	164.75	755			2.43	153.25
Kyasanduka	237	24.0	0.47	0.89	203.03	263	30.7	0.26	3.50	91.83	265	19.0	0.38	6.33	139.62
Mirambi	642	90.0	0.04	0.63		693	82.0	0.07	0.50	20.05	653		1.06	1.8	19.07
Nkugute	121	90.0	0.05	0	5.89	123	99.3	0.04	0.77	19.17					
Nyamogusingiri	618	44.0	0.06	2.00	14.79	760	25.0	0.13	4.03	163.67	741	40.0	0.42	3.99	4.752
Nyungu	430	8.0	0.26			418	19.5	0.22	2.75	183.00	459	29.5	0.37	1.44	33.13

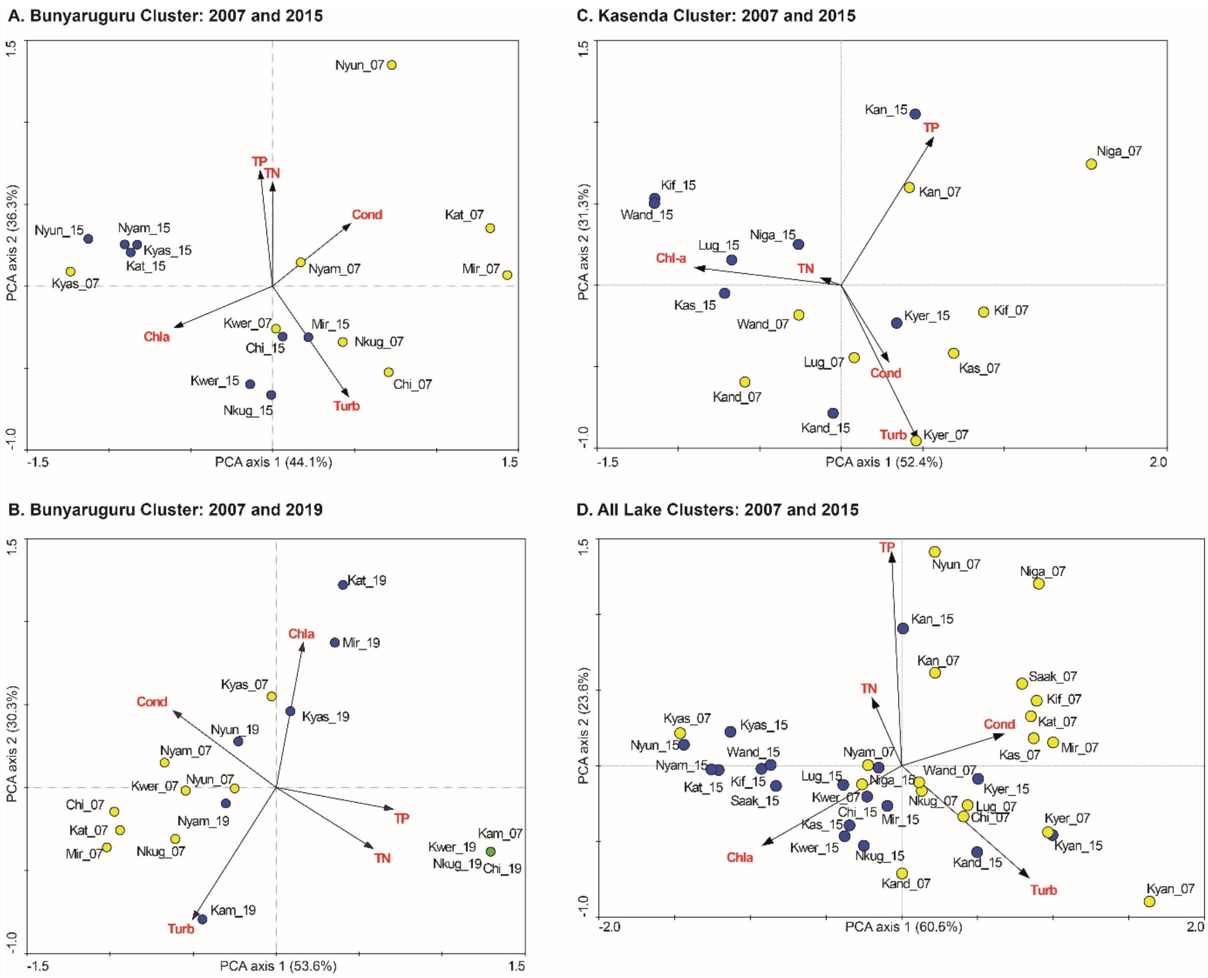

Figure 3. Results of the water chemistry Principal Components Analysis (PCA) carried out on four example datasets. (a) PCA of 2007 and 2015 water chemistry of eight lakes within the Bunyaruguru lake cluster (Lake Kamunzuka was removed from this analysis due the lack of data for 2015). (b) PCA of 2007 and 2019 water chemistry of nine lakes within the Bunyaruguru lake cluster. (c) PCA of 2007 and 2015 water chemistry of eight lakes within the Kasenda lake cluster (Lakes Murusi and Nkuruba were excluded from analysis due to lack of data from 2015). (d) PCA of all lakes from the Fort Portal, Kasenda, and Bunyaruguru clusters that had complementary datasets from 2007 and 2015 (Lakes Kamunzuka, Murusi and Nkuruba were excluded from this analysis). PCA axis 1 and axis 2 percentages are given on each diagram. The arrows represent the dominant water chemistry trends in each analysis (Cond = conductivity, Turb = turbidity, TP = total phosphorus, TN = total nitrogen, Chla = Chlorophyll-a). All data were log-transformed prior to the PCA.

3.2 Lake trophic status

Lakes were assigned a lake trophic status on the basis of their Chl-a content, as defined by Nankabirwa et al. (2019). A minimum of two Chl-a concentration measurements were made at 19 lakes across the Bunyaruguru, Fort Portal and Kasenda crater lake clusters between 2006 and 2019, which were used to assign the lakes a trophic status change (Table 3). The change in trophic status of the lakes over the sampling period has been varied; some lakes across the region experienced no change in trophic status between sampling points, and others experienced a net increase or reductions in trophic status between 2006 and 2019.

Six of the 19 lakes had the same trophic status at each point in time that lake water Chl-a concentration was measured. One lake (Lake Nyungu) experienced no net change in trophic status but did experience a higher trophic status in 2014/15 (hypertrophic) compared to measurements taken in 2006 and 2019 (eutrophic).

Twelve lakes experienced a net change in their trophic status between the earliest and most recent sample collection. Eight lakes experienced a net increase in their trophic status (increase in Chl-a concentration), whereas 4 lakes experienced a decrease in trophic status (reduction in Chl-a concentration).

Table 3. Trophic status of lakes, as defined by Nankabirwa et al. (2019) in 2006 (Mills and Ryves, 2012), 2007 (Rumes et al., 2011), 2015 (Nankabirwa et al., 2019), and 2019 (collected by Hunt, and methodologies described in this paper). Blank cells = missing data / no data collected.

Lake	**Depth** (m)	**Trophic Status**				**Change in trophic status**
		2006	2007	2015	2019	
Bunyaruguru Cluster						
Kyasanduka	2		Hyper	Hyper	Hyper	No change
Nyam.Basin	4.4		Meso	Hyper	Oligo	Decrease
Chibwera	11.7		Meso	Eutro		Increase
Katinda	17			Hyper	Hyper	No change
Mirambi	22			Eutro	Meso	Decrease
Nyungu	27	Eutro		Hyper	Eutro	No net change
Kamweru	45		Meso	Eutro		Increase
Nkugute	58		Oligo	Meso		Increase
Kamunzuka	61	Oligo			Oligo	No change
Fort Portal Cluster						
Kyaninga	57		Oligo	Oligo		No change
Kasenda Cluster						
Kifuruka	5.3	Meso		Hyper		Increase
Kanyamukali	10.8		Meso	Meso		No change
Wandakara	12.1	Meso	Meso	Hyper	Eutro	Increase
Kyerbwato	12.7		Oligo	Meso		Increase
Kasenda	13.5	Oligo		Eutro	Meso	Increase
Lugembe	18.6		Oligo	Eutro		Increase
Nkuruba	34.8		Eutro		Oligo	Decrease
Murusi	57		Oligo		Oligo	No change
Katanda	145		Eutro	Meso		Decrease

3.2 Palaeolimnological records

3.2.2 Lake Kamunzuka

Lake Kamunzuka has a good ^{210}Pb record, with a high surface concentration which declines regularly with depth, reaching equilibrium with the supporting ^{226}Ra at approximately 40 cm (Figure 4). The highest ^{137}Cs concentration occurs at c. 14 cm, in good agreement with the depth of 1963 as calculated from the ^{210}Pb dates using the CRS model (c. 17 cm).

The diatom assemblage from Lake Kamunzuka (Figure 5) is dominated by the epiphytic *Gomphonema gracile* (comprising 60-90% of the assemblage), with a number of notable changes. The planktonic species *Aulacoseira ambigua* is present between AD 1910-1840 (38-28 cm), declining from a maximum abundance of c. 20% to c. 2.5%. This species is succeeded by another planktonic species, *Fragilaria tenera*, which is present from AD 1830 (39 cm) at 20%, and slowly declines to <3% through record until all but disappearing from AD 1930 onwards (25 cm). Four other species are consistently present throughout the core: the planktonic *Staurosira construens* (3-6%) and *Aulacoseira granulata* (c. 7%) and the epiphytic *Encyonema minuta* (c. 5%) and *Gomphonema parvulum* (c. 6%). The most notable change with the records of these species is that from c. 1990 (10 cm) *Staurosira construens*, *Aulacoseira granulata*, and *Encyonema minuta* all decline to <1%, whilst *Gomphonema parvulum* reaches its maximum abundance (c. 20%). These assemblage changes are also demonstrated in the PCA analyses (Figure 5), with declining sample scores throughout the record, but obvious changes occurring c. AD 1870 (34 cm) and AD 1990 (10 cm).

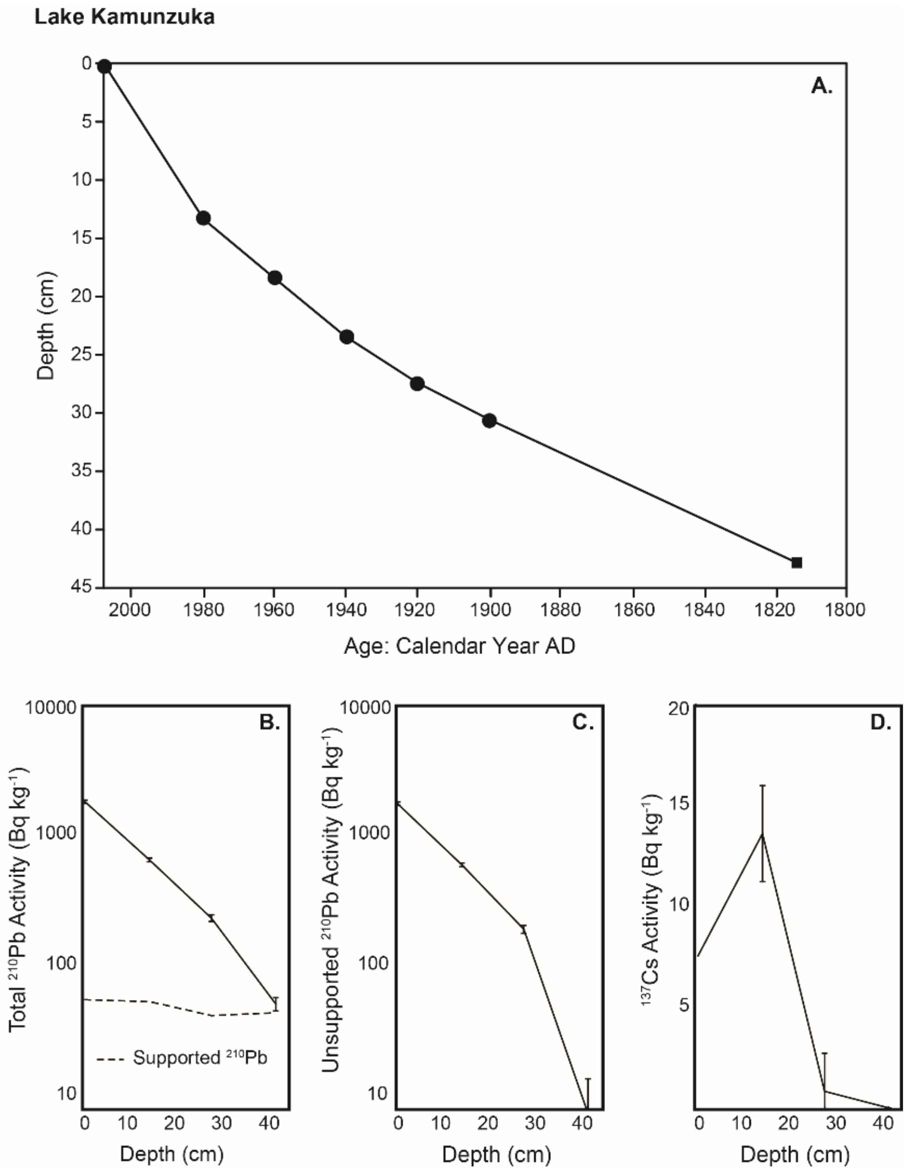

Figure 4. Lead-210 chronology for Lake Kamunzuka. (a) Dates were determined using linear extrapolation between the dated horizons [circles], the basal data [square] is based on extrapolated data. Fallout radionuclides are also shown: (b) total and supported ^{210}Pb, (c) unsupported ^{210}Pb, and (d) ^{137}Cs concentration versus depth.

The sediments are rich in organics, with loss-on-ignition values between 20-40%; carbonate values are low (<5%) (Figure 5). The organic content is stable at c. 20% from AD 1810-1970 (42-15 cm). After AD 1970 the organic content increased steadily to 40%. Likewise, the DMAR is constant at c. 0.05 g cm^{-1} yr^{-1} between AD 1810-1920 (42.5-27 cm), before increasing to 0.1 g cm^{-1} yr^{-1} from AD 1920 (27 cm) (Figure 6). Peak DMAR is reached c. 1980 (0.15 g cm^{-1} yr^{-1}, 13 cm) before declining towards the top of the core.

3.2.3 Lake Nyungu

The ^{210}Pb record from Nyungu, while not irregular, does demonstrate a change of gradient at c. 20 cm, attributed to an acceleration in sedimentation rate (Figure 7). Equilibrium with the supporting ^{226}Ra occurs at c. 25 cm and the highest ^{137}Cs concentration occurs at c. 18 cm. This is in agreement with the position of 1963 as calculated using the CRS model.

There is a clear divide in the diatom assemblage data between AD 1950 (18 cm) and AD 1960 (15 cm) (Figure 8). The earlier part of the record, the assemblage is dominated by the planktonic species

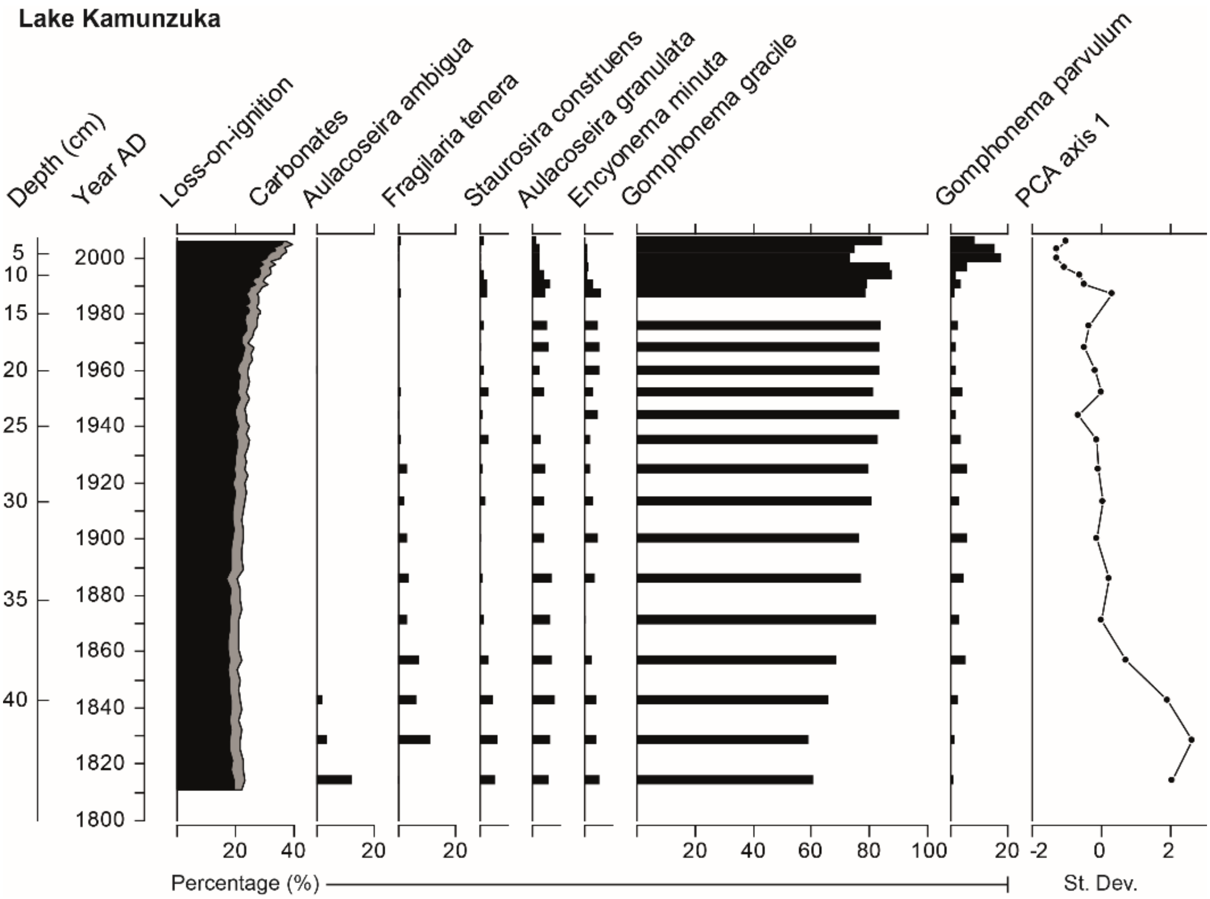

Figure 5. Results of the palaeolimnological analysis of the Lake Kamunzuka sediment core showing the down core results of loss-on-ignition (organic content) and carbonate content. The diatom assemblage data shows all species >5% abundance alongside the PCA axis 1 samples scores.

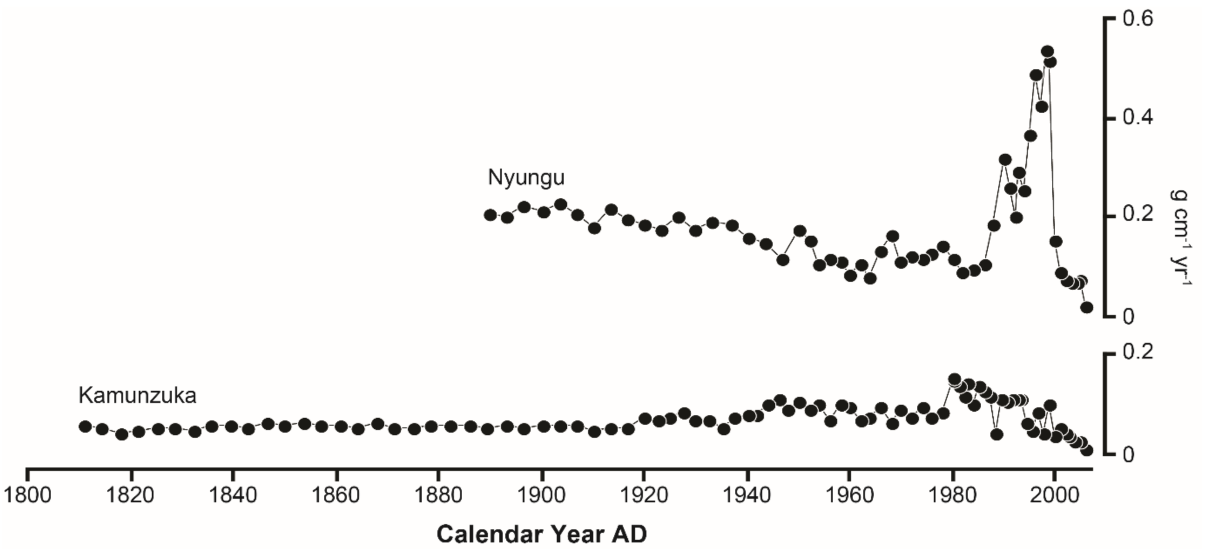

Figure 6. Calculated dry mass accumulation rates (DMAR) from lakes Kamunzuka and Nyungu over the last 200 years.

Nitzschia lancettula, which reaches a maximum abundance of c. 70%. Two epiphytic species, *Amphora copulata* and *Encyonema muelleri*, are also consistently present in quantities of c. 5-15%. There is an obvious decline in the dominant *N. lancettula* between AD 1900 (26 cm) and AD 1910 (24 cm). During this short-lived phase, the aerophilous and shallow water diatoms *Luticola mutica* and *Hantzschia amphioxys* increase to a maximum abundance of c. 20%, as does, although to a lesser extent, *Diadesmis contenta* (c. 10%). From AD 1950 (18 cm), the diatom assemblage switched to a system dominated by the epiphytic *Gomphonema pumilum* and the high nutrient indicator *Nitzschia palea* (10-60% of the assemblage). Other epiphytic and shallow water diatoms (*D. contenta*, *Navicula cryptonella*, *Nitzschia amphibia* and *Gomphonema parvulum*) occur in abundances between 10-20%. It is noted that the excursions in the organic and carbonate data are mirrored with concomitant increases in the aerophilous taxon *D. contenta* at AD 1990 (8 cm) and AD 1998 (4 cm). The results of the DCA (Figure 8) show a decline in sample scores through time, with the major change occurring c. AD 1950.

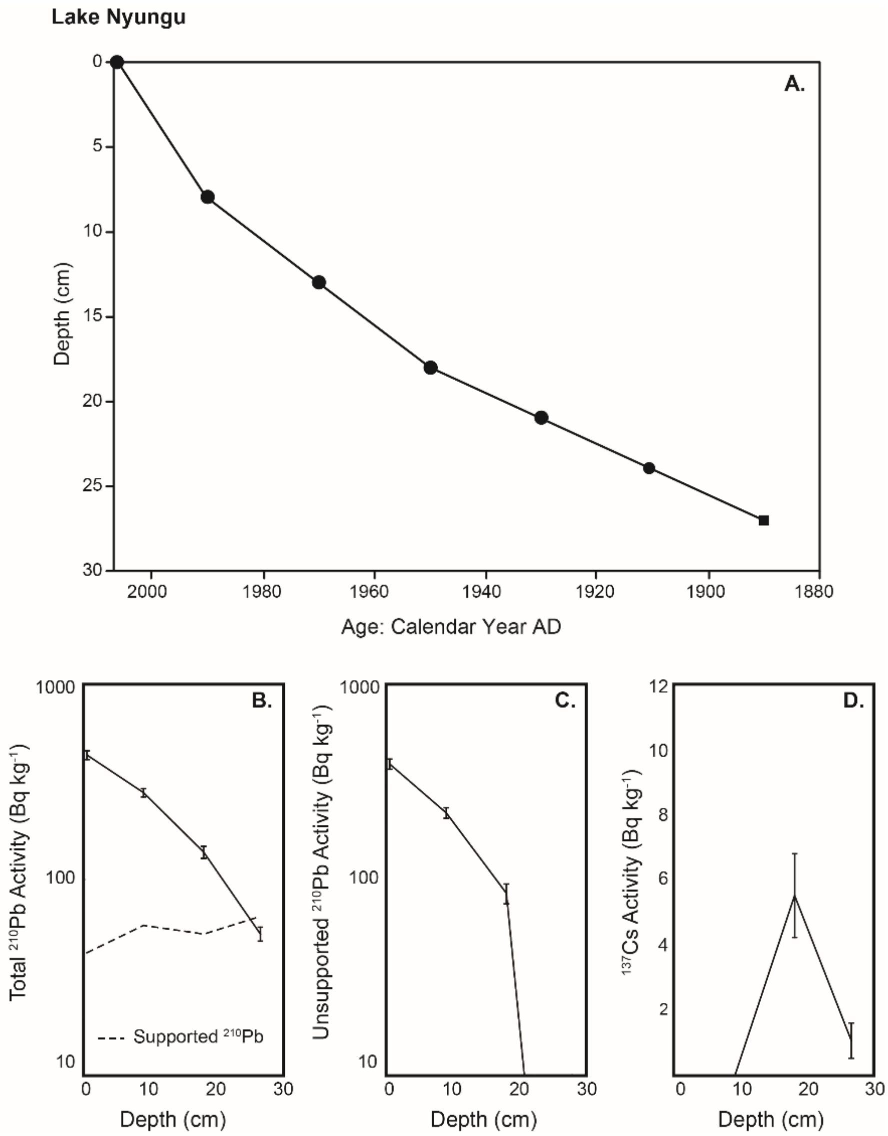

Figure 7. Lead-210 chronology for Lake Nyungu. (a) Dates were determined using linear extrapolation between the dated horizons [circles], the basal data [square] is based on extrapolated data. Fallout radionuclides are also shown: (b) total and supported ^{210}Pb, (c) unsupported ^{210}Pb, and (d) ^{137}Cs concentration versus depth.

Prior to AD 1950 (18 cm), the sediments from Nyungu have a low organic (c. 5%, Figure 6) and low carbonate content (c. 6%). After AD 1950 the sediments became organic-rich, increasing to a maximum of c. 30%. There are 3 notable excursions in the LOI data where values decline to 10-15%, these occur at AD 1970 (13 cm), AD 1990 (8 cm), and AD 1998 (4 cm). Carbonate values also increase to c. 30%. The carbonate record also shows similar data excursion to the organic record, where values drop to c. 15%. The DMAR is generally low and fluctuates between 0.1-0.2 g cm-1 yr^{-1} from AD 1890-1980 (27-11 cm). A substantial and rapid increase in DMAR occurs between AD 1980 (11 cm) and AD 1998 (4 cm) to a maximum value of 0.5 g cm^{-1} yr^{-1}. Values then decline towards the top of the core (to values <0.1 g cm^{-1} yr^{-1}).

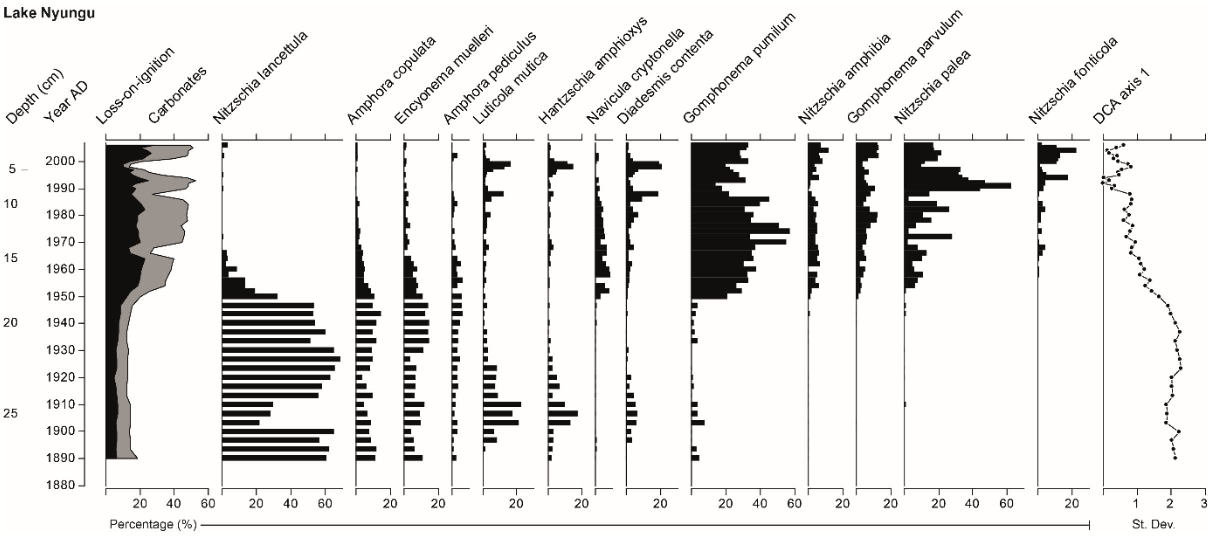

Figure 8. Results of the palaeolimnological analysis of the Lake Nyungu sediment core showing the down core results of loss-on-ignition (organic content) and carbonate content. The diatom assemblage data shows all species >5% abundance alongside the PCA axis 1 samples scores.

4. Discussion

The modern limnology datasets and palaeolimnological studies from Lakes Nyungu and Kamunzuka presented here provide insight into the changes in water quality that the crater lakes have experienced, across multiple timescales, over the past 150 years. The different approaches highlight the challenges associated with working in areas with sparse monitoring data, and the merits that a palaeolimnological approach can have in understanding lake systems that lack long term monitoring datasets. The results of the water chemistry dataset analyses (4.1, 4.2) and palaeolimnological studies (4.4) are discussed below, as well as the challenges associated with working with such sparse water chemistry datasets (4.3) and the role that palaeolimnology can play in informing sustainable lake management (4.5).

4.1 Modern water chemistry

The full 80 crater lake dataset (2.1) comprises lakes that have at least one water chemistry sample in the last 20 years (most commonly, a conductivity measurement); this comprises nearly all of the crater lakes that are documented in the western region of Uganda. To allow for a robust analysis, a criterion of requiring 2 data points from separate years for key parameters reduced this dataset by 75% (to 21 lakes). Some lakes have certain parameters collected more often than others (e.g. conductivity) reflecting the focus of particular research e.g. for developing conductivity transfer functions (Eggermont et al., 2006; Mills and Ryves, 2012) and data collection is often not systematic due to logistical constraints of field campaigns, including time in the field, the crater lake area of focus (higher number of lakes from the Kasenda and Bunyaruguru clusters have been repeatedly sampled) and site-specific access issues.

Tropical African waters have high phosphorus concentrations in comparison to unpolluted European waters. The reason for this excess could be due to phosphorus being limited in its availability to algae, or that there is insufficient demand by algae to exhaust supplies, suggesting an alternative nutrient (e.g. nitrogen) is the limiting growth factor (Kalff, 1983). The relationship between total phosphorus (TP) and total nitrogen (TN) for the lakes studied here is illustrated in Figure 9. The red and blue lines represent the TN: TP ratios of 15:1 and 7:1 (Vollenweider and Kerekes, 1982). Lakes are typically P-limited when the ratio is >15, and N limited when the ratio <7. Across the 3 years in the dataset there is a large amount of scatter, but there is a clear pattern in the data set when comparing between years. The data from 2007 suggest that there was a range in whether lakes were P or N-limited with many sitting between the two, with only 3 sites clearly having a limiting nutrient (2 lakes are clearly N-limited, 1 lake is P-limited). Moving into 2015, whilst there are still many lakes that sit between the 2 ratios, several lakes are clearly P-limited (4 lakes) and N-limited (3 lakes). The clearest shift occurred within the 2019 datasets, where nearly all lakes are now N-limited, which suggests an excess of phosphorus in the lake systems, and follows the hypothesis of Talling and Talling (1965) who suggested that N-limitation rather than P-limitation might be regionally prevalent in eastern Africa.

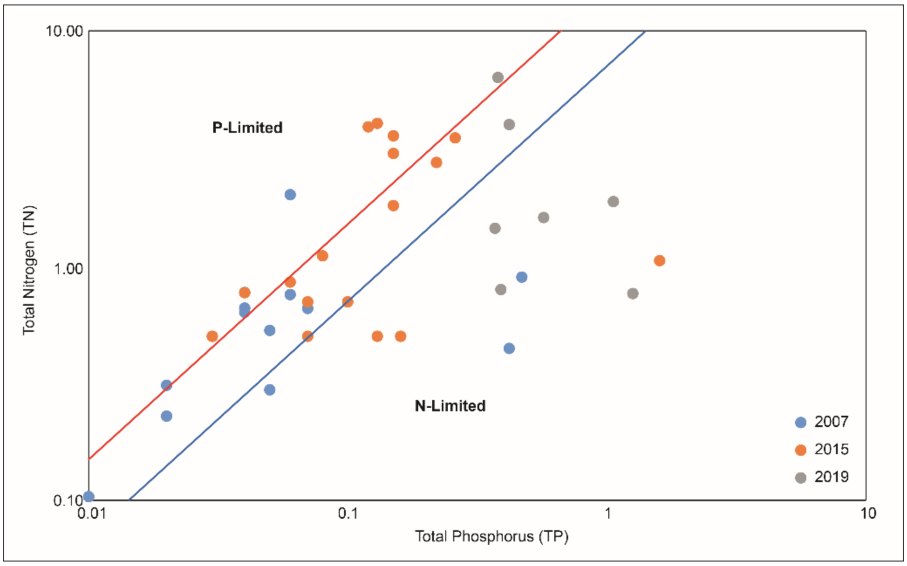

Figure 9. Total phosphorus (TP) versus Total nitrogen (TN) of the 21 crater lakes in each of the year categories. The solid lines represent 7:1 (blue) ratio and 15:1 (red) ratio. Lakes that are phosphorus limited (ratio N: P > 15:1) plot above the red line, those that are nitrogen limited (ratio N: P <7:1) plot below the blue line. Lakes that plot between the two lines may be limited by either phosphorus or nitrogen (Vollenweider and Kerekes, 1982).

The majority of measured nitrogen concentrations in the crater lakes are well below 1.5 mg l^{-1}, although 7 lakes (in at least one of the 3 years) have values that exceed this: lakes Katinda, Kyasanduka, Mirambi, Nyamogusingiri, Saaka, Kifuruka, and Wandakara. The high nitrogen values may be attributable to the large amount of human impact in the lake catchment, and inputs from animal and human waste. However, the distribution of phosphorus values with regards to the quantity of human impact within the lake catchment is less clear. This suggests that the relationship between catchment agricultural activity and total phosphorus values are far more complex and may be due to several confounding factors such as catchment geology and within-lake processes such as phosphorus cycling, affecting deposition and subsequent release of phosphorus from sediments under anoxic bottom waters.

The input of phosphorus to lake systems has likely increased in the recent past due to catchment disturbance e.g. through the clearance and burning of the natural forest for subsistence agriculture. This in conjunction with periods of intense rainfall and the steep crater slopes aids the transport of nutrients to lakes. The retention of phosphorus and nitrogen by undisturbed, well-vegetated catchments means very little is transported to lakes (Borman and Likens, 1970). Conversely, lakes situated in agricultural drainage basins with rich soils (and those receiving e.g. animal manure fertilisers) receive extremely high nutrient loads (Kalff, 2003). Human impacts, such as deforestation can result in a huge response in the aquatic systems due to the modification of catchment hydrology (Borman and Likens, 1970) and through nutrient loss from land to water through erosion and runoff. Subsequent effects are dependent on land use (e.g. bare soil, cultivation or regrowth of 'natural' vegetation). In eastern Africa, the impact of human disturbance is thought to increase in proportion to population growth (Verschuren, 2002).

Climate changes can also influence the loss of nutrients from a catchment to a lake through changes in rainfall, soil moisture, and changes in runoff and erosion. Identifying which of these potential factors drive change in a given lake is difficult (Anderson, 1995; Mills et al., 2017).

4.2 Changes in lake trophic status

While the decline in lake water quality in 7 of 19 lakes across the crater lake region (Table 3) is a cause for concern in terms of declining water quality, the main conclusion that can be drawn is that the nature of change in trophic status in lakes across the region is extremely varied. There is no clear temporal or spatial pattern with regards to the changing trophic status of the lakes. The lack of a regionally uniform change suggests that the drivers of increased algal productivity, as measured by Chl-a, including eutrophication are filtered by individual lakes (Magnuson et al., 2004) or that the drivers of eutrophication within the lakes are, themselves, catchment and lake specific. Whether the lakes are responding to catchment scale change, or are filtering a regional signal, the heterogeneous nature of the trends observed across the lakes highlight the need to take a lake-by lake approach to understanding how each lake is responding to environmental changes, or to take a landscape scale approach in order to understand how different lakes respond to common regional drivers (e.g. Moorhouse et al., 2018).

The drivers of algal blooms in tropical lakes are the nutrient content of lake water, the climate, and the hydrology of the lake systems; nutrient content of lake water is most closely related to lake trophic status in the tropics (Giani et al., 2020). The water chemistry data presented here show that nearly all of the lakes across the region have experienced an increase in either, or both, lake water TN and TP concentrations. It is likely that the increase in TN and/or TP lake water concentrations have had some influence on driving the increase in trophic status observed at seven of the lakes; all of the lakes that experienced an increase in trophic status between 2006 and 2019 experienced an increase in at least one major nutrient (TN or TP), and similarly both the TN and TP concentration of lake water, and the trophic status of Lake Katanda decreased across the study period. However, a number of lakes that experienced an increase in TN and/or TP experienced no change in trophic status, and a number of lakes (including Lakes Nyungu, Mirambi, Nyamogusingiri and Nkuruba) experienced a reduction in lake trophic status. This means that nutrient concentrations of the crater lake waters are not the only driver of changes in lake productivity. Other influences, such as individual lake hydrology, or climate variability on a regional scale may be acting to counteract or exacerbate the influence of changing nutrient flux into the lakes.

The lakes in the study that were hypertrophic during the study period (such as Lakes Kyasanduka, Nyamogusingiri, Katinda, Kifuruka, and Wandakara) tended to be shallower (<20m deep). This could possibly be because shallower tropical lakes tend to be more productive than deeper lakes (Lewis, 1987). More hypertrophic lakes were located in the Bunyaruguru crater lakes than in the Kasenda crater lake clusters, although this may be an artefact of the lakes that were included in the study (more shallow lakes in the Bunyaruguru cluster were sampled than in the Kasenda cluster).

4.3 Comparing water datasets through time

The water chemistry data presented provides a snapshot of the direction and magnitude of change in lake water quality over the course of the past two decades. However, a number of challenges are faced when working with incomplete datasets that have been compiled by multiple researchers, which limits the comparisons that can be made between datasets, and therefore understanding of how the lakes have changed through time.

The earliest conductivity measurements at the crater lakes were made in 1932 (Beadle, 1932) and have been taken sporadically over the course of the 20th Century (Beadle, 1932; Talling and Talling, 1965; Kilham, 1971; Melack, 1978; Kizito et al., 1993; Chapman, 1998). The technologies used to make these measurements differ significantly to those used today, thus limiting our ability to compare these older data to more modern limnological datasets (Kizito et al., 1993). The use of differing technologies and methods to obtain modern limnological data, in particular water chemistry data, means that difficulties in comparing datasets persists, even when working with more recent datasets. For example, different methods are used by Nankabirwa (2019) to other researchers to obtain nutrient concentrations in lake water, and while the same laboratory was used to analyse water samples collected by Rumes, Verschuren, and Mills prior to 2007, samples collected by Hunt (2019) were analysed in a different laboratory, which could introduce further discrepancies.

As the datasets have mostly been collected sporadically during a number of field campaigns during the dry seasons (January-February and June-July), the data have a seasonal bias. As few measurements have been collected during the rainy seasons, understanding of the lakes during these periods is limited. The implementation of ongoing monitoring at a number of lakes, similar to the monitoring project at Lake Nkuruba as part of the Kibale Fish and Monkey Project, which has monitored the lake on a fortnightly basis since 1992 (Saulnier-Talbot et al., 2014), would help counter this bias.

The compilation of the datasets during a number of field campaigns by multiple researchers, each with different aims, means that the lakes visited and the limnological parameters measured and samples taken for analyses varies between datasets. This means that the datasets collected differ from each other, resulting in significant gaps in the datasets, and makes direct comparisons between datasets harder. By standardising the methods used, the types of observations made and the samples collected for analyses across tropical Africa, the comparability of these datasets and the conclusions drawn from them could be vastly improved.

4.4 Palaeolimnological records from Lakes Nyungu and Kamunzuka

The diatom records from lakes Kamunzuka (Fig. 5) and Nyungu (Fig. 7) provide insight into changes in both lake systems through time. Diatoms are microscopic, unicellular algae that have been used extensively to infer past environmental changes in lakes (Battarbee, 2000). Different species of diatoms are sensitive to, or have a preference for living in, waters of specific chemistries. For example, some diatom species can withstand high levels of salinity, whilst others will not tolerate high levels of nutrients. As such, diatoms are an excellent indicator of changes in water chemistry through time, from decades to hundreds of thousands of years (Stoermer and Smol, 1999), and have been used to infer changes in the salinity of lake waters driven by changes in precipitation (Mills and Ryves, 2012) and for understanding the timing and impact of nutrient enrichment of lake waters (Davidson and Jeppesen, 2013). In eastern Africa, correlations have been established between diatom species composition and pH (Gasse et al., 1995), salinity (Hecky and Kilham, 1973), conductivity (Gasse et al., 1995) and ionic composition (Gasse et al., 1983).

Kamunzuka is a deep (c. 60 m) and clear lake, with a large euphotic depth (>20 m) which allows epiphytic *Gomphonema* species (those attached to plants) to dominate alongside the planktonic *Aulacoseira* species. The dominant *Gomphonema* species (*Gomphonema gracile*) has a preference for waters with a low nutrient content (Patrick and Reimer, 1975). The only obvious perturbation that occurs in this lake is during the earliest phase of the record (c. AD 1830) where there is a slight decrease in the relative abundance of *Gomphonema gracile* and a higher percentage of *Fragilaria tenera*, perhaps indicative of large inputs of very fresh waters (Kelly et al., 2005). The presence of *Aulacoseira granulata* throughout the record attests to high silica and high light conditions. For *Aulacoseira* species to occur there must be turbulence within the water column, to aid buoyancy and to keep the genus suspended in the photic zone.

There is coherence between the amount of sedimentation (Fig. 6) and the diatom data, with the most obvious excursion, occurring c. AD 1980-1995, where there is an increase in the DMAR and a concomitant shift in the diatom assemblage, as evidenced by change in the PCA samples scores, driven by the increase in the diatom *Gomphonema parvulum* which is often used as an indicator of environmental stress (Sabater, 2000).

In Lake Nyungu, prior to AD 1950, the diatom assemblage data suggest that the lake was deep and fresh (*Nitzschia lancettula*), with vegetated lake shores (*Amphora copulata*, *Encyonema muelleri*). A major switch in the diatom assemblage occurs at c. AD 1950, and the planktonic freshwater *N. lancettula* disappeared from the record by AD 1965. The loss of the epiphytic diatom species suggests that the previously established littoral vegetation was destabilised, and the once clear water system was replaced by a more turbid lake with an assemblage dominated by periphytic and benthic species, most notably *Gomphonema pumilum* and *Nitzschia palea*. Aerophilous species *Hantzschia amphioxys, Luticola mutica* and *Diadesmis contenta* are also consistently present throughout this zone. The presence of *Gomphonema pumilum* perhaps attests to lower oxygen content in the lake water than the earlier assemblage (Gasse, 1986). The increase and variation in the *Nitzschia palea* record from c. AD 1990 appears to be closely related to increases in the input of catchment sediments to the lake system (Sabater, 2000). *Nitzschia palea* is an indicator of turbid waters with a heavy load of decomposed organic matter (Leland et al., 2001) as well as being indicative of eutrophic/hyper-eutrophic conditions (van Dam et al., 1994).

Overall, Lake Kamunzuka with its more 'natural' catchment reveals very little variation in its diatom assemblage since AD 1810. Conversely, 'impacted' Lake Nyungu indicates a significant shift in the diatom assemblage data in the last c. 50 years, with a change in habitat from a planktonic to a benthic dominated system. The major changes in the diatom flora are coincident with an increase in the flux of sediment to the lake system. Even in Lake Kamunzuka, there is evidence for an increase in sediment delivery to the system in the last 20 years of the core record. The increases in sediment flux to the lakes over the last 20-50 years is not unique to the two systems presented here (e.g. Mills, 2009; Mills et al., 2014; Mills et al., 2018). The near simultaneous increase in sediment delivery to the two lakes suggests that there is a regional driver for changes in the recent record, and this is likely related to major human disturbance of the lake catchments (e.g. clearance of natural vegetation for agriculture). The increase in the dry mass accumulation, inferred to mark an increase in the amount of organic and minerogenic material being delivered to the lake system, is coincident with increases in benthic, periphytic and aerophilous diatom taxa in Lake Nyungu, suggesting a causal link between diatom response and catchment disturbance. Although in many instances sediment influx has decreased in the most recent period (late 1990s), the relative abundance of benthic and periphytic taxa remain high. This could be the result of the crossing of a threshold within the lakes.

There is evidence of increasing human impacts over the last 150 years in the region of western Uganda, with changes in catchment vegetation due to the replacement of forest with agriculture (Ssemmanda et al., 2005). Vegetation changes affect catchment hydrology, and it is likely that the diatom assemblage changes are driven by nutrient enrichment and/or changes in the turbidity of water, and hence light availability (Battarbee, 2000; Verschuren, 2003). The removal of catchment vegetation for small-scale agriculture and plantations could have a large effect on the amount of sediments delivered to the lake and the rates of sediment delivery to the system in the last 50 years is unprecedented when compared to the preceding decades.

The increase in the delivery of sediments to the lake systems is also likely to have caused an increase in the amount of nutrients delivered to the lake system. Increasing nutrients can lead to the deterioration of lake water quality, largely through eutrophication. Cultural eutrophication of lake waters occurs as a result of human activity within the lake's catchment that increases the nutrient input to the aquatic ecosystem, which can in turn increase algal productivity and can lead to water quality issues and deep-water anoxia (Smith, 1998). Whilst many studies have shown that early societies have modified catchments (e.g. removal of vegetation for agricultural purposes) and therefore water chemistries of lakes in Europe (Fritz, 1989), tropical America (Anselmetti et al., 2007) and North America (Ekdahl et al., 2004), the study of human impacts on lacustrine ecosystems and the onset of cultural eutrophication in eastern Africa, has been limited to the larger lakes, such as lake Victoria (Verschuren et al., 2002) and Malawi (Hecky, 2000). The only exception to this is a comparative study of data over a 30-year span (1971-2000) at Lake Saaka, near Fort Portal, which suggested that eutrophication had occurred over the time period in question. Although this study was based on one dataset collected in 1971 (Melack, 1978) and compared to data collected during monthly monitoring between 1995 and 1998, it indicated that the lake had been undergoing cultural eutrophication since the 1970s. This eutrophication was attributed the enlargement of a prison farm and agricultural expansion on the flanks of the crater as well as the introduction of Nile perch in the 1970s which would have caused alterations to the food web, leading to the observed increase in trophic state (Crisman et al., 2001).

It is likely that changes in catchment hydrology (both natural and/or anthropogenic) and the increase in nutrient inputs since the early 1900s has fundamentally, and perhaps permanently, modified the lake ecosystems under investigation. Similar studies from Uganda show enhanced phytoplankton production since AD 1950 and AD 1970 in Lakes Kanyanmukali and Chibwera (Bessems et al., 2008), though only the change in Kanyanmukali is attributed to cultural eutrophication as a result of subsistence agriculture within the lake's catchment.

4.5 Palaeolimnology and lake management

Palaeolimnology is a valuable tool which can be used to provide long term records of ecological and environmental change in lakes, and, therefore, as an evidence-base to inform the future management of lake systems (Sayer et al., 2012). Its use has been proposed to assist with large scale water quality monitoring and restoration projects such as the EU Water Framework Directive (Bennion and Battarbee, 2007). Palaeolimnological studies from the Ugandan crater such as those described here are a promising, but currently underutilised, tool for informing the management of these systems.

Palaeolimnological datasets are a cost-effective way of adding to and extending datasets back in time, which improves our ability to understand the range of drivers of environmental changes (Bennion and Battarbee, 2007) and identify which are particularly important in a given system (Moorhouse et al., 2018). Multi-proxy studies in particular, and their integration with modern limnological and catchment datasets, can establish the relative importance of such drivers (Davidson and Jeppesen, 2013). Furthermore, core data complement monitoring data in terms of temporal scale. While monitoring data is highly sensitive to short term variability, the time integrated nature of palaeolimnological datasets means that the 'noise' associated with high frequency data is smoothed and is therefore can be easier to interpret with regards to long term change (Bennion and Battarbee, 2007).

Palaeolimnology is also able to provide a 'baseline' of conditions for a lake or region prior to catchment disturbance and recent climate changes, as lake monitoring often post-dates these (Bennion et al., 2010). This multi decadal, or centennial perspective is often a far more appropriate baseline with which to compare current lake water conditions to, and for setting management targets in relation to (Bennion and Battarbee, 2007; Bennion et al., 2010).

5. Conclusions

The variability of lakes, both physically and chemically, is well known and has been intensively studied in temperate regions, with many long-term monitoring stations in place. In comparison, tropical lakes are under-studied, with many of the published studies based on just a single sample per lake (Escobar et al., 2020). The lack of knowledge regarding the functioning of these lake systems in tropical regions can lead to generalisations (Hutchinson, 1957, Talling and Lemoalle, 1998) which have consequences in terms of our ability to successfully manage these systems.

The results presented here show a clear regional pattern of lake change in western Uganda over recent decades but highlight the numerous drivers that could drive these changes and that, despite some general patterns, not all lake systems behave in the same way. The importance of a co-ordinated monitoring approach is therefore clear, with palaeolimnology able to provide a much-needed longer term perspective, and a baseline to these recently observed trends. The importance of understanding each lake on its own merits, from a monitoring or palaeolimnological perspective is also highlighted.

Palaeolimnology provides a potentially logistically and economically friendly way of retrospectively monitoring lakes through time, especially when combined with targeted shorter-term monitoring programmes. Combined they provide the potential to inform management decisions to sustain lake ecosystems in a healthy state, for the benefit of all users.

The work described and discussed in this paper leads to a number of specific recommendations for future academic and policy driven research projects for east African lakes:

- A co-ordinated, ongoing monitoring of multiple lakes across the region, including standardisation of field and laboratory practises to allow comparison and amalgamation of datasets.
- Clear protocols for access (for uploading and downloading data) to databases.
- Multiproxy core studies to capture potential drivers and lake responses and to provide benchmarks for management targets.
- A landscape palaeolimnological approach i.e. using multiple sites to understand how different lake systems may respond to common drivers.

Acknowledgements

The authors thank the Uganda National Council for Science and Technology (UNCST permit NS609) and the Uganda Wildlife Authority (UWA permit UWA/COD/96/05) for permission to conduct the required field research. Financial support for this research was provided by grants from the Natural Environment Research Council (NE/D000157/1) to DBR, the British Ecological Society (SR16/1371) to KM, a Doctoral Training Partnership grant (NE/L002604/1) and a British Geological Survey University Funding Initiative stipend to LH. This research was also supported by the British Geological Survey's NC-ODA grant (NE/R000069/1) *Geoscience for Sustainable Futures*. The authors are indebted to Richard Nyakoojo for all his assistance in the field, as well as to the local communities who generously facilitated our access to the lakes so we could undertake sampling. The authors also thank

the reviewers and editors for their suggestions and contributions to this manuscript.

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