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Latest Pleistocene and Holocene primary producer communities and hydroclimate in Lake Victoria, eastern Africa

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ABSTRACT

The Lake Victoria ecosystem is emblematic of the catastrophic effects that human activities, particularly cultural eutrophication, can have on freshwater biodiversity. However, little is known about the long-term spatial and temporal pattern of aquatic primary paleo-production (PP_{aq}) and producer communities in Lake Victoria and how these patterns relate to past climate variability, landscape evolution, lake hydrology, mixing regimes, nutrient cycling, and biodiversity dynamics in the past 17 kyr. We use sediments from four well-dated cores along a transect from offshore to nearshore sites, and exploit XRF element scanning and hyperspectral imaging data, TC, TN, bSi, $\delta^{13}C$ and $\delta^{15}N$, and sedimentary pigments to investigate paleolimnological variability and change. Our findings demonstrate that changes in PP_{aq} and algal communities during the past 17 kyr were closely related to hydroclimatic changes, lake mixing, and nutrient availability. During the wetland phase (16.7–14.5 cal ka BP), PP_{aq} levels remained generally low, while chromophytes and chlorophytes dominated the algal community. Following the rapid lake level rise (~14.2 cal ka BP) during the early African Humid Period (AHP), PP_{aq} levels steadily increased, accompanied by a shift towards cyanobacteria and chromophytes. During the Holocene, our results suggest repeated short-lived arid intervals (~10.5, ~9, 7.8–7.2, ~4, and 3.2–3.0 cal ka BP) and two distinct periods of enhanced lake mixing associated with high PP_{aq} and high diatom productivity: the first one between 11 and 9 cal ka BP, which coincided with the maximum of the AHP (high precipitation, high wind, enhanced mixing), and the second, less pronounced one, between 7 and 4 cal ka BP. Between these two periods (i.e. 9–7 cal ka BP) we observe reduced diatom productivity, relatively low PP_{aq} , and high C/N ratios, suggesting conditions with more stable lake stratification, likely associated with reduced wind strength, and some nutrient limitation (N and P). Finally, the drier conditions around the end of the AHP (ca. 4 cal ka BP) and during the late Holocene were associated with decreasing lake mixing and increasing dominance of cyanobacteria. Given our reconstruction of PP_{aq} over the past 17 kyr, we conclude that the levels in the 20th century are unprecedentedly high, consistent with the massive human-mediated impact on the Lake Victoria ecosystem including biodiversity loss.

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1. Introduction

Lake Victoria, the largest freshwater lake in the tropics, is renowned for its unique aquatic biodiversity (Sayer et al., 2018) and holds significant socio-economic value for the surrounding countries (Nyamweya et al., 2023). Over the course of the last century, however, Lake Victoria has faced profound environmental challenges including eutrophication, the introduction of invasive species, and land use changes in the catchment, among other challenges, that have substantially altered the ecological functioning and sustainability of ecosystem services (Gikuma-Njuru and Hecky, 2005; Njagi et al., 2022; Sitoki et al., 2010).

In Lake Victoria, eutrophication due to anthropogenic activities has been documented to have left signatures that date back the 1920s (Hecky et al., 1994) and led, for instance, to the development of hypoxia and harmful algal blooms (Hecky et al., 1994; Onyango et al., 2020), increased abundances of primary producers, shifts in zooplankton composition, loss of fish biodiversity and, finally, to a much simpler food web structure (Kaufman, 1992; van Zwieten et al., 2016). However, given the complex interaction between abiotic and biotic factors controlling aquatic ecosystems, the interconnectivity between catchment and lake processes, and the relatively short observational periods, it is unclear whether currently observed changes and states of the aquatic ecosystem exceed the range of past long-term patterns of variability (Johnson et al., 1996; Temoltzin-Loranca et al., 2023a; Wienhues et al., in press). Additionally, it is uncertain to what extent changes in the aquatic ecosystem are controlled by the manifold potential determining factors (climate, nutrient cycles, vegetation, and others).

Aquatic primary production is frequently used to assess the trophic status of lake ecosystems (Jones and Smol, 2024; Michelutti and Smol, 2016). Several methods exist to reconstruct long-term (centennial to multi-millennial) variability of aquatic primary production (PP_{aq}) from lake sediments (e.g., organic C, N, bSi, diatom-inferred total P, sedimentary chlorophylls and their diagenetic products), but interpretations can be quite challenging. This is because PP_{aq} can be affected by many potentially interacting factors, such as climate (temperature, solar radiation, wind), nutrient dynamics in the catchment and the lake, hydraulic changes, lake mixing, light conditions and transparency of the lake water, and aquatic food web structure (Jones and Smol, 2024). Furthermore, basin-wide assessments of PP_{aq} can be complicated by large spatial variability within a lake, which is also documented from contemporary studies for Lake Victoria (Frank et al., 2023; Gikuma-Njuru et al., 2013). It is also well established that interpreting sedimentary PP_{aq} proxies can be challenging because they can undergo substantial diagenetic alteration (Rydberg et al., 2020).

Records of sedimentary photosynthetic pigment biomarkers and their diagenetic products can offer more detailed insight into past communities of primary producers (mainly phytoplankton), although their low taxonomic resolution limits species-level distinction. Nevertheless, these records can serve as informative indicators of associated ecological conditions (e.g. light and nutrient conditions, thermal stratification) and aquatic food web structure (Gikuma-Njuru et al., 2013; Leavitt and Hodgson, 2001). Analysis of sedimentary pigments is common in mid- and high-latitude or high-elevation lakes, but rare in tropical and subtropical lakes, particularly in Africa (Loakes et al., 2018; Meyer et al., 2018; Saulnier-Talbot et al., 2018; Uveges et al., 2020). In such conditions, high temperatures and accelerated decomposition enhance the potential for pigment degradation already in the water column, making them less likely to be preserved in the sediment (Buchaca et al., 2019). It remains an open question whether sedimentary pigments from warm tropical lakes such as Lake Victoria yield interpretable and reliable data useful for paleoenvironmental interpretations.

Hence, the objective of our study is to investigate: (i) the detectability and degree of preservation of pigments in the sediments of Lake Victoria and their use as proxy indicators of PP_{aq} under tropical conditions, (ii) to explore the spatio-temporal variability of PP_{aq} and primary producer communities since the Late Pleistocene re-filling of Lake

Victoria after 17 cal ka BP and, (iii) to examine the likely environmental factors controlling primary production during the latest Pleistocene and Holocene. To reach these objectives, we use sediments from four well-dated cores along a transect from offshore (63 m water depth) to near-shore (13 m water depth) that span the last 17 kyr (Temoltzin-Loranca et al., 2023a). The transect embraces a wide range of ecological conditions across the lake. The recently refined chronology of the lake's refilling during the latest Pleistocene (Wienhues et al., in press) and new information on regional vegetation dynamics and fire regimes from palynological and charcoal evidence (Temoltzin-Loranca et al., 2023a, 2023b) provide the hydroclimatic and catchment-process context for changes in PP_{aq}, along with the documented shifts in invertebrate and fish dynamics (King et al., 2024; Ngoepe et al., 2023, accepted). A better picture of the time-space transgressive variability of PP_{aq} and its underlying causes in Lake Victoria will help to better understand trajectories of the lake ecosystem evolution under multiple stressors through time. Our results may also provide information on lake eutrophication and its effects on evolutionary dynamics of biodiversity generation and loss by delivering new insights into potential first-order effects of internal changes in the lake's biogeochemical conditions.

2. Materials and methods

2.1. Study area

Lake Victoria (0.5 °N to 3.0 °S; 68,800 km², 1135 m asl) is located in equatorial eastern Africa between two branches of the East African Rift Valley (Fig. 1). The lake is relatively shallow, with a mean water depth of ~40 m and a maximum water depth of 68 m (Johnson et al., 1996).

Modern Lake Victoria is a hydrologically open lake and responds sensitively to rainfall variations (Beverly et al., 2020; Yin and Nicholson, 1998). The hydrological budget is controlled by direct precipitation (>80% of incoming water) and lake surface evaporation (~70% of outgoing water) (Yin and Nicholson, 1998). River runoff makes only a limited contribution to the water input (Crul, 1995) and the lake drains through the Victoria Nile in the north. The tropical climate is characterized by two distinct rainy seasons with long rains (March–May) and short rains (October–December). Moist air masses derive from the Indian and Atlantic Oceans, respectively, and are mainly governed by the interplay between the north-south migration of the Afrotropical rain belt and the west-east movement of the Congo Air Boundary (CAB).

Currently, Lake Victoria is monomictic, with the water column overturning during the cooler and windier dry season from May to August. Progressive eutrophication during the 20th century resulted in more stable lake stratification and anoxic bottom waters (Hecky et al., 1994; Verschuren et al., 2002), which are estimated to cover more than 40% of the lake's bottom area (Hecky et al., 1994). The rise in aquatic primary production was accompanied by a shift from diatoms to cyanobacteria blooms and this coincided, along with the introduction of Nile perch in the 1950s, with a dramatic loss of fish biodiversity (Mugidde, 1993; Hecky et al., 1994; Stager et al., 2009; Ngoepe et al., accepted).

2.2. Sediment chronologies

A series of UWITEC piston cores were obtained in October 2018 along a depth transect off the eastern shoreline (Fig. 1A-B). From multiple parallel cores at each coring site, continuous master composite cores were established for four coring sites namely LVC18-S1 to LVC18-S4 (hereafter referred to as LV1 to LV4). The water depths at the coring sites range from 13.4 to 63 m below the modern lake level (m.b.l.l.) (Fig. 1C-D) (Wienhues et al., in press). Radiocarbon chronologies for LV1, LV2, LV4 (Temoltzin-Loranca et al., 2023a), and LV3 (Wienhues et al., in press) were established based on sieved, handpicked and taxonomically identified terrestrial plant macrofossils and charcoal using ¹⁴C AMS MICADAS dating and Bacon age modeling (Blaauw and

Christen, 2011). Details of these complex chronologies are provided in Temoltzin-Loranca et al. (2023a). The stratigraphic positions of the ^{14}C dates in the composite cores are marked in Fig. 1D.

2.3. Geochemical methods

Multiple non-destructive geochemical analyses (XRF and hyperspectral imaging) on fresh split core halves were performed prior to discrete subsampling for biogeochemical analyses (10 or 20 cm intervals, 1–3 cm³; Table S1).

Scanning X-ray fluorescence (XRF) was carried out using a Cr-anode (for LV1-3) and both Mo- and Cr-anode X-ray tube (LV4) on the ITRAX core scanner at the Institute of Geological Sciences, University of Bern. XRF measurements were performed at 50 mA, 30 kV, and 30 s integration time with 5 mm (LV4, 1 and 2) and 10 mm (LV3) intervals. For further analyses, we selected key XRF elements and elemental ratios based on data quality and interpretations of interest (Davies et al., 2015): Zr, Ti, Fe, and K represent lithogenic sediments; Si/Ti is interpreted as biogenic Si (bSi) and Rb/K relates to chemical weathering and hydroclimate.

Hyperspectral imaging (HSI) scans were performed on fresh split-core halves following Butz et al. (2015). The relative absorption band depth index (RABD655–680max) was used to quantify the absorption trough of total green chloropigments (TChl including chlorophyll *a*, *b*, and colored degradation products) and is interpreted as total algal abundance and a proxy for aquatic paleo-productivity (Michelutti and Smol, 2016). Further methodological details are described in Butz et al. (2015) and Zander et al. (2022).

Total carbon (TC), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were measured on homogenized, freeze-dried samples packed in tin capsules using a ThermoFisher Flash-

EA 1112 coupled with a ConFlo IV interface to a ThermoFisher Delta V isotope ratio mass spectrometer (IRMS) at the Geological Institute, ETH Zurich. Isotope ratios are reported in the conventional δ -notation with respect to atmospheric N₂ (AIR) and VPDB (Vienna Pee Dee Belemnite) standards, respectively. Analytical reproducibility of the measurements is better than 0.2 ‰. Due to the absence of inorganic carbon in the sediment (tested by CNS analysis on ashed samples), samples were not acidified prior to isotopic analysis. Thus, TC reflects total organic carbon (TOC) in these samples.

Biogenic silica (bSi) analysis followed the wet-alkali method of Ohlendorf and Sturm (2008). Extracts were measured with ICP-MS (Agilent ICP-MS 7700x). Organic matter was removed by H₂O₂ prior to leaching (Mortlock and Froelich, 1989). The solid residual after bSi leaching was used for grain size distribution analysis by laser diffraction, using a Malvern Mastersizer 2000 instrument (Fig. S4).

For LV1, sequential phosphorus extraction was performed on 200 mg homogenized, dry samples following the standardized SMT protocol of the European Commission (Ruban et al., 1999, 2001; Tu et al., 2021; Williams et al., 1976). Phosphate concentrations were determined photometrically through the malachite green method (Ohno and Zibilske, 1991; Tu et al., 2021). Analytical efficiency was controlled with the certified reference sediment material (CRM) BCR-684 and showed good agreement (Table S2).

Sedimentary pigments were extracted following Sanchini and Grosjean (2020). The pigment extracts were quantified with high performance liquid chromatography (HPLC) at the CNR Water Research Institute in Verbania, Italy (method by Lami et al., 2000). All HPLC pigment concentrations were expressed as nMol per g of organic carbon to minimize matrix dilution effects by clastic sediment (Lami et al., 2000).

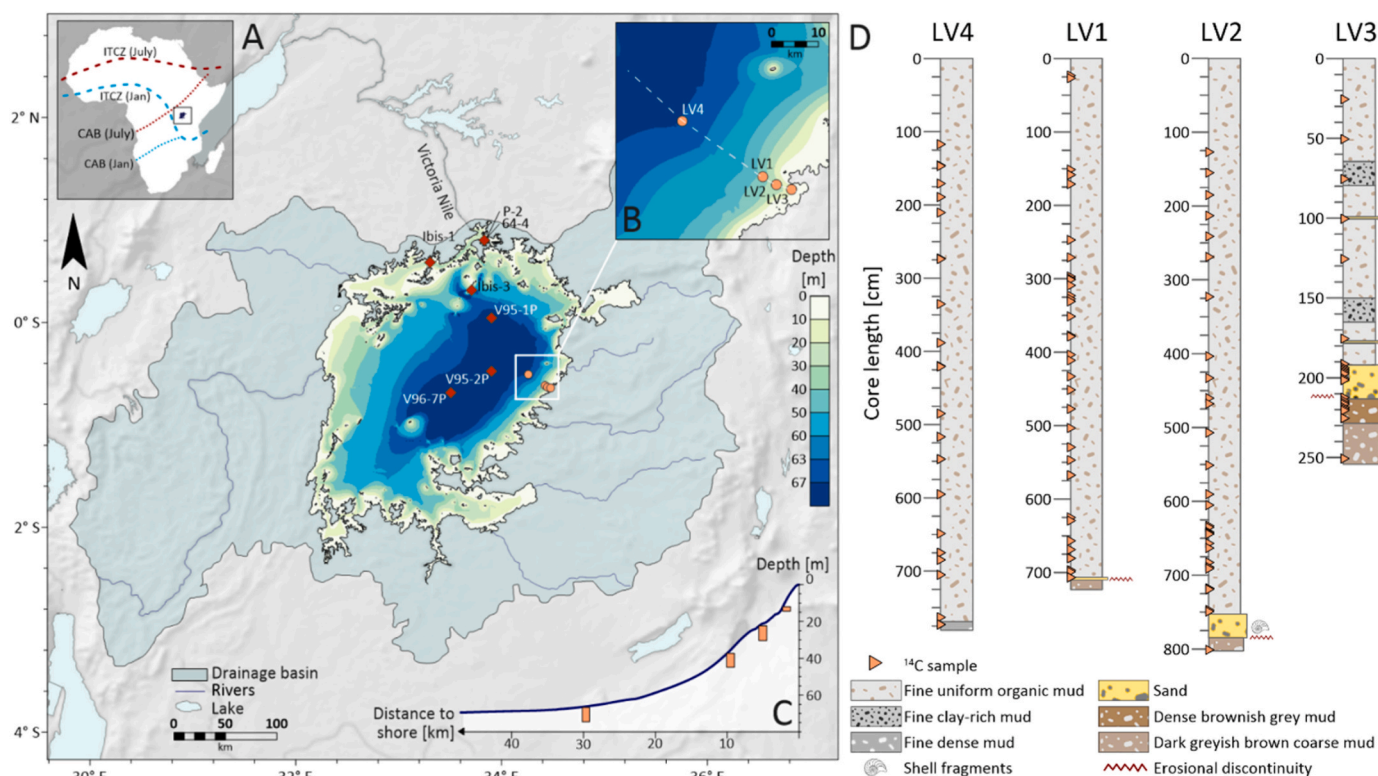


Fig. 1. Catchment and bathymetry of Lake Victoria with sediment cores (LVC18-S1 to LVC18-S4; hereafter referred to as LV1 to LV4, this study, orange circles) and previously collected cores (red diamonds) (A) Inset map of the African continent with the location of Lake Victoria and the position of the Intertropical Convergence Zone (ITCZ) and CAB during the months January and July. (B and C) Inset map and depth profile of the coring transect (adapted from Wienhues et al., in press). (D) Sediment core lithologies from LV1-4. The positions of ^{14}C dates are denoted as triangles (Temoltzin-Loranca et al., 2023a, Wienhues et al., in press).

2.4. Statistical analyses

All statistical analyses were performed using R v4.1.2 (R Core Team, 2021). XRF and HSI data were averaged to 0.5 cm resolution (for LV3 at 1 cm). The data were transformed using the centred log ratio (clr) transformation (Aitchison, 1982) and scaled prior analyses. A principal component analysis (PCA) was conducted on a correlation matrix using the `veganrda` function (Oksanen et al., 2022). Unconstrained cluster analysis was done using the `ward.D2` clustering method with the Euclidean distance (Murtagh and Legendre, 2014) to delineate sediment sections with similar geochemical compositions (lithotypes). Additionally, stratigraphically constrained cluster analysis (CONISS) clustering (Grimm, 1987) was applied to divide the core sequences into sediment units using the R package `rioja` (Juggins, 2015). The number of significant clusters and principal components was determined based on the broken-stick model (Bennett, 1996).

A separate CONISS clustering was performed on the HPLC sedimentary pigment dataset (pigment zones). We selected pigments that can be associated to algal groups. Pigment concentrations were Hellinger-transformed and scaled prior to analysis. A broken-stick model was used to determine the number of pigment zones (Bennett, 1996).

3. Results and interpretation

3.1. Lithotypes and primary production

At our deepest coring site (LV4), cluster analysis on selected biogeochemical XRF and HSI proxies revealed five lithotype-clusters (hereafter lithotypes) and five CONISS zones (Units I – V), whereby the boundaries of the lithotypes and the units closely match each other (Fig. 2).

The basal sedimentary Unit I in LV4 (16.7–14.5 cal ka BP; 778–692 cm; Fig. 2; coring site at 63 m water depth) is characterized by clastic, fine, dense mud with high Zr, Ti, Fe, and K counts and low PP_{aq} (low TChl, Br, Si/Ti), representing sedimentation in a landscape with shallow, episodically dry ponds. These ponds were surrounded by extended wetlands during the dry period prior to 16.2 cal ka BP (Wienhues et al., in press). The highest values of clastic indicators (Zr, Ti, Fe, K) are found in the basal part of the core where dry bulk density is high and water content low. From 16.2 cal ka BP onwards, fine uniform organic mud was deposited, still in a pond-wetland environment.

In Unit II (between 14.5 and 11.5 cal ka BP; 692–565 cm), the deposition of fine, uniform, organic mud continues. At 14.2 cal ka BP, a

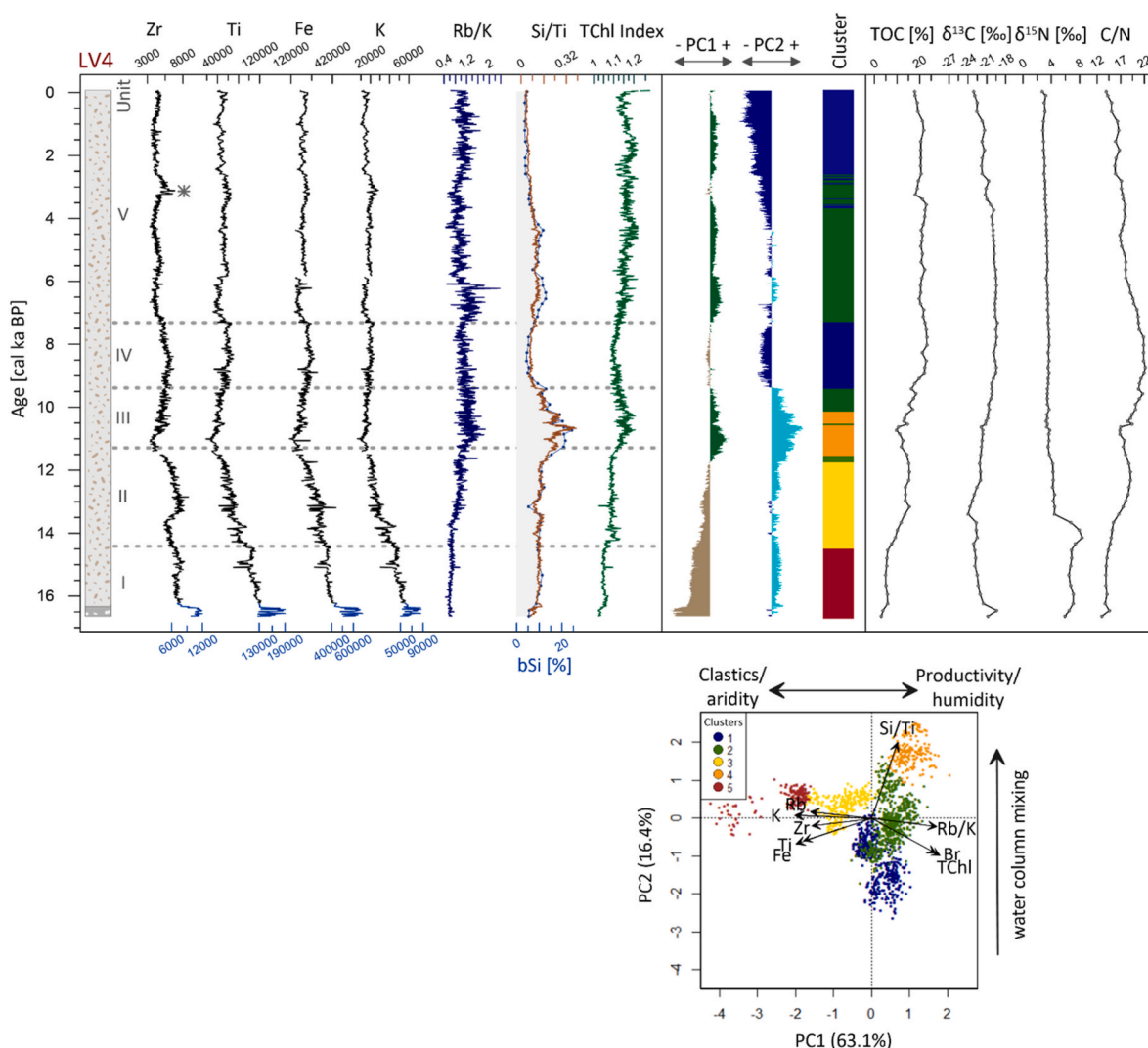


Fig. 2. Selected bio-geochemical variables (XRF, HSI, bSi, TOC, $\delta^{13}C$, $\delta^{15}N$, and atomic C/N ratio) and PCA scores plotted against age for LV4. For Zr, Ti, Fe, and K, the blue color refers to the scale at the bottom. The colored bar shows the lithotypes identified by unconstrained cluster analysis. The stratigraphically constrained cluster boundaries (Units I–V) are shown as horizontal dashed grey lines. The position of the potential cryptotephra is indicated with an asterisk (Lane et al., 2018). The principal component biplot shows the first two principal components with loadings of each variable depicted as black arrows. Data points in the PCA biplot are grouped and colored by cluster/lithotype. The corresponding figures for LV1–3 are shown in Supplementary Material (Figs. S1–S3).

first marked increase of PP_{aq} is recorded (TChl), whereas lithogenic indicators (Ti, Fe, K) continuously decrease towards a minimum at 11.2 cal ka BP. In this period, Si/Ti largely correlates with bSi concentrations, suggesting the predominantly biogenic origin of excess Si (Si/Ti; silicified algae, Brown, 2015). The sediments of Unit II reflect deposition in the rapidly infilling lake between 14.2 and 13 cal ka BP and the subsequent establishment of the modern lake with an overflow towards the Nile (Wienhues et al., in press).

Sediments of Unit III (11.5–9.5 cal ka BP; 565–427 cm) still consist of fine, uniform, organic mud. At the onset of the Holocene, a further pronounced increase in PP_{aq} is observed. Smear slide analysis and high bSi, Si/Ti values suggest that the increase in TChl in Unit III is mostly related to diatoms. In Lake Victoria, high diatom abundance has been interpreted mainly as indicative of enhanced water column mixing (Gikuma-Njuru et al., 2013; Johnson et al., 1998; Stager et al., 2003; Stager and Johnson, 2000; Stager and Mayewski, 1997). Most likely, allochthonous input of nutrients from the catchment was enhanced due to increased rainfall during that time (Cockerton et al., 2015; Kendall, 1969). A rapid increase in precipitation is also supported by elevated Rb/K ratios and a further lake level rise around 10.8 cal ka BP (Wienhues et al., in press). The relatively low values of clastic indicators (Zr, Ti, Fe, K) are related to enhanced deposition of biogenic components in the sediment (matrix effect, bSi >20%) and higher sedimentation rates (Temoltzin-Loranca et al., 2023a) rather than reduced allochthonous sediment flux.

Unit IV (9.5–7.2 cal ka BP; 427–326 cm) continues with the deposition of fine uniform organic mud. In contrast to the diatom-rich Unit III, sediments of Unit IV suggest lower PP_{aq} (TChl), specifically lower diatom production (bSi, Si/Ti), which points towards reduced mixing and enhanced water column stratification. Rb/K remains at high levels suggesting continuing strong chemical weathering (Davies et al., 2015, Wienhues et al., in press) and humid hydroclimatic conditions.

Sediments of Unit V (7.2 cal ka BP – Present; 326–0 cm) still consist of fine uniform organic mud. Visually, there is no difference to the sediment in Unit IV. Conditions remained overall very stable during the mid-to-late Holocene. Unit V starts with a local maximum in diatom production (high bSi and Si/Ti, enhanced lake mixing) and Rb/K (chemical weathering, hydroclimate), and a concomitant local minimum in clastic indicators between 7.2 and 5.8 cal ka BP. Overall, PP_{aq} (TChl) remains very high with slightly increasing trends towards 1 cal ka BP followed by weakly decreasing trends in the last millennium. BSi concentrations start declining already around 4.2 cal ka BP. Peaking TChl values in the uppermost part of the core reflect the contemporary eutrophication evident since the last century (Hecky et al., 1994; Verschuren et al., 2002). A short-term peak of Zr at 3 cal ka BP may correspond to a cryptotephra layer previously described in the V95–1P core and dated to 3151–2537 cal yr BP (Lane et al., 2018). This aligns with a prominent anomaly of magnetic susceptibility observed in several other LV cores (Johnson et al., 2000).

PCA of the entire LV4 core shows that negative scores of PC axis 1 (PC1, 63.1% of the variance, Fig. 2) are associated with clastic lithogenic indicators (Zr, Ti, Fe, K, Rb) whereas positive PC1 scores are associated with PP_{aq} (TChl, Br, Si/Ti) and humid hydroclimate (Rb/K). Therefore, the scores of PC1 reflect the change from clastic sedimentation under late-glacial dry conditions to organogenic sediment driven by increasing PP_{aq} and humidity at the onset of the Holocene (11.7 cal ka BP). Accordingly, PP_{aq} maxima are found between 11.7 and 9.5 cal ka BP and, with a few exceptions, from 7.2 cal ka BP onwards. PC axis 2 (PC2, 16.4% of the variance) is mainly driven by Si/Ti (diatom productivity; interpreted as lake mixing; Stager and Johnson, 2000). Accordingly, positive PC2 scores suggest well-mixed conditions between 16.5 and 9 cal ka BP, in particular between 12 and 9 cal ka BP, and around 6 cal ka BP whereas periods with higher water column stability are found between 9 and 7 cal ka BP and from 4 cal ka BP onwards.

For comparison, the lithotypes, clusters, and PCA of the cores from the shallower sites (LV1–LV3) are shown in Figs. S1–S3. Despite the differences in water depth at the coring sites, the lithotypes in LV1, LV2

and LV3 exhibit a geochemical composition which is similar to the one observed in LV4 (the colors in Figs. S1–S3 represent similar lithotypes as in LV4, Fig. 2). Significant differences among the cores are found in the basal sand layers in LV2 and LV3, and in two clay layers in the near-shore core LV3. At the deepwater sites (LV1 and LV4), the variability in the sediment composition is primarily explained by changes in PP_{aq} (PC1) and water column mixing (PC2). Conversely, at shallower sites (LV2 and LV3), sediment variability is increasingly controlled by clastic components and grain size (PC2 in LV2, PC1 in LV3). Furthermore, and in contrast to the offshore sites, bSi concentrations correlate only poorly with Si/Ti ratios at the more littoral sites, suggesting that nearshore Si sources are more mixed. Overall bSi concentrations are substantially lower in the cores LV1 (max. 4 wt%, 38 m water depth) and LV2 (max. 9 wt%, 23 m water depth) than in the centre of the lake at LV 4 (max. 15 wt%, 63 m water depth). This agrees with the increasing relative importance of clastic sediments with greater proximity to the shore.

The frequency and position of the cluster and zone boundaries reveal differences between the four cores along the transect. Notably the deepwater core LV4 exhibits the most pronounced alterations in the geochemical composition during the initial part of the record after 16.7 cal ka BP until 7.2 cal ka BP. In contrast, the intermediate cores LV1 (38 m.b.l.l.) and LV2 (23 m.b.l.l.) demonstrate higher variability in the mid-to-late Holocene. In the case of LV1 (38 m.b.l.l.), periods of elevated PP_{aq} (TChl, bSi) are observed from 6 to 3.2 cal ka BP and from 1.8 cal ka BP onwards. Similarly, LV2 shows enhanced PP_{aq} (TChl, bSi) from 1.7 cal ka BP onwards and less pronounced between 8.7 and 6.2 cal ka BP.

Among all cores, the nearshore core LV3 (13 m.b.l.l.) displays the largest and most visible lithological changes. In contrast to the three other cores, LV3 shows two clay-rich layers (rich in K, K/Al) between 10.7 and 9.5 cal ka BP and between 6.5 and 5.5 cal ka BP, respectively. In LV3, PP_{aq} (TChl) increases substantially around 2.5 cal ka BP whereas PP_{aq} in LV1, 2, and 4 remains largely stable until the 20th century and increases rapidly thereafter. A distinct Zr peak around ~8.4 cal ka BP is observed in both LV1 and LV2, but not in LV4 and LV3. The reasons are not known but could be related to some differential sediment reworking at that time. A cryptotephra is not reported for this time. Additionally, a second local maximum of Zr in LV1 and LV2 around 3.0–1.9 cal ka BP could correspond to the Zr peak associated with the cryptotephra (Lane et al., 2018) in LV4 around 3 cal ka BP.

3.2. Bulk organic geochemistry

In LV4 (63 m.b.l.l.), the TOC content ranges between 3 wt% at the bottom of the core (>16.4 cal ka BP) to high values around 20 wt% in the Holocene (Units IV–V from 9.5 cal ka BP onwards, Fig. 2). The marked decline of TOC concentrations in the diatom-rich Unit III (11.2–9.5 cal ka BP) is attributable to increased bSi and sedimentation rates during that time (Temoltzin-Loranca et al., 2023a). In the more near-shore cores LV1 and LV2, TOC concentrations decrease with increasing lithogenic proportions (Figs. S1 and S2).

In LV1, LV2 and LV4 cores, $\delta^{13}C$ values span from –24 to –19 ‰ (Fig. 1, S1 and S2). Prior to 13.5 cal ka BP, more negative $\delta^{13}C$ values in LV4 likely reflect the abundance of swamp vegetation which yields more negative values than phytoplankton (Meyers, 1997). All cores show a significant trend towards less negative values during lake infilling and establishment (ca. 13.5 cal ka BP and early Holocene) and trends towards more negative values in the mid- and late Holocene. During the Holocene, TOC and $\delta^{13}C$ are positively correlated and reach maxima between 9.5 and 7.3 cal ka BP. The positive correlation suggests a close link between organic matter remineralization and the lake's carbon cycle (Talbot and Lærdal, 2000). Here, high values indicate good organic matter preservation related to more stable water column stratification (low diatom productivity) during that time.

In all cores, the $\delta^{15}N$ values are relatively high with values up to +8.3‰ (LV4) notably in the lower parts of the cores (Fig. 2, S1 and S2) when shallow pond and wetland environments prevailed. In all cores,

$\delta^{15}\text{N}$ values drop sharply at the time of lake level transgression at 13.5 cal ka BP in LV4 (63 m.b.l.l.), at 12.6 cal ka BP in LV1 (38 m.b.l.l.) and at 11.5 cal ka BP in LV2 (23 m.b.l.l.), respectively, when the Nile outflow established northward (Wienhues et al., in press). Afterwards, throughout the Holocene, $\delta^{15}\text{N}$ values remained remarkably stable within a very narrow range (mean values LV1, LV2 and LV4 between 1.9 ‰ and $3.4 \pm 0.5 \text{ ‰}$). LV1 and LV2 show stable $\delta^{15}\text{N}$ values in the early Holocene and slightly negative trends between 8 and 1.2 cal ka BP ranging between +2.7 and +1.2 ‰, and positive trends in the last two millennia. Our data are consistent with the $\delta^{15}\text{N}$ pattern described in the offshore core V95–2P (Talbot et al., 2006).

The C/N ratios in LV4 show a general increase from C/N = 13 (at 16 cal ka BP) to a maximum of C/N = 22 between 10 and 7.3 cal ka BP, followed by decreasing trends to C/N = 14 in modern times (Fig. 2). Similar trends are reproduced in LV1 and LV2, albeit with generally lower values (C/N = 10–16; Figs. S1 and S2). These C/N values are above the values that are typically found in organic matter of purely planktonic origin (C/N < 10; Meyers, 1997). However, smear slide analysis revealed predominantly algal sources of organic matter and did not support terrestrial origin. Talbot and Lærdal (2000) ascribed high C/N ratios in Lake Victoria sediments to algal growth under N-deficient conditions (Healey and Hendzel, 1980; Hecky et al., 1994) and proposed adjusted C/N thresholds for aquatic organic matter sources in the lake (Fig. 3a). Following this argument, nitrogen limitation appears to be most pronounced in the deep water (LV4) and progressively less limiting in shallower regions of the lake (LV1 and LV2; Fig. 3a). This spatial pattern could be explained by closer proximity of the more nearshore sites to N sources from the catchment or stronger light limitations because of more turbid conditions at near-shore sites (Fadum and Hall, 2023; Guildford et al., 2003).

Additionally, Fig. 3b indicates a linear relationship between TOC and C/N. Accordingly, highest C/N values coincide with maximal organic matter (TOC %), peaking between 9 and 7 cal ka BP. From 7 cal ka BP onwards, TOC remains relatively high, while the C/N ratios decline, suggesting a change in organic matter production and preservation.

3.3. Phytoplankton pigment stratigraphy

The sedimentary pigments provide specific information about algal communities. Pigment taxonomic affiliations and their interpretation follow those of Bianchi and Canuel (2011) and Leavitt and Hodgson (2001): Chlorophyll *a* and its derivatives pheophorbide *a*, and pheophytin *a*, and β - β -carotene are indicators for total phytoplankton

biomass and are used as proxies for paleo-productivity (Michelutti and Smol, 2016). Pheophytin *a* occurs in senescent algae, and pheophorbide *a* potentially indicates zooplankton grazing. Diadinoxanthin, diatoxanthin, and fucoxanthin are mainly associated with chromophyte algae (diatoms, dinoflagellates, and chrysophytes). Dincoxanthin and peridinin indicate dinoflagellate algae, whereas alloxanthin is associated with planktonic cryptophytes. Lutein is found in green algae (chlorophytes). Echinenone and zeaxanthin are marker pigments for cyanobacteria, whereas myxoxanthophyll and canthaxanthin are specifically common in colonial cyanobacteria. The pigment oscillaxanthin is characteristic of the filamentous cyanobacterium *Oscillatoria* (Lami et al., 2000). Pigments with episodic occurrence and unidentifiable carotenoids were not included in our analyses but are listed in Table S1.

The CONISS analysis on sedimentary pigments in LV4 revealed four pigment zones (PZ) (Fig. 4a):

PZ-LV4-I (>16.4 cal ka BP; 758 – 778 cm): In the lowest strata of the deep-water site LV4 (>16.4 ka), one single cyanobacteria pigment (myxoxanthophyll) could be detected in its degraded form, suggesting that preservation conditions for pigments and organic compounds were overall poor. This is expected for sediments in a dry environment with frequent desiccation and sub-aerial exposure (Wienhues et al., in press).

PZ-LV4-II (16.4–14.1 cal ka BP; 758 – 668 cm): Green algae (lutein) prevailed, alongside with some chromophytes (diadinoxanthin, fucoxanthin). The presence of fucoxanthin is surprising since this pigment is generally reported as labile (Hurley and Armstrong, 1990). Cyanobacteria (myxoxanthophyll, canthaxanthin, echinenone) are detected continuously but at low concentrations (normalized to C_{org}). Alloxanthin (cryptophytes) and lutein (green algae) are abundant. The high concentrations of pheophorbide *a* and low concentrations of chlorophyll *a* (Fig. 4a and 5) suggest grazing by zooplankton. According to Uveges et al. (2020) and Itoh et al. (2007) lutein is better preserved in zooplankton fecal pellets.

PZ-LV4-III (14.1 – 5.2 cal ka BP; 668 – 168 cm): Most carotenoids show similar patterns between 14.1 and 5.2 cal ka BP with peak relative abundances between 11 and 10 cal ka BP followed by a relative decline ca. 9 cal ka BP and stable conditions until 5.3 cal ka BP (Fig. 2). Diatoxanthin, a pigment indicative of diatoms, emerges at the onset of this pigment zone 14.2 cal ka BP. Increasing abundance of cyanobacteria is suggested by myxoxanthophyll, zeaxanthin, and echinenone between 13.5 and 12.5 cal ka BP. Pheophorbide *a*, indicative of zooplankton grazing (Carpenter et al., 1988; Leavitt and Carpenter, 1990), rises between 14.1 and 9.5 cal ka BP, whereas Chl *a* and pheophytin *a* remain at low levels. Around 13.5 cal ka BP and between 8 and 5 cal ka BP,

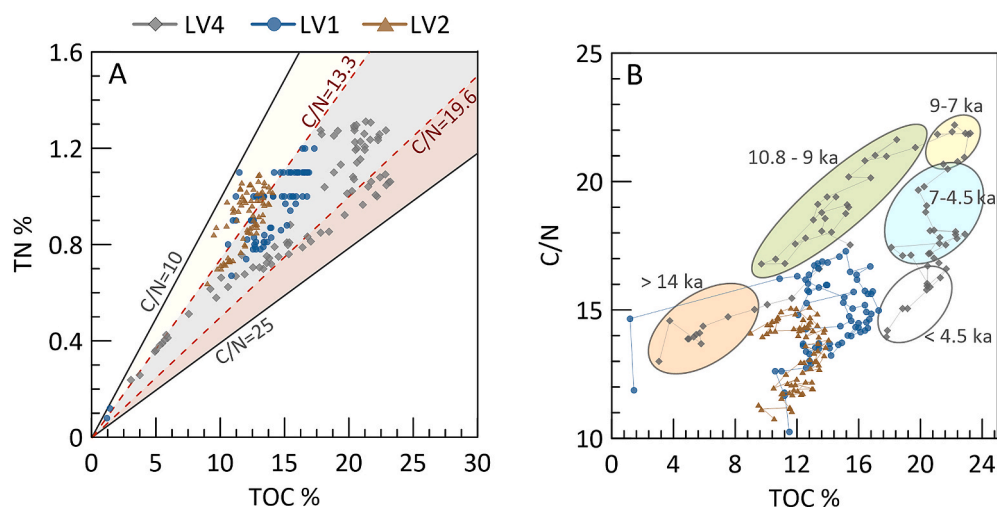


Fig. 3. (A) TOC vs. TN for the cores LV4, LV1, and LV2. C/N boundaries for endmembers (aquatic or terrestrial organic matter; Meyers, 1997). Dashed lines indicate algal C/N composition under moderate and severe nitrogen deficiency (Talbot and Lærdal, 2000). (B) TOC vs C/N for the cores LV4, LV1, and LV2. The LV4 data is subdivided into distinct diatom productivity periods in Lake Victoria presented in Fig. 7.

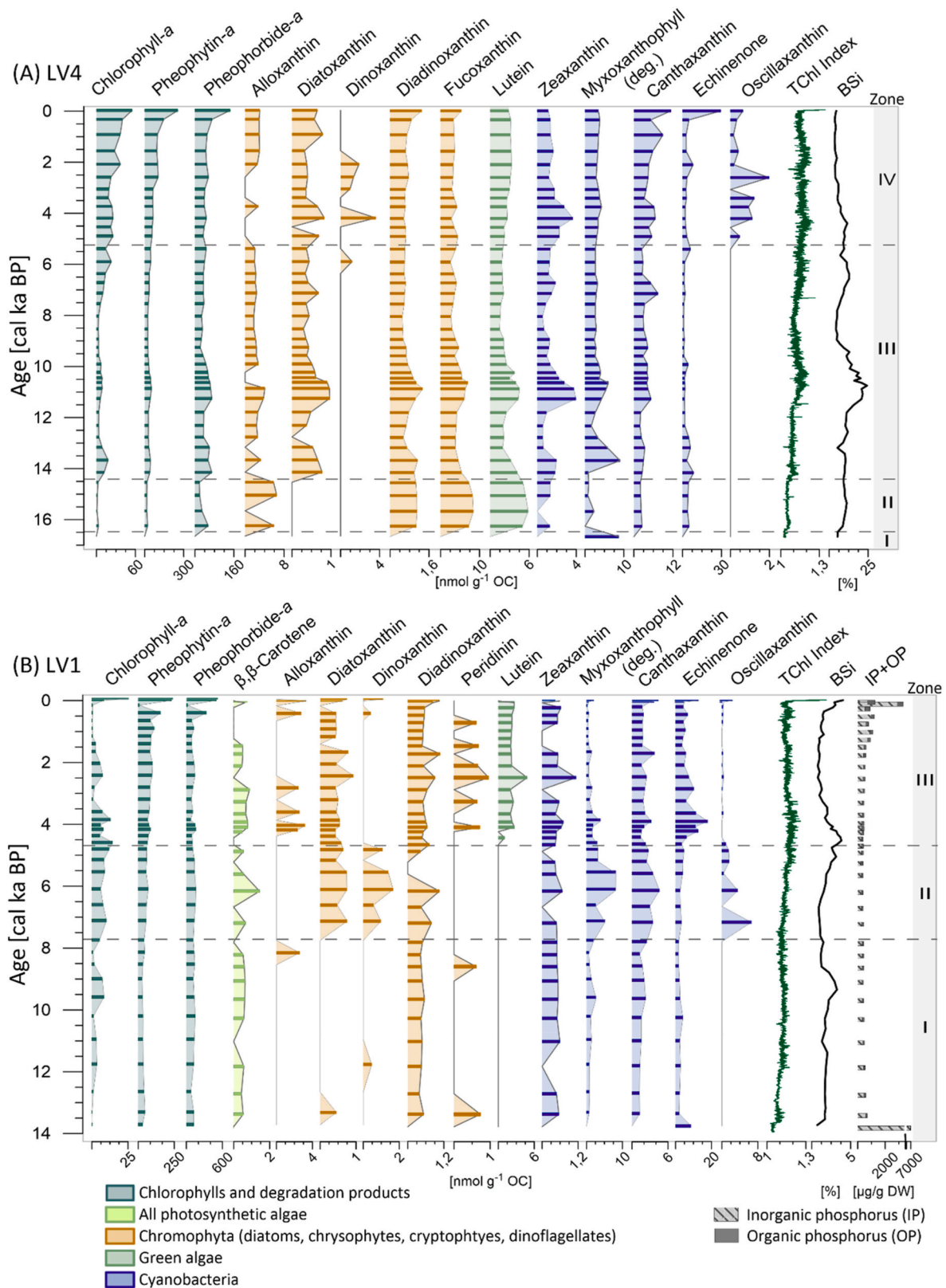


Fig. 4. HPLC sedimentary pigment stratigraphy for (A) LV4 and (B) LV1. Pigment zones were defined by CONISS analyses (far right). TChl Index, BSi, IP, and OP were not included in the cluster analyses.

elevated Chl *a* values suggest better pigment preservation conditions (Swain, 1985). PZ-LV4-III corresponds to the period of rapid lake infilling and the establishment of the modern lake with the Nile overflow (Wienhues et al., in press).

PZ-LV4-IV (5.2 cal ka BP – Present; 168 – 0 cm): The uppermost pigment zone shows a rise in TChl (chlorophylls and diagenetic products) indicating increasing phytoplankton production and/or better pigment preservation. Oscillaxanthin points to a shift to more eutrophic

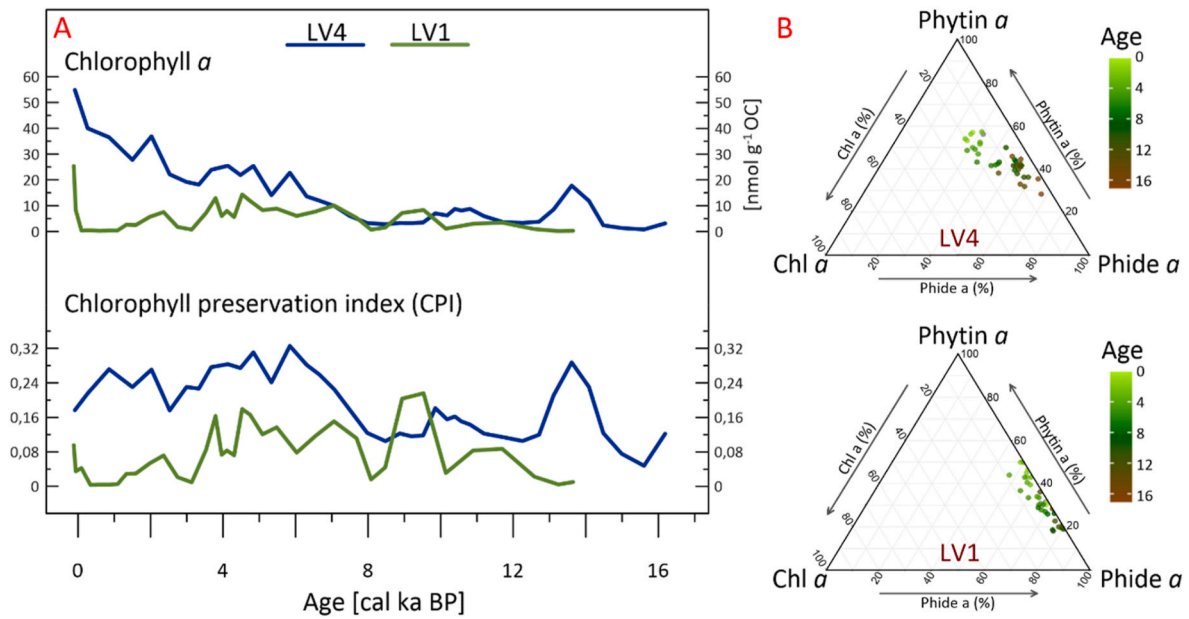


Fig. 5. (A) Time series of Chl *a* and CPI (Chlorophyll Preservation Index) for LV4 and LV1. (B) Ternary diagram for Chl *a* and its degradation products (pheophytin *a* and pheophorbide *a*). Colors indicate the age of the data points (cal ka BP).

conditions as *Oscillatoria* blooms are often found at the initial phase of eutrophication in lakes (Havens et al., 1998). Interestingly, the dinoflagellate-associated dinoxanthin appears along with oscillaxanthin, whereas peridinin, another dinoflagellate pigment, is absent. In contrast, cryptophytes likely became outcompeted since alloxanthin disappears as oscillaxanthin levels peak (5.2–2.4 cal ka BP). The predominance of zeaxanthin (cyanobacteria) over lutein (green algae) suggests a temporal cyanobacteria dominance between 5.2 and 3.6 cal ka BP. Other cyanobacteria pigments (myxoxanthophyll, echinenone) remain relatively constant. Finally, high pigment concentrations (chlorins, cyanobacteria, TChl) in the topmost samples represent the recent eutrophication of the lake.

At LV1 (37 m.b.l.l.), CONISS revealed three pigment zones covering the last 13.7 kyr (Fig. 4b):

PZ-LV1-I (13.7–7.7 cal ka BP; 722–490 cm): This zone is dominated by cyanobacteria (zeaxanthin, canthaxanthin, myxoxanthophyll, echinenone) and some chromophytes, mainly diatoms (diadinoxanthin). Whereas β,β -carotene was not detected in LV4, it is relatively abundant in LV1. Overall, relative pigment concentrations are variable, and low Chl *a* values suggest relatively poor pigment preservation. This limits further interpretations in this zone.

PZ-LV1-II (7.7–4.7 cal ka BP; 490–370 cm): This PZ reveals the most diverse pigment spectra and highest pigment concentrations of the entire core, suggesting a diverse phytoplankton community. During this

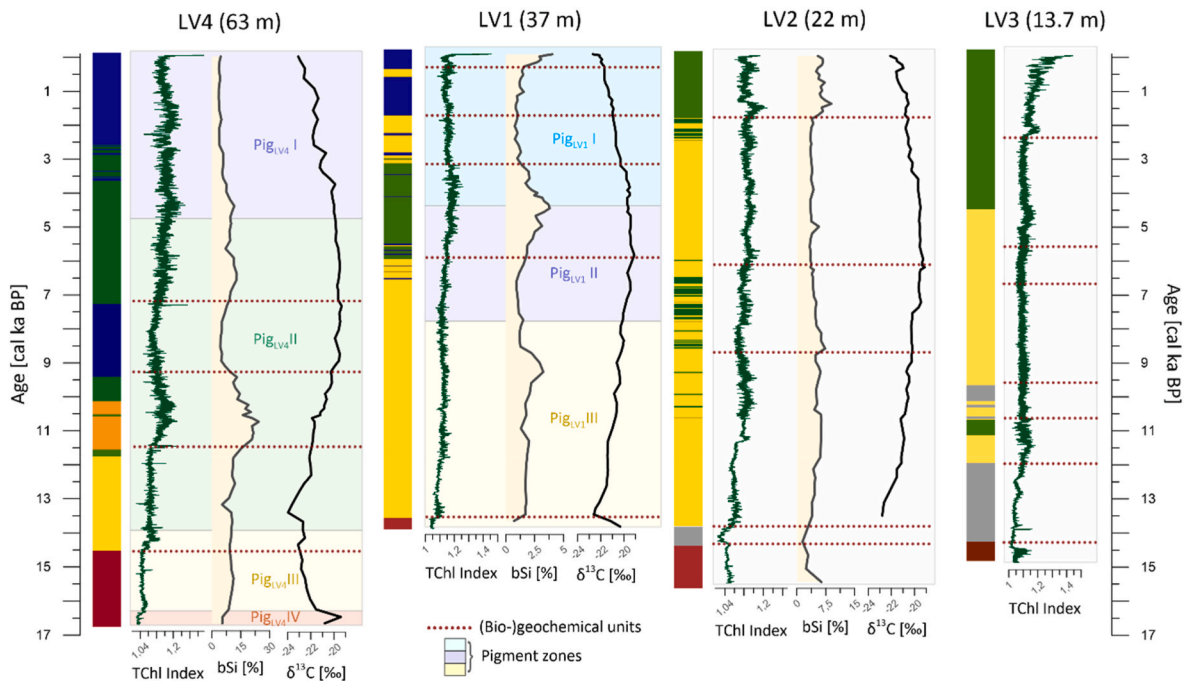


Fig. 6. Compilation of lithotypes, TChl, bSi, $\delta^{13}\text{C}$, sedimentary units (Fig. 2, S1–3) and pigments zones (Fig. 4) across the transect with the four sediment cores (LV1 to LV4).

phase, colonial cyanobacteria (myxoxanthophyll, canthaxanthin and oscillaxanthin) dominate under better stratified water column conditions (low bSi values between 7.7 and 6 cal ka BP; Fig. 6). Enhanced algal blooms and reduced light exposure (better preservation) likely contributed to elevated Chl *a* values during this period. Furthermore, chromophytes (diatoxanthin, dinoxanthin) become abundant. Notably, the pigment composition of PZ-LV1-II resembles that observed in PZ-LV4-IV, suggesting similar conditions in the mid-Holocene mid-shore and late Holocene offshore.

PZ-LV1-III (4.7 cal ka BP – Present; 370 – 0 cm): From 4.7 cal ka BP onwards, the pigments reflect the presence of green algae (lutein), dinoflagellates (peridinin), other siliceous algae (diadinoxanthin, diatoxanthin), and cyanobacteria (echinenone, zeaxanthin, canthaxanthin). The very labile pigment peridinin (dinoflagellates) is sporadically detected within this zone, suggesting good pigment preservation. Cryptophytes (alloxanthin) episodically appear between 4.2 and 2.5 cal ka BP and in the last 500 years. Overall, chlorophyll *a*, β , β -carotene and TChl decrease until reaching a minimum in the 19th century whereas derivatives such as pheophytin *a* and total phosphorus (TP; Figs. 4b, S5) gradually increase.

3.4. Chlorin and pigment preservation

The ratios between chlorophyll *a* and its degradation products are often used to evaluate the degree of pigment degradation and/or zooplankton grazing (Bianchi and Canuel, 2011). In Lake Victoria overall, the chlorophyll degradation products pheophytin *a* and pheophorbide *a* are the most abundant sedimentary pigments (Fig. 5b) suggesting substantial cellular senescence and/or zooplankton grazing in

the water column. Other chlorophyll degradation products such as pyropheophytin, pyropheophorbide, or chlorophyllide were not detected.

Relative to its degradation products, Chl *a* was detected only at low concentrations (<22% in LV4 and <15% in LV1) with highest values at the top of both cores. Only the deepwater site LV4 displays a gradual rise in Chl *a* from 7 cal ka BP onwards, along with an overall greater relative proportion of Chl *a* to the chlorin content (Fig. 5a and b). This trend could be attributed to the gradual increase of hypolimnetic hypoxia as a result of enhanced stratification (low bSi, Fig. 2) and, hence, better pigment preservation at the deep-water site LV4 compared to LV1. Chl *a* is especially sensitive to dissolved oxygen (Leavitt and Hodgson, 2001).

In both cores, the ratio between pheophytin *a* (general cell senescence) and pheophorbide *a* (cell destruction by grazing; Bianchi and Canuel, 2011) increases from older to younger ages (Fig. 5b) suggesting that zooplankton grazing was the dominant process for Chl *a* degradation prior to ca. 8 cal ka BP, whereas cell senescence was more important thereafter.

The Chlorophyll Preservation Index (CPI; Chl *a*/(Chl *a* + pheophytin *a*)) is used as an indicator of pigment preservation/degradation (Buchaca and Catalan, 2008) and reveals substantial fluctuations at both sites through time (Fig. 5a). At LV4, high CPI values suggest better preservation of pigments around 14 cal ka BP and from 7 cal ka BP onward. At LV1, high CPI values are recorded around 9 and between 8 and 4 cal ka BP. Among other factors, differences in light exposure and sedimentation might contribute to these local periods of better pigment preservation. Nevertheless, the CPI ratio is generally low in LV, emphasizing the high degradation activity in this tropical system.

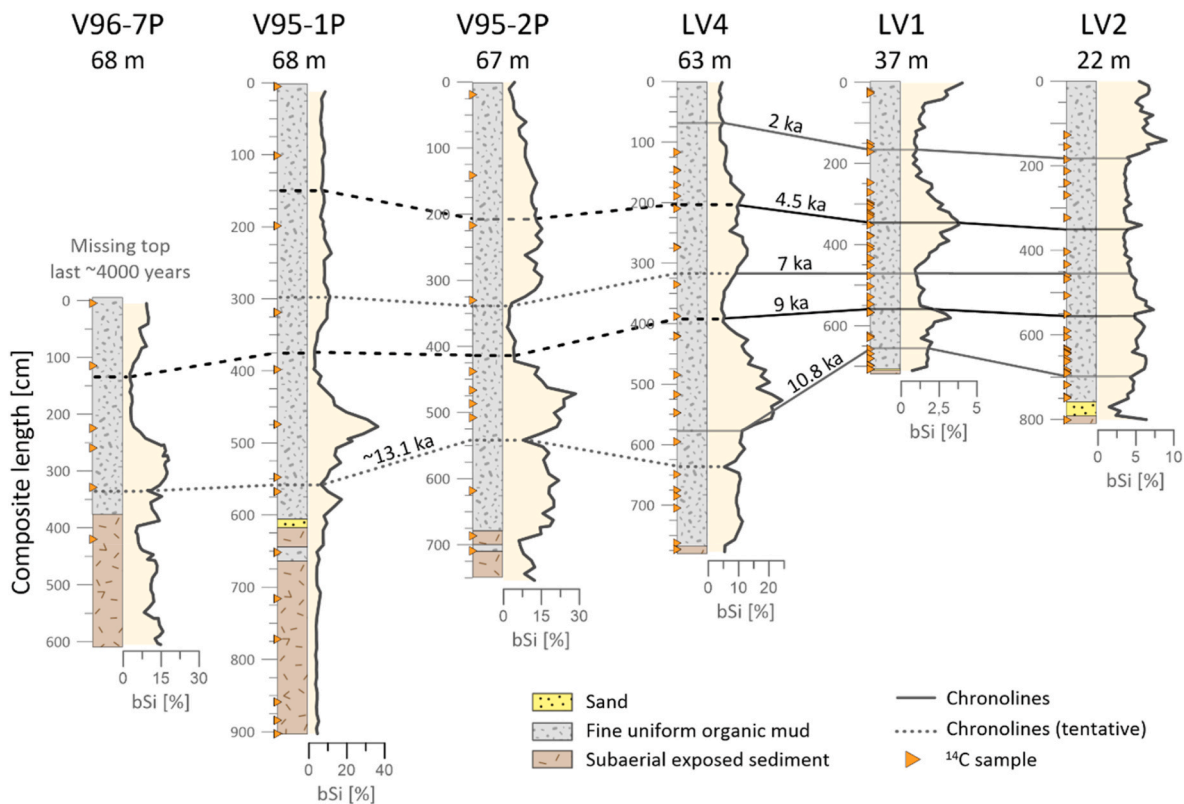


Fig. 7. Compilation of bSi records across Lake Victoria displayed in composite core lengths (Beuning et al., 2002; Talbot and Lærdal, 2000; Verschuren et al., 1998, and three LV cores from this study) and isochrones of phases with high (low) bSi values. Schematic core lithologies were derived from sediment descriptions in the literature (Beuning et al., 2002; Talbot and Lærdal, 2000; Verschuren et al., 1998; Wienhues et al., in press). Orange triangles mark ¹⁴C dates. The bSi records from V95-3P and V95-6P have only one ¹⁴C date and were omitted but display distinctly different bSi profiles (see full figure in Supplementary Material; Fig. S6). Note the different scales of the x-axis.

4. Discussion

Overall, our results suggest that it is possible to quantify spatio-temporal variability of PP_{aq} in a tropical lake based on biogeochemical analyses, and to provide insights into the underlying abiotic and biotic processes that determine PP_{aq} over the past 17 kyr of Lake Victoria's history, from its initial infilling to the onset of cultural eutrophication.

4.1. Pigment preservation

Studies of sedimentary pigments in tropical lakes are still limited. In tropical and relatively shallow Lake Victoria, it is reasonable to assume that elevated microbial activity, seasonal mixing and regular oxygenation of the water column favoured transformation and degradation of photosynthetic pigments. In general, some pigment degradation is evident in the dominance of chlorophyll derivatives in both cores LV1 and LV4 and low CPI (Fig. 5). Notably, the degree of chlorophyll preservation is better with greater water depth (better in LV4 than in LV1). This is consistent with findings from other pigment studies showing that shallower and near-shore regions tend to experience elevated levels of photodegradation and/or higher grazing activity. Both processes lead to the degradation of photosynthetic pigments (Cuddington and Leavitt, 1999).

The intermediate site LV1 (37 m.b.l.l.) is currently located within the range of the seasonal mixed layer depth, which is between 25 and 40 m (Hecky et al., 1994; Mugidde, 1993; Ramlal, 2002). Therefore, at site LV1, the highly variable degree of pigment preservation (CPI) and episodic occurrence of very labile peridinin (Fig. 4b) might be the combined result of changes in the mixed layer depth and oxygenation, water turbulence, exposure to light (photooxidation) and zooplankton grazing. Unfortunately, factoring out the relative importance of each of these environmental variables is not possible at the current stage of our research. Oxygen depletion also currently occurs periodically in the deep waters of Lake Victoria (LV4), potentially favouring pigment preservation (Hecky et al., 1994; MacIntyre et al., 2014). This is in line with the higher proportion of Chl *a* relative to its degradation products in LV4, and the persistent presence of the very labile carotenoid fucoxanthin (Fig. 4a) which is known to degrade quickly (Hurley and Armstrong, 1990; Repeta, 1989).

Cyanobacterial pigments are persistently found throughout both cores. These pigments are known to be more stable and less affected by grazing activity (Leavitt and Hodgson, 2001). These effects could result in over-representation of cyanobacteria compared with producers of more labile carotenoids. Nevertheless, the discernible but expected degradation signature in the phytopigments, and the structure of the pigment stratigraphies (pigment zones) suggest that major shifts in phytoplankton communities are preserved and can be cautiously interpreted. The deepwater site LV4 appears to be the least affected, providing more reliable pigment data, while interpretations from LV1 should be approached with greater caution.

4.2. The transition from wetlands to an exorheic lake

Prior to the rapid and massive lake level rise at 14.0–13.6 cal ka BP, the area of modern Lake Victoria was covered by a tropical wetland environment with relatively shallow ponds (<16.7 ka, Wienhues et al., in press). Between 16.2 and 14.1 ka, sedimentary pigments indicate the presence of a chlorophyte and chromophyte algal assemblage, which includes cryptophytes, during this phase of shallow water conditions (Zone_{LV4} II; Fig. 4) which markedly differs from the diatom-cyanobacteria phytoplankton composition after ~14.1 cal ka BP (i.e. the phase of the lake-level rise). The sediments show low values in TOC, TChl, and other pigments (e.g., diatoxanthin, myxoxanthophyll), more negative $\delta^{13}C$ values, and predominance of clastic sediments: overall an environment with low PP_{aq} and poor pigment preservation in shallow water conditions with light and oxygen exposure and possible

sediment reworking. The low $\delta^{13}C$ values, pollen data (Temoltzin-Loranca et al., 2023a) and *n*-alkanes (Cockerton et al., 2015) suggest abundant *Typha* macrophytes covering extended wetland areas in the LV basin during that time. Emergent macrophytes play a crucial role in wetlands and shallow lake systems by modulating chemical and physical parameters (e.g. nutrient levels, light, and turbulence), shaping the phytoplankton community structures and biomass. This may have had propagating impacts on zooplankton, fish, and the aquatic food web in general (Scheffer and Jeppesen, 1998; They et al., 2014; Zeng et al., 2012). For example, field surveys in tropical lakes indicate that macrophytes can induce a shift from cyano- to chloro- and cryptophyte dominance (Finkler Ferreira et al., 2018; Fonseca and Bicudo, 2010).

With the major lake-level rise and establishment of the outflow to the Nile river between 14.1 and 13.6 (Wienhues et al., in press), a gradual decrease in chlorophytes and chromophytes was observed, accompanied by a rise in PP_{aq} , as evidenced by the TChl, Chl *a* and pheophorbide *a* levels. The rise of the lake level was likely the cause for a reduction in mixing as suggested by a temporal peak of cyanobacteria and the presence of the diatom *Nitzschia fonticola* (Stager and Johnson, 2000).

4.3. Mixing and nutrient dynamics shaping primary paleo-production

The phytoplankton distribution in tropical lakes is especially sensitive to mixing dynamics, including the extent of the mixed layer and the duration of deep mixing, both driven by interannual climate variability (e.g. Sarmiento et al., 2006; Talling, 1966). Also in Lake Victoria, water column mixing, combined with light availability, largely controls the modern seasonal distribution of phytoplankton (Cózar et al., 2012).

Currently in Lake Victoria diatoms constitute the major plankton community during the well-mixed windy season from April to September offshore (MacIntyre et al., 2014). This mixing period is characterised by high nutrient and low light conditions. In contrast, cyanobacteria and chlorophytes become more abundant during the rainy season with reduced wind activity and density gradients (MacIntyre et al., 2014), low nutrient and high light conditions in the epilimnion. This shift in phytoplankton composition has been attributed to the ability of diatoms to grow under turbulent and light-limited conditions, whereas buoyant cyanobacteria are favoured by stable water column conditions (Reynolds, 1987, 2006). Today, the lake-wide convection over the water body is seasonally driven by southeastern and north-western monsoonal winds, which are linked to the seasonal movement of the intertropical rain belt and the Indian Ocean temperature (Cózar et al., 2012; MacIntyre et al., 2014). These processes may also have played a role in the past and provide a conceptual model to link past monsoonal activity and hydroclimate with lake mixing and nutrient availability and, finally, PP_{aq} and primary producer communities.

Our record of diatom paleo-production (bSi; Fig. 7), along with the interpretation of Stager and Johnson (2000) and Stager et al. (2003) from other sectors of Lake Victoria, suggests two periods with sustained water column mixing (bSi maxima) and nutrient recycling between 10.8 and 9 cal ka BP and, less pronounced, between 7 and 4.5 cal ka BP, separated by a period with enhanced stratification (local bSi minimum) between ca. 9 and 7 cal ka BP. In LV4, the changes of the mixing regimes (bSi record) are also reflected in changing lithofacies (strong mixing in clusters 4 and 2, rather stratified conditions in cluster 1; Fig. 2), in the PC2 loadings (positive during mixing phases) and K/Rb ratios (enhanced precipitation and erosion during periods with strong mixing; Fig. 2). Although water column temperature is generally positively correlated to the lake's water column stability, this pattern is not reflected in the TEX₈₆ water temperature record (Berke et al., 2012).

The isochronic alignment of all existing bSi records from Lake Victoria (Fig. 7; Beuning et al., 2002; Johnson et al., 1998; Talbot and Lærdal, 2000) highlights spatial heterogeneity in diatom production within the lake. This heterogeneity is expected due to varying sedimentation regimes, wind patterns, mixing dynamics, shaping the nutrient distribution across different regions of the lake.

Nevertheless, similar patterns emerge in bSi records from core sites in closer proximity and/or at comparable water depths. This suggests that changing hydroclimatic conditions at the onset of the Holocene and the mid-Holocene had profound impacts on nutrient dynamics and algal community compositions, with substantial spatial heterogeneity across various regions within the lake. This observation is most relevant because it documents the imperative of a large number of cores from different sites to capture the full ecosystem variability in space and time. The extent to which the observed spatial variation in diatom and algal dynamics in Lake Victoria reflect differential degradation of biomarkers or real spatial-temporal shifts in primary production remains unclear at the current stage of our research.

The first maximum in diatom productivity 10.8–9 cal ka BP can be attributed to exceptionally wet conditions and enhanced monsoonal activity at the onset of the Holocene as recorded over eastern Africa (Garcin et al., 2007; Gasse, 2000; Talbot et al., 2007). In LV, these humid conditions with strong monsoonal activity led to a positive water balance (P/E) and high lake level during that time (Wienhues et al., in press; Berke et al., 2012; Stager and Mayewski, 1997). Sufficient delivery of nutrients from the catchment (N, P, and Si) was concomitant with high input of weathered material (Rb/K) during this time (Cockerton et al., 2015). Efficient recycling of hypolimnetic nutrients during times of deep mixing may have contributed to a widespread and sustained increase in PP_{aq} , which is particularly visible in LV4 (Fig. 4). Importantly, Cockerton et al. (2015) found that Si was not a limiting factor for diatom productivity but, instead, favoured the proliferation of heavily silicified diatom species, particularly *Aulacoseira* spp., previously identified in offshore, deep-water and shallow-water cores from Lake Victoria during this period (Stager and Johnson, 2000; Stager and Mayewski, 1997).

In contrast, the decline in bSi across offshore sediment cores between 9 and 7 cal ka BP (Fig. 7) would reflect increased lake stratification. During this period, diatom frustules are absent in the core V95–2P (Stager and Johnson, 2000); TChl concentrations were relatively low and clastic input reduced (LV4; Figs. 2 and 5a). It is conceivable that a combination of factors contributed to the reduction of silicifiers and the general shift in algal assemblages offshore: reduced water column mixing and N limitation (maxima in C/N ratios, Fig. 5b) may have out-competed diatoms in favour of cyanobacteria (visible in LV1), and/or the preservation conditions of diatom frustules in the sediment were poor.

Nutrient limitation in the lake could also be the result of better N retention in the dense rainforest which prevailed in the catchment during that time (9–7 cal ka BP; Temoltzin-Loranca et al., 2023a). Dense rainforest could also efficiently capture Si, reduce Si flux to the lake (Street-Perrott and Barker, 2008) and limit diatom growth. However, Cockerton et al. (2015) concluded that, at least in core V95–1P, the Si pool was sufficient during that time. Nutrient enrichment studies in LV have shown that, today, phytoplankton biomass is primarily limited by light which, during periods of stratification and clear water, could result in moderate P and N deficiency (Guildford et al., 2003; Guildford and Hecky, 2000). Indeed, offshore N limitation around 9–7 cal ka BP is supported by very high C/N ratios (Fig. 3b). Evidence for P limitation during this time is provided by the very low sedimentary total phosphorus (TP) concentrations (mostly inorganic P) in LV1 between 13 and ~4 cal ka BP (Fig. 4b). The green alga *Botryococcus* is adapted to low P and N conditions, thriving in oligotrophic to mesotrophic environments (Smittenberg et al., 2005). Its notable peak between 9 and 6 cal ka BP in the offshore core V95–1P, as inferred from lipid biomarkers (Cockerton et al., 2015), provides evidence for the inference of nutrient deficiency in that period. The bSi profile from LV3 (Fig. 7) and diatom assemblages from nearshore, shallow water cores Ibis-1 and 64-4 lack the period of low diatom production (Stager et al., 2003; Stager and Mayewski, 1997) that is evident in the deepwater cores. This suggests that the discussed nutrient-deficient conditions were restricted to the deepwater regions of the lake.

The transition from the early to mid-Holocene has been interpreted as a transition towards moderate water column mixing (Stager and Johnson, 2000). This is evident in the second bSi maximum during the mid-Holocene offshore around 7 cal ka BP (Fig. 7), and it began with respect to diatom assemblages in nearshore cores at ~8 cal ka BP (Stager et al., 2003; Stager and Mayewski, 1997). Mixing increases the nutrient availability in the photic zone. Interestingly, this is best seen at LV1 (intermediate water depth), whereas this bSi maximum is only moderately expressed in the deepwater cores (Fig. 7). Increased diatom productivity during that time is not reflected in the phytoplankton biomarker stratigraphy at LV4 (Fig. 4); this could be related to the labile nature of diatom pigments and the enhanced degree of pigment degradation (Fig. 5). Stager and Johnson (2000) and Stager and Mayewski (1997) found abundant *Nitzschia* spp. in this interval, a diatom group with weakly silicified frustules and the authors inferred an environment with suppressed mixing and low Si/P ratios, pointing to some Si limitation. Similar conclusions were reported by Cockerton et al. (2015) for this time. Supporting evidence for enhanced stratification is also found in the pigment zone II at LV1 (7.7–4.7 cal ka BP; Figs. 4 and 5), showing enhanced cyanobacteria, less severe N limitation (lower C/N ratios, Fig. 3b) and better pigment preservation. Maxima in $\delta^{13}C$ and total organic carbon (TOC) point to a less pronounced degradation of organic matter, which is in line with less oxygenated bottom water conditions reported by Talbot and Lærdal (2000) for that time.

The termination of the AHP with increasing aridity after 5–4 cal ka BP (Gasse, 2000) had a substantial impact on the lake ecosystem. Both cores LV4 and LV1 reveal the change in the pigment zone largely at the same time (4.7–4.4 cal ka BP; Fig. 6), marking the gradual decrease of $\delta^{13}C$ in all cores whereas PP_{aq} (TChl) remains relatively high. Subsequently, diatom productivity decreased systematically (Fig. 7) suggesting gradually increasing lake stratification across Lake Victoria towards the late Holocene. After 5 cal ka BP, expanding savanna, increasing fire activity, and emerging anthropogenic impacts (during the Iron Age ~2.4–1.1 cal ka BP) likely enhanced erosional and atmospheric influx of P and N to the lake (Battistel et al., 2017; Temoltzin-Loranca et al., 2023a). Total sedimentary P has notably increased after 2 cal ka BP.

Unprecedentedly high values of TChl in the 20th century suggest that, at least at coring sites LV1, LV3 and LV4, PP_{aq} values and eutrophication of the past decades have exceeded the range of variability Lake Victoria has experienced in the past 17 kyr. This is not the case for most of the other proxies analysed in this study.

4.4. Primary production and regional hydroclimatic changes

It has been demonstrated in several eastern African lakes (Loiselle et al., 2014; Stager et al., 2009; Tierney et al., 2010; Wolff et al., 2011) that climate variability influences lake water mixing and, ultimately, shapes PP_{aq} and producer communities. Also, the water balance greatly depends on the regional hydroclimate (Olaka et al., 2010).

In general, the lake-level evolution of Lake Victoria during the past 17 kyr agrees with regional hydroclimate records (e.g. Lakes Tana and Chala) and follows broadly northern hemisphere summer insolation strength, although with non-linear responses (Fig. 8). Arid conditions prevailed in eastern Africa and the Lake Victoria area during the Latest Pleistocene, especially during the early Heinrich Stadial 1 (18.3–16.3 cal ka BP; (Stager et al., 2011; Yang et al., 2023). Whereas regional hydroclimate proxies (δD_{wax}) show a rather gradual increase in moisture at the beginning of the African Humid Period after 16 cal ka BP (Fig. 8; deMenocal et al., 2000), Lake Victoria filled-in with a delay but very rapidly between 14.2 and 13.5 cal ka BP (Wienhues et al., in press). The wetland – shallow pond environment transformed into the deep exorheic lake of modern size. The increase in precipitation and concomitant rapid lake-level rise had profound impacts on the vegetation in the region, causing the spread of Afrotropical forests (Kendall, 1969; Temoltzin-Loranca et al., 2023a; Van Zinderen Bakker and Coetzee, 1988) and affecting aquatic primary producers and lake ecology.

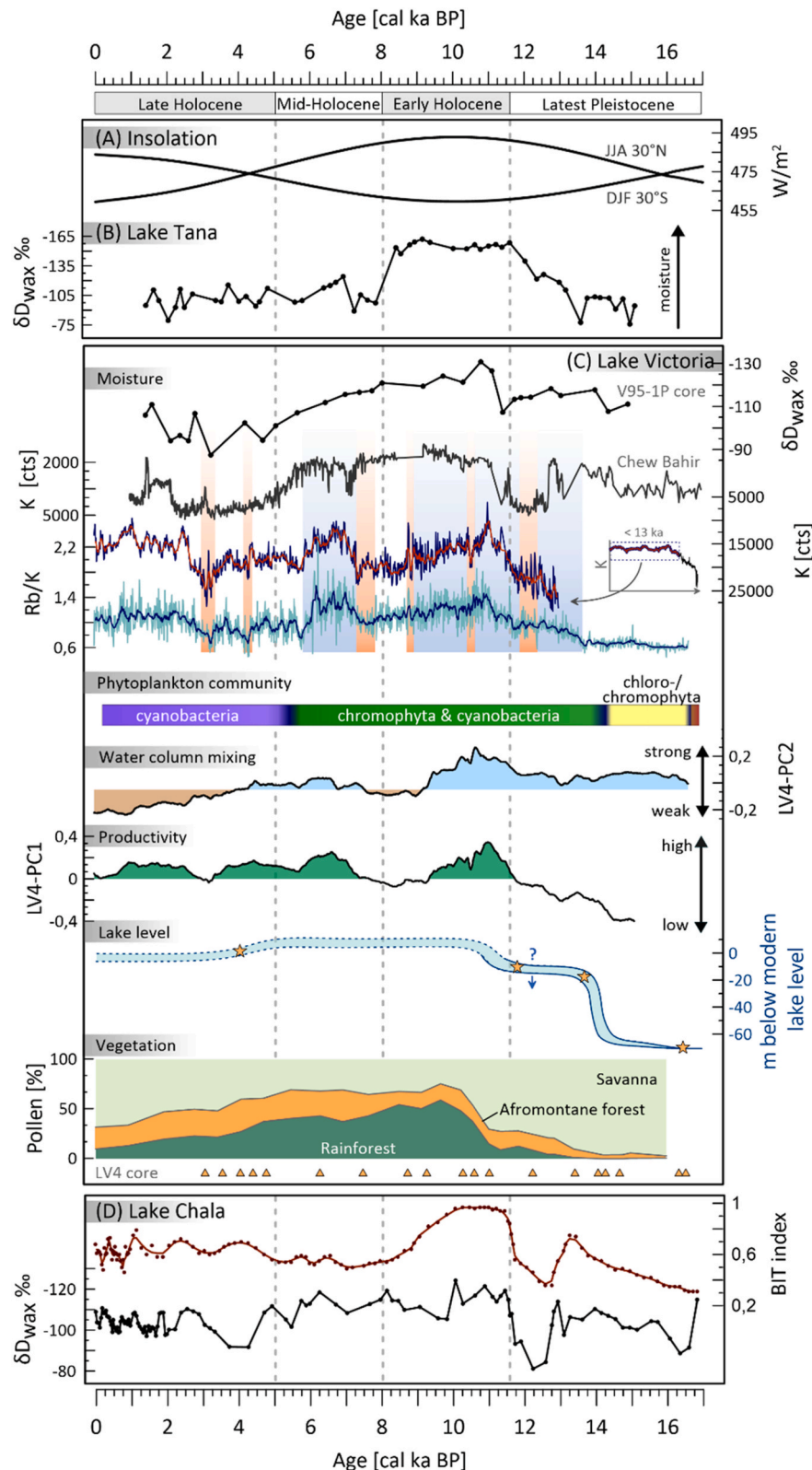


Fig. 8. The Lake Victoria record in the context of regional paleoclimate records. $\delta D_{leaf\ wax}$ indicates hydroclimate variability (amount and source effects). (A) Summer (JJA) and winter (DJF) insolation (Berger and Loutre, 1991). (B) $\delta D_{leaf\ wax}$ of Lake Tana (Costa et al., 2014). (C) $\delta D_{leaf\ wax}$ of Lake Victoria (Berke et al., 2012), K from Chew Bahir (Foerster et al., 2012), K and K/Rb from LV4. Note the reversed scale for K. Dry and wet phases are highlighted (blue and red shading). Pigment-based phytoplankton community changes, LV4-PC1 (primary production) and LV4-PC2 (water column mixing), estimated lake level with tie points (this study; Wienhues et al., in press; Stager et al., 2005), catchment vegetation (Temoltzin-Loranca et al., 2023a, LV4). (D) Chala BIT (branched and isoprenoid tetraether) index (Verschuren et al., 2009) and $\delta D_{leaf\ wax}$ of Lake Chala (Tierney et al., 2011).

Specifically, PP_{aq} increased, and chloro- and chromophyte assemblages typical for wetlands were replaced by chromophyte and cyanobacteria dominated assemblages in the pelagic areas of the lake (Fig. 8c).

Impacts of the Younger Dryas climate event (12.8–11.6 cal ka BP; YD), a period of significant aridity in eastern Africa (Castañeda et al., 2016; Meyer et al., 2020), has not been identified in Lake Victoria's pollen and δD_{wax} records up to now (Berke et al., 2012; Temoltzin-Loranca et al., 2023b). However, a detailed inspection of the Rb/K records (Fig. 2) and, more specifically, of the profile records in LV4 (Fig. 8c) reveals a pause of the wetting trend and lake-level rise (Wienhues et al., in press) during the YD period. The Rb/K and K records of LV4 show striking similarity (although much weaker in the amplitude) with the K minima in the Chew Bahir record from southern Ethiopia (4.77°N, 36.84°S; (Foerster et al., 2015, 2012). Moreover, the similarity with the Chew Bahir K record (Foerster et al., 2012) allows us to identify, with confidence, other short-lived dry intervals in the Lake Victoria basin ~10.5, ~9, between 7.8 and 7.2, ~4 and between 3.2 and 3.0 cal ka BP (red shading in Fig. 8c).

At the beginning of the Holocene, monsoonal moisture transport abruptly intensified (Talbot et al., 2007). Regionally, wet conditions were established in the Early Holocene (11.5–9 cal ka BP; Berke et al., 2012; Costa et al., 2014; Tierney et al., 2011, 2008) and rainforest expanded in the Victoria catchment (Temoltzin-Loranca et al., 2023a, Fig. 8c). Maximum summer/winter inter-hemispheric insolation contrast is argued to have caused warming in the western Indian Ocean and enhanced southeastern monsoon over eastern Africa (Abram et al., 2007, 2020; Tierney et al., 2011; Verschuren et al., 2009) and, ultimately, increased seasonality and windiness in the Lake Victoria region. Accordingly, the lake was well mixed and primary production reached a local maximum; particularly diatom production was high (Fig. 8c). According to Costa et al. (2014) also the eastward displacement of the Congo Air Boundary provided additional moisture from the Atlantic Ocean and Congo basin rainforests. The second half of the AHP appears to be more moderate in wind strength and rainfall amount (Liu et al., 2017). A gradual drying and cooling trend from 9 to 8 cal ka BP towards the mid Holocene occurred in the region, likely causing a reduction of tropical rainforests and moderate expansion of subtropical Afrotropical vegetation (Berke et al., 2012; Kendall, 1969; Temoltzin-Loranca et al., 2023a). A more abrupt change in hydroclimate conditions occurred around 8 cal ka BP, known as the Early-Mid Holocene climate Transition ~8 cal ka BP (EMHT; Stager and Mayewski, 1997). This transition is evidenced by a drastic shift in diatom assemblages, indicating reduced mixing in the northern part of the lake. The causes of these different sensitivity and responses of algal communities across the lake remain unknown.

Regionally, this coincides with relatively dry mid Holocene conditions in easternmost equatorial Africa (Chala BIT index) attributed to insolation-induced reduced monsoonal intensity (Stager et al., 2003; Verschuren et al., 2009) (Fig. 8d). These relatively subtle climatic changes were apparently enough to reduce water column mixing and aquatic primary production (notably diatoms) basin-wide between 9 and 7 cal ka BP (Figs. 6–8). Primary producer assemblages offshore remained dominated by chromophytes and cyanobacteria. It is conceivable that enhanced lake stratification led to nutrient deficiency in the photic zone during that time (Fig. 3b).

With the termination of the AHP, the climate became gradually drier from 6 cal ka BP onwards, although with spatiotemporal variations (Berke et al., 2012; Shanahan et al., 2015) and the catchment vegetation opened with the expansion of savanna (Temoltzin-Loranca et al., 2023a). As a result of declining lake levels, Lake Nabugabo separated from Lake Victoria ~5 kyr ago (Stager et al., 2005) and shallow-water diatom assemblages established in the Pilkington Bay (Stager et al., 2003). A regional drought around 4–3 cal ka BP has been documented in several eastern African records (e.g. Tierney et al., 2011; Foerster et al., 2012). Droughts around that time are also found in the Rb/K and K records of LV4 (Fig. 8c) and coincide with increased biomass burning in

the Lake Victoria catchment (Temoltzin-Loranca et al., 2023a). With the late Holocene drying trend, water column mixing got gradually reduced and enhanced stratification established. Accordingly, diatom productivity decreased (Fig. 6) and the mid Holocene chromophyte and cyanobacteria-dominated communities were more prominently represented by cyanobacteria (Fig. 8).

5. Conclusions

Motivated by the need to better understand the long-term spatial and temporal structure of changes in PP_{aq} and producer communities, and to explore the utility of sedimentary pigments in tropical lakes, we investigated four sediment cores along an offshore to nearshore transect covering the past 17 kyr. Our findings reveal a strong connection between hydroclimate variations, lake mixing, nutrient availability, and primary production, shedding light on changes in the lake's primary producers and algal communities over time. Furthermore, this study places the anthropogenic eutrophication of the 20th century, which has profoundly altered the aquatic ecosystem of Lake Victoria, in a Latest Pleistocene-Holocene context, emphasizing the long-term trajectory of the lake's primary productivity.

We draw the following conclusions.

- During the initial wetland phase (16.7–14.5 cal ka BP), Lake Victoria exhibited low PP_{aq} , predominantly characterized by chloro- and chromophytes. The presence of emergent aquatic macrophytes likely played a role in shaping the lake's ecosystem and phytoplankton community during this period.
- The rapid rise in lake level after 14.2 cal ka BP and the establishment of deep exorheic lake, resulted in increased PP_{aq} and a shift towards a dominance of chromophytes and cyanobacteria in the algal community.
- The Holocene was marked by two distinct phases of increased lake mixing, higher primary production, and enhanced diatom productivity. The first phase occurred between 11 and 9 cal ka BP during the peak of the African Humid Period (AHP), characterized by intensified precipitation, wind activity, and water column mixing. A less pronounced second phase was observed between 7 and 4 cal ka BP. Between 9 and 7 cal ka BP, a prolonged period of stable water column conditions with low diatom productivity and nutrient limitation (nitrogen and phosphorus) occurred. Although the precise driving factors remain unclear, periods of stratification were possibly related to reduced wind stress.
- Significant changes during the mid-to-late Holocene coincided with a gradual drying and the termination of the AHP around 5–4 cal ka BP. Reduced lake mixing led to an increasing dominance of cyanobacteria. Notably, the total chlorophyll levels in the 20th century reached unprecedented levels in the light of the past 17 kyr.
- The K and Rb/K profiles clearly reflect hydroclimate oscillations, including the Younger Dryas (YD) and short-term dry intervals throughout the Holocene.

This research provides valuable insights into the past dynamics of Lake Victoria's primary productivity and phytoplankton composition, offering a glimpse into the magnitude and direction of changes in the lake's primary producers over time.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be available on PANGAEA database.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2024.108599>.

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