The paleolimnological perspective on the evolution of the Lake Victoria ecosystem

Inaugural dissertation
of the Faculty of Science,
University of Bern

presented by

Giulia Wienhues

from Münster (Westfalen), Germany

Supervisor of the doctoral thesis
Prof. Dr. Martin Grosjean
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Abstract

Lake Victoria is a key example of both exceptional biodiversity and increased human pressure leading to ecosystem degradation. Although this lake is known for one of the most diverse and renowned radiations of endemic fish species, many of which are facing extinction, the origin and evolutionary linkage of these species to past climate fluctuations, nutrient cycles, and plankton communities have remained unknown. This thesis aims to shed light on the paleoenvironmental context of aquatic evolution in Lake Victoria over space and time by studying four long sediment records across a depth transect ranging from deep-water to nearshore, shallow-water sites.

The initial study addresses the key question of how Lake Victoria refilled during the Latest Pleistocene and the paleoclimate conditions influencing its re-emergence after a dry period. By reconstructing the hydrological variability of the lake through a detailed analysis of four new sediment cores, the research sheds light on previously debated aspects of its refilling history following the Latest Pleistocene desiccation. The analysis reveals that extensive wetland ecosystems existed before the current lake was established, suggesting rapid refilling driven by changing precipitation. This refined history aligns with regional climate records, highlighting complex past conditions in Eastern Africa.

The second study investigates spatiotemporal changes in primary production within Lake Victoria over the past 17,000 years and their link to environmental factors. To gain a comprehensive understanding of Lake Victoria's long-term paleolimnological evolution, we employed a multiproxy approach on a set of long sediment cores. The results reveal phases of ecosystem shifts driven by hydroclimate, mixing, and nutrient availability. During the initial wetland phase, green algae and chromophytes dominated. With lake-level rise during the African Humid Period, aquatic productivity increased, leading to cyanobacteria and chromophyte dominance. Strong mixing and high primary production with diatom blooms characterized the early and mid-Holocene.

A collaborative study examines eutrophication and ecological consequences in Mwanza Gulf over the past century. This study of short sediment cores from this southern embayment indicates that the lake is sensitive to human impacts, such as increased nutrients and rising water levels, which can lead to eutrophication and disruption of the food web. The study's key findings indicate a gradual increase in algal production since the 1920s, reaching its peak in the 1980s, which reflects the growing eutrophication of the lake. Additionally, the study reveals the significant impact of the 1960s lake-level rise on cladocerans, indicating the effects of habitat alteration. Finally, the study found no clear evidence of predation control or grazing pressure on plankton communities.

Collectively, this thesis unravels the past of Lake Victoria's ecosystem, revealing its interconnected evolution with climate and human development over thousands of years. By integrating advanced methodologies and various biogeochemical markers, it paints a detailed picture of the lake's changing conditions, highlighting the diverse environments within this large tropical ecosystem, and provides important baseline conditions for interpreting the evolutionary trajectories in Lake Victoria.

Acknowledgements

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First and foremost, I would like to thank my long-standing supervisor, Prof. Martin Grosjean, who has been a guiding force since my bachelor thesis. His unwavering support, from my early days as a student research assistant to pursuing a Climate Science Master and eventually embarking on a PhD, has been invaluable.

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Special thanks to my fellow paleolims. Those from the early days: Christoph, Ivan, Tobi, Raphi, Andrea, Stamatina, Luyao, Paul, Aurea and Daniela. And those from the new days: Petra, Chuxian, Stan, Noé, Sergio, Emmanuel, Ann-Kathrin, and Sarah. Special thanks to Aurea, for being the best office mate I could have hoped for. I am grateful to Petra and Chuxian for their invaluable discussions about science and life, unwavering support, and all the sweets you kept our research group fueled with. Petra, I deeply appreciate your assistance with formatting my thesis and more. I would also like to thank Daniela for her endless support in the lab and beyond.

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Lastly, to my parents and sister, thank you for your support, no matter where I went or whatever I did, even if it involved studying ancient lake mud.

This thesis is dedicated to my late father, Michael Wienhues, who taught me about nature, science, and the value of lifelong learning.

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List of Abbreviations

AHP	African Humid Period
AMS	Accelerator Mass Spectrometry
AP	Apatite Phophate
CE	Common Era
CAB	Congo Air Boundary
CFCS	Constant Flux: Constant Sedimentation
CI	Confidence Interval
CONISS	Constrained Incremental Sums of Squares cluster analysis
CPI	Chlorophyll Preservation Index
CRS	Constant Rate of Supply
DBD	Dry Bulk Density
EAHP	Eastern African Humid Period
HPLC	High Performance Liquid Chromatography
HS1	Heinrich Stadial 1
HSI	Hyperspectral Imaging
ICP-MS	Inductively Coupled Plasma Mass Spectrometry
ITCZ	Intertropical Convergence Zone
IP	Inorganic Phosporus
IRMS	Isotope Ratio Mass Spectrometer
ka	kiloannum
LGM	Late Glacial Maximum
LOI	Loss on Ignition
LV	Lake Victoria
MICADAS	Mini Carbon Dating System
MI	Missing Inventory
NAIP	Non-apatite inorganic Phosphorus
OP	Organic Phosphorus
PC(A)	Principle Component (Analysis)
PP_{aq}	aquatic primary paleo-production
PZ	Pigment Zone
RABA	Relative Absorption Band Area
RABD	Relative Absorption Band Depth
RIA	Randomized Intervention Analysis
SMT	European Standard, Measurement and Testing
CRM	Certified Reference Material
TC	Total Carbon
TChl	Total Chlorophyll
TN	Total Nitrogen
TOC	Total Organic Carbon

TP	Total Phosphorus
YD	Younger Dryas
XRF	X-ray Fluorescence

Chapter 1

1. Introduction

1.1 General motivation

Freshwaters as a whole are a hotspot for biodiversity and provide irreplaceable services for both nature and society, influencing biogeochemical processes, ecological dynamics, ecosystem productivity, and human health and welfare from local to global scales (Albert et al., 2021). Despite their vital value, these ecosystems are increasingly threatened by human activities and environmental change (Carpenter et al., 2011; Dudgeon et al., 2006; Strayer & Dudgeon, 2010). The long-term protection of freshwater ecosystems is largely dependent on understanding the underlying physical processes and assessing natural conditions before disturbance. This understanding is particularly important in tropical regions that harbor over 80% of the world's freshwater fish but experience some of the most rapid land-use changes on Earth (Barlow et al., 2018).

Eastern Africa stands out as a region of remarkable ecological and evolutionary significance, assembling hotspots of both human origins and biodiversity. Through its central location between the two branches of the East African Rift System, Lake Victoria is a critical site in understanding the intricate interplay between paleoclimate and biodiversity. In addition, Lake Victoria served as a stark example of increased human pressure, eutrophication, and subsequent ecosystem collapse. The lake houses some of the most diverse and renowned radiations of endemic fish species, many of which have already vanished or are currently under threat of extinction (Hecky et al., 2010; Kaufman, 1992; Witte et al., 2012). Although the modern assemblages are extensively studied, direct evidence of the origin and drivers of this exceptional biodiversity including their evolutionary linkage to climate fluctuations, nutrient cycles, and plankton communities are virtually unknown.

Continuous sediment records have emerged as valuable tools to assess the sensitivity of lake ecosystems to environmental or climate changes across various time scales (Adrian et al., 2009). By analyzing various indicators, from sediment geochemistry to fossil remains embedded in the sediment, these records provide a rich paleoenvironmental context of the lake's past and hold immense value in resolving paleoclimatic, biogeographic, and evolutionary debates in the tropics (e.g. Dommain et al., 2022; Saulnier-Talbot et al., 2018).

As part of the interdisciplinary SNSF Sinergia Lake Victoria Project, the present thesis aims to contribute to the understanding of the paleoenvironmental context of aquatic evolution in Lake Victoria by analyzing the sedimentary record to reconstruct the lake's aquatic conditions in response to past climatic and environmental changes.

1.1.1 The SNSF Sinergia Lake Victoria Project and research objectives

As this thesis is part of the SNSF Sinegia Lake Victoria Project, the aim is to reconstruct the evolutionary history of the Lake Victoria ecosystem, investigate the influence of external factors on species assemblages, and explore the ecosystem changes linked to lake eutrophication and mass extinction in the last century of Lake Victoria (Fig. 1.1). By examining sediment cores, the project integrates approaches from paleolimnology, evolutionary biology, and paleoecology to provide detailed and quantitative reconstructions of past environments. These sediment cores along an onshore-offshore gradient provide a spatial-temporal framework for tracing the lake's evolution and habitat transitions over time (Sinergia project proposal 2018).

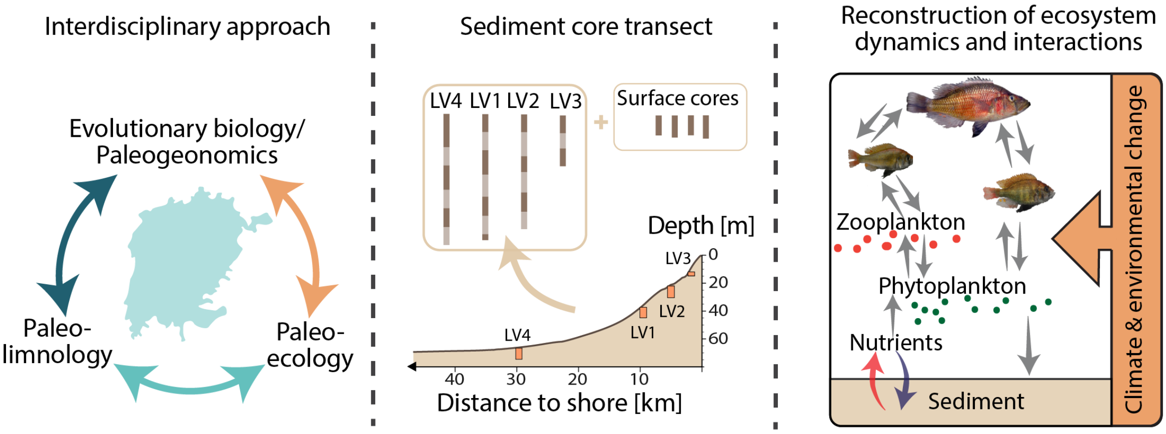

FIGURE 1.1: Schematic view on the SNSF Sinergia Lake Victoria project approach.

The project will thus help to understand (Sinergia project proposal 2018):

- The interaction between physical environments and species during the emergence and maintenance of a biodiversity hotspot.
- The role of climate and environment and species during the emergence of cichlid fishes
- The origins of genome variation crucial for cichlid fish radiation and the processes involved in assembling this variation into numerous new species.
- The impact of cichlid radiation on ecosystem dynamics, particularly exploring the reciprocal relationships between ecosystem and food web structure and the adaptive radiation of cichlid fishes.

The overall project consists of four work packages:

I. A paleolimnology perspective on the evolution of the Lake Victoria ecosystem
II. Diversity and diversification – the adaptive radiation (= rapid diversification) of cichlid fishes in Lake Victoria
III. Lake Victoria plankton and benthos dynamics – interactions with cichlid radiation
IV. Diversification and ecosystem functioning – a dynamic relationship with eco-evolutionary feedbacks

This thesis presents the paleolimnological and geoscientific results as part of the first work package and focuses on the paleoenvironmental and climatic aspects influencing nutrient and paleoproductivity in the lake. The primary objectives of this thesis are:

(1) How did Lake Victoria refill during the Latest Pleistocene? And what were the paleoclimate conditions that influenced its re-emergence?
(2) What are the spatiotemporal changes in primary production in Lake Victoria over the last 17 ka? And how are these changes influenced by environmental factors?

(3) When did anthropogenic eutrophication begin in the Mwanza Gulf of Lake Victoria? And what are the associated ecological changes that have occurred over the past century?

1.2 Research background

1.2.1 Paleoclimate variability in eastern Africa

The hydroclimate in Eastern Africa is characterized by two major convergence zones: The seasonal migration of the Intertropical Convergence Zone (ITCZ) following the solar maximal radiation and the Congo Air Boundary (CAB), which defines the confluence of Atlantic- and Indian-Ocean-derived moist air masses (Fig. 1.2). On longer timescales, orbital variations account for variations in ocean-land contrasts and sea surface temperature influencing the monsoonal systems (e.g., Kutzbach and Street-Perrott, 1985; Saji et al., 1999; Schreck and Semazzi, 2004). While the primary drivers of the regional hydroclimate variability are well understood, their impact on each study site as well as their relative influence, are areas of ongoing research and discussion. Therefore, the following section highlights the key paleoclimate events that have impacted the region.

During the Last Glacial Maximum (LGM), Eastern Africa experienced severe and widespread aridity, which reached its peak during northern-hemispheric Heinrich Stadial 1 (HS1) (~17.5-14.5 ka; Yang et al., 2023). This aridity is apparent in various paleoclimate records, such as Chew Bahir Basin (Foerster et al., 2012), Lake Chala (Verschuren et al., 2009), Lake Tanganyika (Tierney et al., 2010; Tierney et al., 2008), and Lake Malawi (Castañeda et al., 2009), as well as in significant reduction in lake levels across the region (Gasse, 2000). Lake Victoria completely desiccated during this period (e.g. Johnson et al., 1996, further discussion in chapters 3, and 4). A successive period of aridity in tropical eastern Africa occurred during the Younger Dryas (YD) (12.6–11.7 ka) (deMenocal et al., 2000; Gasse, 2000; Gasse et al., 2008), although lipid biomarker records suggest that the timing and severity of this drought event varies across the region. Pronounced responses to the YD drying were found in the Lakes Chala and Tanganyika (Tierney et al., 2008, 2011). In contrast, Lake Tana (Costa et al., 2014) and Lake Victoria displayed either no or muted signals in lipid biomarkers (Berke et al., 2012; Wienhues et al., accepted, Chapter 5).

After the YD termination, the Indian Ocean monsoon experienced a strong resurgence (Talbot et al., 2007), leading to a rapid onset of moist conditions in eastern Africa. The period of increased humidity is commonly known as the African Humid Period (AHP) (e.g. deMenocal et al., 2000; Gasse, 2000), or more precisely as the Eastern African Humid Period (EAHP) (11–5 ka) at the regional level (Tierney et al., 2011). Maximum regional humidity is widely recorded in various hydroclimate records in the region in the early Holocene (e.g. Barker et al., 2004; Gasse, 2000), succeeded by a moderately humid mid-Holocene period (e.g. Baxter et al., 2023; Stager and Mayewski, 1997). Regional differences are observed in the termination of the AHP (~5 ka), ranging from gradual to abrupt transition (e.g. Liu et al., 2017; Tierney and deMenocal, 2013). In the late Holocene, arid conditions prevailed in eastern Africa, marked by abrupt regional drought between ~4.7 and 3.2 ka is commonly recorded in paleoclimate archives (Verschuren et al., 2009).

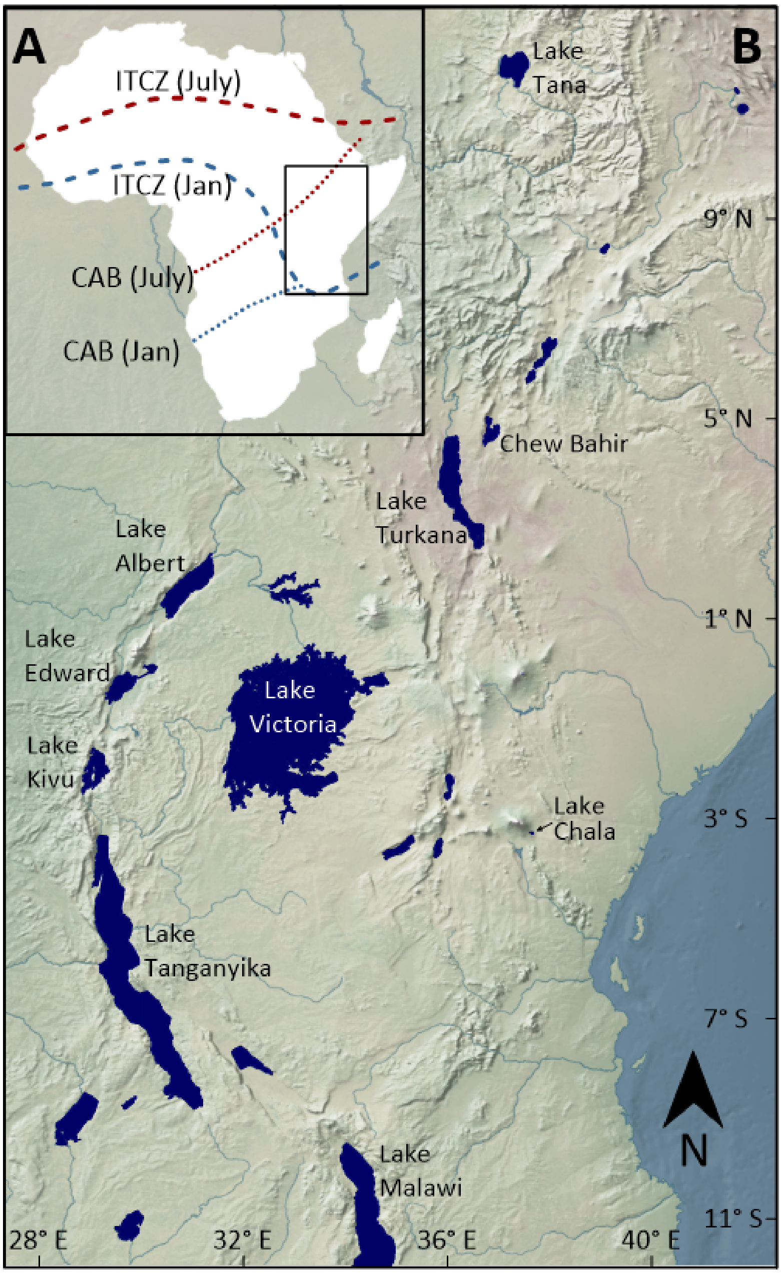

FIGURE 1.2: Map of lakes in eastern Africa and July and January positions for ITCZ and CAB (inset).

While these overarching paleoclimate patterns are evident in eastern Africa, each lake exhibits varying sensitivity to external forcings influenced by lake parameters, location, and local topography (Olaka et al., 2010). To this end, this thesis presents novel high-resolution sediment records from Lake Victoria that contribute to the understanding of the dynamic relationship between hydroclimatic changes and the lake system.

1.2.2 Biodiversity

The endemic cichlid fish in several of the African Great Lakes stand as the most striking examples of explosive speciation, where hundreds of cichlid fish species evolved rapidly within the same ecosystem, each developing unique ecological adaptations to exploit specialized niches (Fig. 1.3, Salzburger et al., 2014). This remarkable diversification is primarily attributed to the dynamic geological and paleoclimate history, which has affected the age, depth, and hydrographic connectivity of the lakes in the region. For instance, past changes in hydroclimate caused significant fluctuations in lake levels (Danley et al., 2012). In contrast to the extremely deep and ancient Lakes Tanganyika and Malawi, which retained significant water bodies despite lake-level drops of 100-250 m (e.g. Cohen et al., 2007; McGlue et al., 2008), Lake Victoria stands as a relatively young, shallow lake (<70 m water depth), having undergone complete desiccation and mass extinction during the latest Pleistocene ~17 ka ago (e.g. Johnson et al., 1996; Wienhues et al., in press, Chapter 4 of this thesis).

One of the main enigmas arising is how Lake Victoria's cichlids managed to repopulate and speciate rapidly following desiccation. The discovery of the desiccation event in Lake Victoria's geological history has led to more complex hypotheses about the lake's cichlid evolution. Some hypotheses suggest that the cichlid radiation in Lake Victoria was fueled by recent speciation events while others propose that the lake's current diversity is the result of refugia that survived the desiccation event (e.g. Elmer et al., 2009; Seehausen, 2002; Seehausen et al., 2003; Verheyen et al., 2003). It highlights the importance of continuous biogeochemical and palaeoecological records to understand the environmental context and lake response to perturbations when studying the impact of climate change in shaping the biodiversity of aquatic ecosystems (e.g. Cohen et al., 2022). This approach has been successfully used in other ancient lake systems (e.g. Albrecht & Wilke, 2008; Ivory et al., 2016; Wilke et al., 2020).

The study of Lake Victoria sediments, which cover the entire sedimentation history of the modern lake, can help to address these questions and provide the paleoenvironmental and paleoclimatic context for interpreting evolutionary history.

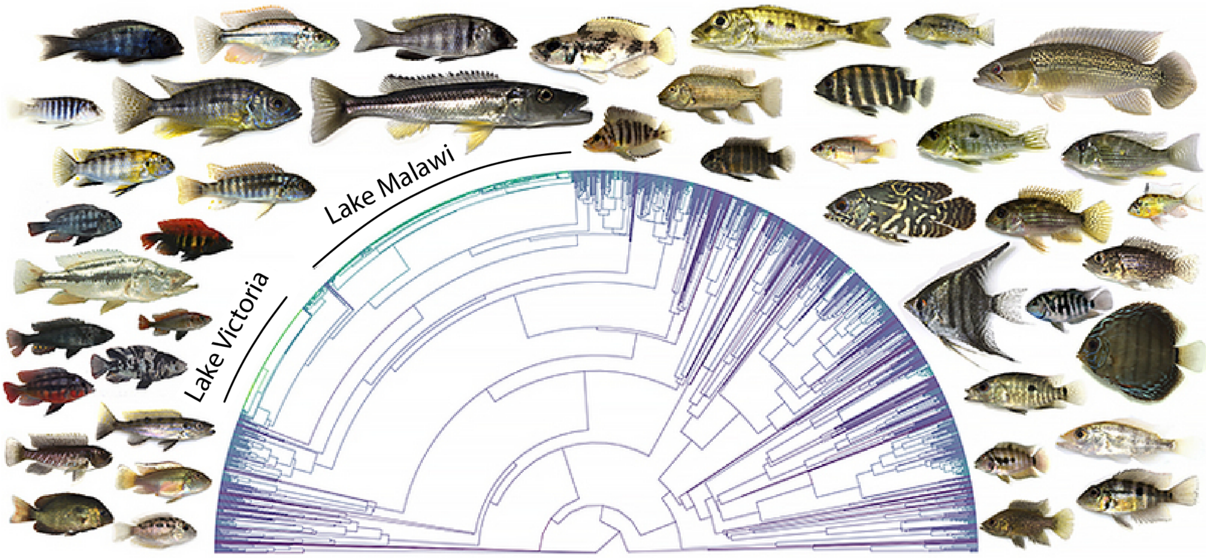

FIGURE 1.3: Macroevolutionary history of cichlid speciation and their morphological diversity. The two fastest radiations, Lake Victoria and Lake Malawi, are highlighted in green (adapted from McGee et al., 2020).

1.2.3 Environmental change and eutrophication

The Lake Victoria catchment is one of the most densely populated areas in Africa, while the lake itself supports one of the world's largest inland fisheries (Juma et al., 2014). Land use changes, increased nutrient loading, and the introduction of exotic species triggered eutrophication, causing a cascading effect on Lake Victoria's biodiversity (Downing et al., 2014).

Early signs of eutrophication in Lake Victoria date back to the 1920s (Hecky et al., 2010; Njagi et al., 2022; Verschuren et al., 2002). Agriculture, deforestation, and wastewater discharge increased nutrient inputs from agriculture, resulting in phytoplankton blooms that peaked in the mid-1980s (Hecky, 1993). This has led to a decline in water transparency, a increase in bottom water anoxia, and a shift in phytoplankton community composition towards dominance by cyanobacteria (Hecky, 1993; Verschuren et al., 2002), while the zooplankton community shifted to small species dominance (Gophen et al., 1995; Mwebaza-Ndawula, 1994; Wanink et al., 2002). In addition, cyanobacteria dominance caused increasing concentrations of cyanotoxins (e.g., microcystin) in the water (Onyango et al., 2020).

In 1954, the Nile perch, a large predatory fish, was introduced into Lake Victoria. This species rapidly expanded its population and reached high densities in the 1980s. Simultaneously, a decline in the diversity and biomass of haplochromine cichlid fishes was observed. These endemic fishes were once the dominant fish species in the lake (Witte et al., 1992). The introduction of Nile perch is thought to have played a major role in this decline (Witte et al., 2007). Although the haplochromine population recovered in the last decades (Seehausen et al., 1997), the species diversity remains well below pre-Nile perch levels (Kishe-Machumu et al., 2015; Witte et al., 2000).

The interconnectivity of these events and processes in the food web has motivated numerous research studies focusing on how eutrophication and fishing pressure have altered the ecology of Lake Victoria in all aspects of the food web from algae to fish. Analyzing changes in nutrient concentrations, algal community and abundance, and zooplanktivorous fish density over time in sediments an provide valuable insights into this complex issue.

1.3 Outline of the thesis

In many respects, Lake Victoria is a unique study site to address questions about lake responses to paleoclimate changes and ecosystem interactions on millennial to decadal time scales. In the following chapters, this thesis provides a detailed characterization of the paleolimnological conditions of Lake Victoria with a focus on sedimentological analysis of physicochemical variables, nutrient dynamics, ecosystem paleoproductivity, and algal communities.

Chapter 2 provides a detailed introduction to the study site and methods employed in this thesis. Summaries of co-authored publications demonstrate the contribution of this thesis to the overall project.

Chapter 3 summarizes previous paleoenvironmental research with a focus on sediment cores and
chronologies. The extensive and detailed literature review is central to the contextualization of the investigations presented in the subsequent chapters.

Chapter 4 focuses on the re-filling history of Lake Victoria after its desiccation in the latest Pleistocene. By combining chrono-lithostratigraphy of a set of sediment cores and palynological evidence, this chapter presents a refined and robust lake-level reconstruction, enabling the investigation of shifts in aquatic habitats.

Chapter 5 investigates the hydroclimate variability and primary production responses in Lake Victoria from the latest Pleistocene to the Holocene. Based on an extensive multivariate dataset, it provides a more accurate, time- and space-transgressive view on environmental changes in the lake and determines major phases of ecosystem change.

Chapter 6 focuses on anthropogenic eutrophication and associated ecological changes in the Mwanza Gulf, a southern embayment in Lake Victoria, over the past century. Through an in-depth analysis of sediment surface cores, this chapter unravels the timing and extent of alterations in phytoplankton and zooplankton assemblages in relation to changes in fish community structure.

Chapter 7 synthesizes the major findings and conclusion of the present thesis. An outlook is given for future research on Lake Victoria.

Appendix I complements Chapter 3 by providing a summary table of Lake Victoria sediment cores and their chronologies and references to the original publications.

Appendix II contains a detailed overview over all analyzed cores and established core composites.

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Chapter 2

2. Study sites and methodology

2.1 Site description – Lake Victoria

Lake Victoria (0.5°N to 3.0°S; 1135 m a.s.l.) is situated in the depression between the two branches of the East African Rift System and is the world's largest tropical lake (surface area of 68,800 km^2). With a maximum water depth of 68 m and an average water depth of 40 m (Johnson et al., 1996), the lake is relatively shallow compared to the surrounding Rift Valley lakes. The lake's bathymetry reveals a shallow bowl-shaped basin devoid of prominent topographic features and characterized by gentle slopes.

Hydrology: Lake Victoria's water balance is predominantly influenced by rainfall and evaporation. Over 80% of the water entering the lake comes from direct precipitation, while approximately 70% of the water leaving the lake evaporates into the atmosphere (Beverly et al., 2020; Yin & Nicholson, 1998, 2002). River runoff makes a small contribution to the lake's overall water input (Crul, 1995). The lake drains northward via the Victoria or White Nile, which accounts for 24% of the water loss. The outflow has been controlled since 1959 (Nalubaale Dam; Kull (2006)).

Climate (Fig. 2.1 A and B): The tropical climate is controlled by seasonal rainfall migration, creating two distinct rainy seasons from March to May (long rains) and October to December (short rains) (Nicholson, 2018). Moist air masses originate from the Indian and Atlantic Oceans and are primarily controlled by the interplay between the northward and southward movements of the Afrotropical rain belt (widely known as the Intertropical Convergence Zone, ITCZ), and the westward and eastward shifts of the Congo Air Boundary (CAB).

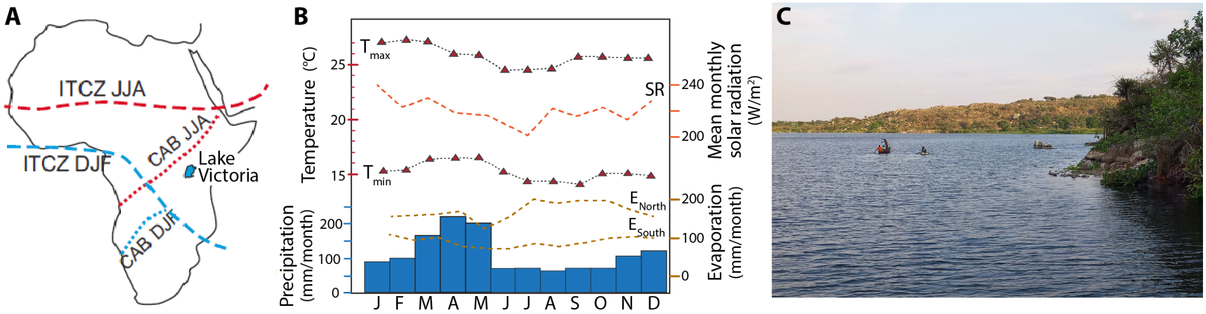

FIGURE 2.1: Location and climate context of Lake Victoria. **(A)** Boreal summer (JJA) and winter (DJF) position of the Intertropical Convergence Zone (ITCZ) and Congo Air Boundary (CAB).**(B)** Climate pattern after Spigel and Coulter (1996). **(C)** Picture of the eutrophic Mwanza Bay (© G. Wienhues)

Limnology: Lake Victoria is currently classified as holomictic, with the water column undergoing a complete overturn once a year during the cool and windy dry season from May to August. Stratified water column conditions and bottom water anoxia were caused by progressive eutrophication in the 20th century (Hecky et al., 1994; Verschuren et al., 2002). Rising nutrient levels also led to changes in phytoplankton composition, transitioning from diatoms to cyanobacteria, a trend that is most evident in the protected and shallow embayments of

Lake Victoria (Fig. 2.1C) (Meyers & Teranes, 2001; Silsbe et al., 2006). These disruptions to the lake's ecosystem have had a devastating impact on fish biodiversity, with the introduction of Nile perch in the 1950s exacerbating the situation (Hecky et al., 1994; Mugidde, 1993; Stager & Mayewski, 1997).

2.2 Methodology

This section summarizes the key methodologies used in this thesis (Fig. 2.2). More details about the methods can be found in the respective chapters (Chapters 3, 4, and 5).

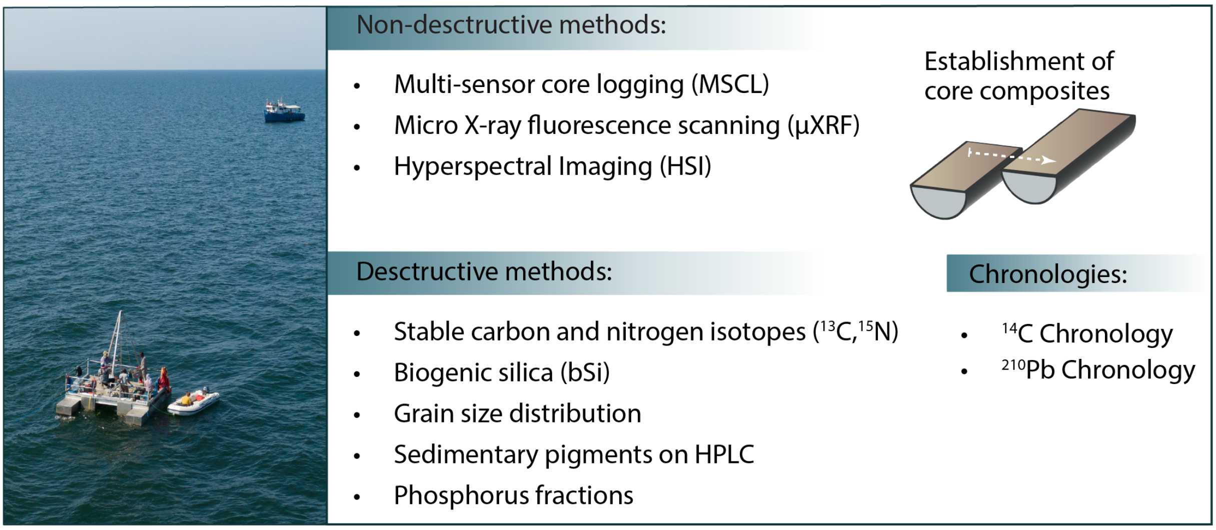

FIGURE 2.2: Schematic summary of workflow and multi-proxy data set generated in this thesis. Picture of the coring platform on Lake Victoria in 2018 (©M. Muschick).

2.2.1 Core retrieval and composite stratigraphy

Sediment cores for the present thesis were retrieved during a field campaign in 2018. A series of sediment cores were extracted using a UWITEC piston corer along a nearshore to offshore transect from the eastern shoreline (Fig. 2.3B). Multiple cores were collected at four different coring sites, designated as LVC18-S1 to LVC18-S4 (hereafter LV1 to LV4). The water depths at these coring sites ranged from 13.4 to 63 meters below the modern lake level (m.b.l.l. in October 2018) (Fig. 2.3C). Additionally, short surface cores were retrieved at the sites LV1 and LV3 mainly for chronological assessment of the sediment top (LVC19-S1 and S3). In the southern Mwanza Gulf, several short surface cores were obtained using UWITEC gravity corer (Fig. 2.3D). The cores SC12, SC14, and SC19 were subsequently selected for further analysis.

The cores were split lengthwise, and the core halves were sedimentologically described following Schnurrenberger et al. (2003) as well as initially examined using non-destructive analytical techniques: micro X-ray fluorescence (μXRF) and hyperspectral spectral scanning (HSI) (more details in Chapters 4, 5, and 6).

For the coring sites LV1, 2 and 4, a continuous composite sediment sequence was created from parallel cores (Appendix II). The stratigraphic correlation between the core sections was established using tie points from elemental profiles derived from XRF data (example Figure

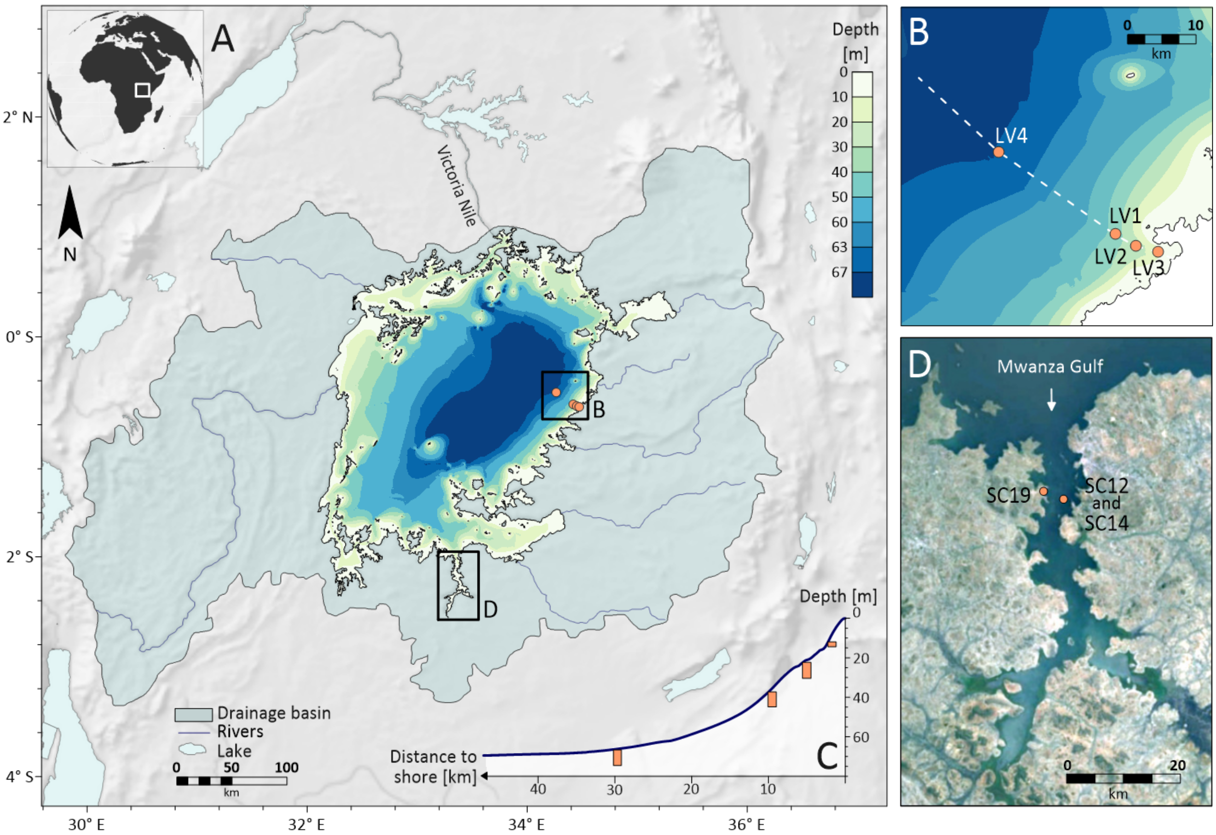

FIGURE 2.3: **(A)** Catchment and bathymetry of Lake Victoria with the indicated location of the long and surface coring sites modified from Wienhues et al. (in press). **(B)** Inset map of the coring transect with the long cores LVC18-S1 (LV1), LVC18-S2 (LV2), LVC18-S3 (LV3), and LVC18-S4 (LV4). **(C)** Depth profile of the coring transect in distance to the shoreline. Bathymetric data are from Hamilton et al. (2022). **(D)** Inset satellite image of the Mwanza Gulf with the location of the surface cores SC12, SC14, and SC19 (Google, 2024)

AII.1 in Appendix II). Due to the homogeneous nature of the sediment, the sediment cores lacked visual markers. Core LV3 is a single continuous piston core, and the three core segments were simply added together. An overview of the cores used in this thesis in presented in Table 2.1. Detailed tables of the composite correlation can be found in Appendix II.

2.2.2 Chronologies

Sediment chronologies were determined by radiocarbon dating of handpicked macroscopic charcoal pieces and terrestrial plant macrofossils. For the piston cores (LV1, 2, and LV4), we used the precise chronologies developed by Temoltzin-Loranca et al. (2023a). The age-depth model for core LV3 is presented in Wienhues et al. (accepted) (Chapter 3). All samples were analyzed with the MICADAS system at the University of Bern (Szidat et al., 2014) and calibrated with IntCal20 (Reimer et al., 2020). Age-depth models were constructed using the software rbacon (Blaauw & Christen, 2011; Blaauw et al., 2021).

The age of the surface cores (SC12, SC19, LVC18-S1, and LVC18-S3) was determined by radionuclide dating, utilizing alpha spectrometry for ^{210}Pb (measured indirectly by ^{210}Po) and gamma spectrometry for ^{226}Ra and ^{137}Cs at the University of Gdansk (Tylmann et al., 2016). The

TABLE 2.1: Summary of piston and surface cores taken during coring campaign 2018, including the analyses applied on each core.

Core ID (Segments)	Coordinates	Depth [m]	Coring Site	Composite Core (short name)	Analyses applied on composite core
Piston cores (offshore to nearshore)					
LVC18-4L (1 – 10)	01°02,966′S 33°47,768′E	63.0	4	LVC18-S4 (LV4)	HSI, XRF, δ^{13}C, δ^{15}N, bSi, Pigments, Grain Size
LVC18-1B (1 – 7)	01°06,979′S 33°54,811′E	37.6	1	LVC18-S1 (LV1)	HSI, XRF, δ^{13}C, δ^{15}N, bSi, Grain size, Pigments, Phosphorus
LVC18-1C (1 – 6)	01°06,982′S 33°54,804′E	37.6	1		
LVC18-2E (1 – 9)	01°07,850′S 33°56,779′E	22.6	2	LVC18-S3 (LV2)	HSI, XRF, δ^{13}C, δ^{15}N, bSi, Pigments, Grain Size
LVC18-2F (1 – 8)	01°07,849′S 33°56,779′E	22.6	2		
LVC18-3J (1 – 3)	01°08,344′S 33°58,593′E	13.4	3	LVC18-S3 (LV3)	HSI, XRF
Surface cores (offshore to nearshore)					
LVC18-1-S1*	01°06,914′S 33°55,146′E	37.0	1	(LVC18-S1)	^{210}Pb, XRF, HSI
LVC18-3-S2	01°06,914′S 33°55,146′E	10.0	3	(LVC18-S3)	^{210}Pb, XRF, HSI
* The sediment core was not further used due to the loss of the uppermost sediment section, as indicated by ^{210}Pb and HSI analyses.					
Surface cores (Mwanza Gulf)					
LVC18-TSG-SC12	02°33,473′S 32°52,470′E	14.5	G	(SC12)	^{210}Pb, XRF, HSI, δ^{13}C, δ^{15}N, Pigments, Phosphorus
LVC18-TSG-SC14	02°33,473′S 32°52,470′E	14.5	G	(SC14)	XRF, HSI, (invertebrates)
LVC18-TSI-SC19	02°33,015′S 32°51,023′E	10.5	I	(SC19)	^{210}Pb, XRF, HSI, δ^{13}C, δ^{15}N, Pigments, Phosphorus

^{210}Pb chronologies were determined by commonly used model algorithms: The constant rate of supply (CRS), constant flux with constant sedimentation (CFCS) (Appleby, 2001) as well as the Bayesian plum model (Aquino-López et al., 2018). Calculating ^{210}Pb ages by multiple models helps to assess their sensitivity and performance compared to each other. All data sets were tested (and corrected) for missing ^{210}Pb unsupported inventories according to Tylmann et al. (2016).

2.2.3 Non-destructive sediment analyses

On the full core segments, magnetic susceptibility (MS) and sediment density (γ-ray attenuation) was measured with a GEOTEK multi-sensor core logger (MSCL) at the Institute of Geological Sciences, University of Bern. However, the data obtained from the sediment cores was not used due to the interference caused by the surrounding iron-containing tape.

X-ray fluorescence (XRF) analysis was conducted on split core halves to assess changes in the elemental composition of sediments from Lake Victoria, serving as indicators of significant shifts in the lake's environment (Davies et al., 2015). XRF measurements were performed at 50 mA, 30 kV, and 30-second integration time over 5 mm intervals (LV4, 1, and 2, surface cores) and 10 mm intervals (LV3). The scans were conducted using an ITRAX core scanner equipped with a Cr- and Mo-anode X-ray tube at the Institute of Geological Sciences, University of Bern. The selection of key elements for analysis was guided by the quality of the data and the research questions of interest.

In addition, hyperspectral imaging (HSI) core scanning was performed on fresh core halves to gain information about paleoproduction in Lake Victoria. A hyperspectral camera (Specim PFD4K-65-V10E; 400–1000 nm) was used with exposure 120 ms, aperture f/1.9, field of view 90.2 mm, frame rate 8.0 Hz, and scanning speed 0.55 mm/s. The analysis of the spectral data follows the methodology outlined by Butz et al. (2015). The relative absorption band depth index (RABD655–680max) was utilized to quantify the absorption trough of total green chloropigments (TChl, including chlorophyll *a*, *b*, and colored degradation products), which serves as an indicator of aquatic primary production and/or total algal biomass (Leavitt & Hodgson, 2001; Michelutti & Smol, 2016). Detailed instrumental and methodological descriptions can be found in Butz et al. (2015) and Zander et al. (2022).

2.2.4 Destructive analytical techniques

Additional analytical techniques were performed after taking discrete samples. The sampling strategies employed are thoroughly detailed in the individual research articles (Chapters 3, 4, and 5).

The concentration and isotope composition of nitrogen and carbon (TC%, TN%, δ^{13}C, δ^{15}N) in the sediments of Lake Victoria were simultaneously determined 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 N_2 (AIR) and the V-PDB (Vienna Pee Dee Belemnite) standards, respectively. For δ^{13}C and δ^{15}N calibration, atropine ($\delta^{13}C = -21.4‰$, $\delta^{15}N = -2.9‰$), peptone ($\delta^{13}C = -15.64‰$, $\delta^{15}N = 6.67‰$), and nicotinamide ($\delta^{13}C = -42.2‰$, $\delta^{15}N = -1.99‰$) in-house standards with known carbon and nitrogen content and isotopic composition. Measurement reproducibility for both nitrogen and carbon was better than 0.2‰. Carbon and nitrogen analysis on ashed sediment samples (loss-on-ignition at 550°C) confirmed the absence of inorganic carbon. Therefore, samples were not acidified before isotopic analysis (Kennedy et al., 2005), and total carbon (TC) values represent total organic carbon (TOC) in Lake Victoria's sediments.

Biogenic silica (bSi) was determined following the wet-alkali method of Ohlendorf and Sturm (2008). Accordingly, 100 mg of freeze-dried sediment was extracted using 1M NaOH solution at 90°C for 3h. Organic matter was removed by H_2O_2 prior to leaching (Mortlock & Froelich, 1989). Extracted Si was measured with inductively coupled plasma mass spectrometry (Agilent ICP-MS 7700x). Lithogenic elements (Fe, Al) were simultaneously measured for lithogenic Si correction (Mortlock & Froelich, 1989). The solid residual after bSi leaching was used for grain size distribution analysis. To avoid the formation of flocs, a dispersion solution comprising sodium hexametaphosphate $(NaPO_3)_6$ and sodium carbonate (Na_2CO_3) was applied. After ultrasonic treatment, the samples were measured by laser diffraction (Malvern Mastersizer 2000 equipped with an automated wet dispersion unit) at the Institute of Geography, University of Bern. Due to instrumental bias during the grain size measurement that noticeably affected the grain size distribution in the clay and silt fraction, the data was deemed unreliable and therefore not used. The biogenic silica as well as the grain size analysis were applied to the offshore cores LV1, LV2, and LV4.

Sequential phosphorus (P) extraction was applied to the offshore core LV1, as well as the two surface cores SC12 and SC19 from Lake Victoria following the protocol developed by the Standards, Measurements, and Testing (SMT) of the European Commission (Ruban et al., 1999, 2001; Tu et al., 2021). Three independent extractions using NaOH and HCl were carried out to measure five P fractions: non-apatite inorganic P (hereafter referred to as Fe–P), calcium phosphate apatite (AP), inorganic P (IP), organic P (OP), and total P (TP). Analytical efficiency was assessed by analyzing certified reference sediment material (CRM) BCR®-683. Extractable P concentrations were measured colorimetrically in 4ml macro-cuvettes using the malachite green method at an absorbance of 610 nm (Ohno & Zibilske, 1991) with the spectrophotometer (Shimadzu UV-1800). Separate standard calibration curves were prepared and measured for each measurement batch and sample matrix. The obtained results from offshore site LV1 yielded no evidence of substantial phosphorus fractionation in Lake Victoria. Considering the time- and labor-intensive nature of this analysis, the limiting amount of sample material, and the inconclusive results, it was decided to not proceed with this analysis on subsequent long cores.

Sedimentary pigments were analyzed on two offshore cores (LV1 and LV4) and two surface cores (LV12 and LV19). The pigments were extracted by using 95% acetone following the procedure outlined by Sanchini and Grosjean (2020). The quantification of pigment extracts was carried out using high-performance liquid chromatography (HPLC) at the CNR Water Research Institute in Verbania, Italy, following the method described by Lami et al. (2000). All HPLC pigment concentrations were expressed as nMol per gram of organic carbon, as recommended by Lami et al. (2000). The analysis was restricted to taxonomically diagnostic pigments.

2.3 Co-authored publications

Building upon the data and research presented in this thesis, this section summarizes my contribution in the co-authored publications. Figure 2.4 provides an overview of these publications.

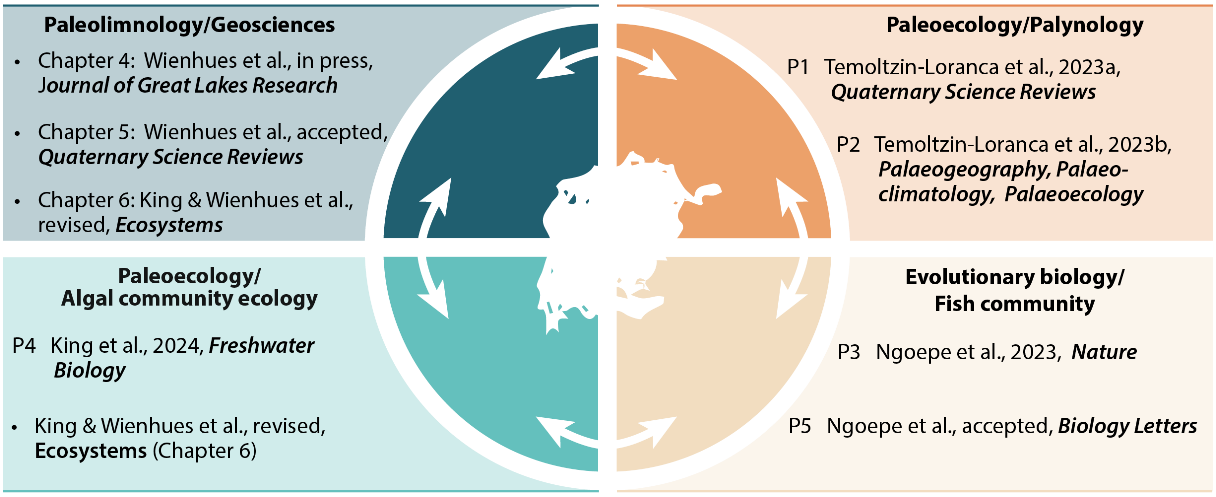

FIGURE 2.4: Co-authored publications (P1 to P5) from the Lake Victoria Sinergia Project (state: Feb. 2024).

P1: A chronologically reliable record of 17,000 years of biomass burning in the Lake Victoria area

Yunuen Temoltzin-Loranca, Erika Gobet, Boris Vannière, Jacqueline F.N. van Leeuwen, **Giulia Wienhues**, Sönke Szidat, Colin Courtney-Mustaphi, Mary Kishe, Moritz Muschick, Ole Seehausen, Martin Grosjean, Willy Tinner

Quaternary Science Reviews (2023a)

This study presents a new chronological framework for a set of sediment cores from Lake Victoria. It provides a continuous and independent radiocarbon chronology based on macroscopic charcoal and novel palynological and charcoal records for three sediment cores along a transect (LV1, 2, and 4). The palynological data served additionally as a biostratigraphic control across this transect. The data revealed that, during the Last Glacial Maxima and Heinrich Stadial 1, a dominant savanna landscape prevailed, characterized by low fire frequency before 15 ka and increased fire occurrence between 15 and 14 ka. Subsequently, the Afromontane forest expanded as warmer and wetter conditions promoted rainforest growth, leading to a decline in fire events, notably during the Eastern African Humid Period (11.5 to 5 ka). A peak in fire activity was noted at the end of this exceptionally humid period around 5 ka. However, unexpectedly low fire frequencies followed during the Iron Age and subsequent periods. These results reveal that long-term vegetation dynamics in the Lake Victoria area were mainly driven by (hydro-)climate, at least until the early Iron Age (~ 2.4 – 1.1 ka), when human impact became important. Fire activity may have been controlled by combined factors such as fuel availability, temperature, and moisture.

I contributed to this by joining the core opening campaign and scanning all core segments (XRF and HSI) prior to subsampling. Based on these scans, I created and provided the master core composite. Furthermore, I actively discussed, reviewed, and commented on the manuscript text.

P2: Long-term ecological successions of vegetation around Lake Victoria (East Africa) in response to latest Pleistocene and Early Holocene climatic changes

Yunuen Temoltzin-Loranca, Erika Gobet, Boris Vannière, Jacqueline F.N. van Leeuwen, **Giulia Wienhues**, Colin Courtney-Mustaphi, Mary Kishe, Moritz Muschick, Leighton King Pavani Misra, Nare Ngoepe, Blake Matthews, Hendrik Vogel, Oliver Heiri, Ole Seehausen, Martin Grosjean, Willy Tinner ***Palaeogeography, Palaeoclimatology, Palaeoecology* (2023b)**

The study presents a refined high-resolution palynological and macrocharcoal (woody and herb charcoal) record from offshore core LV4 during the Late Pleistocene-Holocene transition (16.6 to 9 ka), a period that involves major hydroclimate changes. A special focus lays on the drivers of ecological successions from savanna to Afromontane and tropical rainforest at Lake Victoria. By the end of the widespread drought in eastern Africa during the Heinrich Stadial 1 (~16.5 ka), arboreal taxa (Celtis and Podocarpus) expanded at the expense of savanna, followed by the spread of Afromontane tree species (Olea and Macarang) around 15.5 – 15 ka. Herb macrocharcoal influx indicates that mainly grasses fueled fires in the savanna. As temperatures and humidity continued to rise (13.2 – 10.7 ka), Afromontane vegetation dominated by Olea expanded towards the lowlands and tropical rainforests established, and woody-dominated fuel types started to replace grassland fires. By the onset of the Holocene, the tropical savanna had largely been replaced by tropical rainforest, while Afromontane forests moved to higher elevations. These results suggest that the biome reorganization was primarily driven by moisture and temperature changes.

Similar to the first co-authored publication, I contributed to this study by joining the core opening campaign, providing the master composite as well as the elemental ratios (Zr/Ti and Rb/Zr) shown in this article. Furthermore, I reviewed and provided feedback on the manuscript.

P3: A continuous fish fossil record reveals key insights into adaptive radiation

Nare Ngoepe, Moritz Muschick, Mary A. Kishe, Salome Mwaiko, Yunuen Temoltzin-Loranca, Leighton King, Colin Courtney Mustaphi, Oliver Heiri, **Giulia Wienhues**, Hendrik Vogel, Maria Cuenca-Cambronero, Willy Tinner, Martin Grosjean, Blake Matthews, Ole Seehausen

***Nature* (2023)**

The study presents a fossil-based reconstruction of the Lake Victoria fish assemblages and provides insights into the temporal development of an adaptive radiation community through time and a deeper understanding of the evolution of the lake's fish diversity. A set of sediment cores (LV1 to LV4) were screened for fish teeth, which were morphologically assigned to five fish families (catfish, cyprinoids, radiating haplochromine cichlids, and non-radiated oreochromine cichlids). This fossil data set was discussed in light of key evolutionary diversification concepts: (i) ecological versatility (= the ability of species to access new resources and populate a wider range of habitats), (ii) ecological opportunity (= the opening of new ecological niches and availability of resources), (iii) hybrid ancestry (= the genetic diversity stemming from hybridization events of ancestral lineages), and (iv) priority effect (= possible early habitat occupation or monopolization by haplochromine cichlids). It was observed that initially, all major fish taxa colonized the shallow wetland environment in the Victoria basin. However, as the lake level rose, only haplochromine cichlids colonized in the deep and open-water habitats, while other taxa remained in littoral inshore habitats. These results support the differential habitat versatility of cichlid fishes compared to other fish groups and that ecological versatility was key to the adaptive radiation of cichlid fishes in Lake Victoria. The coincidence of ecological opportunity with ecological versatility and hybrid ancestry was crucial for the explosive adaptive radiation that occurred in Lake Victoria. Furthermore, the simultaneous arrival of all major fish taxa as the modern lake formed contradicts the notion of ecological priority effects in the early stages of the lake's evolution.

My contributions to this study included joining the core opening campaign, providing the master composite as well as the reconstruction of the lake formation and lake-level dynamics, capturing the transition from the wetland environment to a deep and open lake in the latest Pleistocene, and the age-depth model for core LV3, employed in this study. I was involved in discussions about sedimentological, geomorphological, and environmental dynamics characterizing the aquatic habitats across the core transect in Lake Victoria.

P4: Temporal dynamics of invertebrate community assembly in Lake Victoria since the Late Pleistocene based on chitinous remains

Leighton King, Colin Courtney-Mustaphi, Maria Cuenca-Cambronero, **Giulia Wienhues**, Nare Ngoepe, Moritz Muschick, Yunuen Temoltzin-Loranca, Hendrik Vogel, Martin Grosjean, Willy Tinner, Andrew Cohen, Mary Kishe, Oliver Heiri, Ole Seehausen, Blake Matthews

***Freshwater Biology*, 2024**

This study analyzed the fossil remains of invertebrates in a Lake Victoria sediment core to trace changes in invertebrate community composition and gain insights into their temporal dynamics in response to climatic and environmental variability. For this end, chitinous remains of chironomids and midges (Chaoboridae) from one sediment core (LV1) were examined. The study identified four distinct phases in the invertebrate community, each corresponding to different climatic and environmental conditions. First, colonizing species became established, followed by a transition from benthic to pelagic species indicating rising water levels in response to increasing humidity during the Late Pleistocene-Holocene transition (13.7 – 9.1 ka). A high abundance of dipteran larvae and high diatom production corresponds to the Holocene African Humid Period (9.1 – 4.7 ka). The subsequent appearance of the littoral Cladocera Alona

(~4.7 ka) coincides with the end of the African Humid Period, suggesting the establishment of seasonal wind-driven oxygenation of the water column. During the last 1.3 ka, increasing planktonic cladoceran assemblages dominated the invertebrate community, which are most likely linked to human impact and food availability.

My contributions to this study included participating in the core opening campaign, providing the master composite, and through discussions and comments on the manuscript text. Additionally, I provided the biogenic silica data for the cores LV1 and LV4, which facilitated the comparison of the invertebrate data with previous studies from Lake Victoria at different water depths.

P5: Testing alternative hypotheses for the decline of cichlid fish in Lake Victoria using fish teeth time series from sediment cores

Nare Ngoepe, Alenya Merz, Leighton King, **Giulia Wienhues**, Mary A. Kishe, Salome Mwaiko, Pavani Misra, Martin Grosjean, Blake Matthews, Colin Courtney Mustaphi, Oliver Heiri, Andrew Cohen, Willy Tinner, Moritz Muschick, Ole Seehausen

***Biology Letters*, accepted**

This study examines the impact of various factors, including eutrophication, fishing pressure, and the introduction of non-native species on the haplochromine cichlid fish community of Lake Victoria during the 20th century. By analyzing fish teeth time series from two surface cores (SC9 and SC14) in the Mwanza Gulf, the study reveals a significant decline in cichlid populations preceding the arrival of the Nile perch. This indicates that eutrophication and associated ecosystem changes likely played a more significant role in the decline of cichlids than the introduction of Nile perch.

My contribution to this study included core splitting, core picture scans, and providing the hyperspectral data sets for each surface core, which were crucial for visually correlating to the ^{210}Pb dated cores and providing feedback on the manuscript.

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Chapter 3

3. Paleoenvironmental research at Lake Victoria

Lake Victoria has captivated scientific interest for several decades. This chapter provides a comprehensive overview of the paleoenvironmental research conducted on Lake Victoria, setting the stage for the detailed investigations presented in the subsequent Chapters 4, 5, and 6.

3.1 Sediment cores from Lake Victoria

Previous research on Lake Victoria has played a crucial role in deciphering its complex history. Figure 3.1 presents a comprehensive review of the sediment cores and their lithologies. Pioneering studies in the 1960s and mid-1980s provided valuable insights but focused on sites at intermediate water depth (namely the cores: P2, 64-4, and Ibis-1 also known as Damba core, and Ibis-3; (Kendall, 1969; Stager, 1984; Stager et al., 1986; Talbot & Livingstone, 1989). The International Decade for the East African Lakes (IDEAL) project in the mid-1990s marked a significant advance involving extensive piston coring and seismic surveys, and provided multiple offshore cores from the deposition center (e.g., Johnson et al., 1996; Scholz et al., 1998) (see Fig. 3.1A).

The precise timing of Lake Victoria's desiccation remained controversial due to repeated re-assessments of radiocarbon ages (Stager et al., 2002) and re-interpretations of the same stratigraphy (e.g. for core V95-2P; Beuning et al., 1997b, 2002; Johnson et al., 1996; Stager & Johnson, 2000; Talbot & Lærdal, 2000; Verschuren et al., 1998, see Table AI.1), whereby the wide range of radiocarbon ages is partly attributed to the quality of the dated material (mostly bulk samples, or pollen-algae fraction, few charcoal dates) and analytical constraints in the past. Overall, this resulted in a variety of interpretations of Lake Victoria's desiccation and re-filling history.

The seismic profiles from the year 1998 reveal a persistent discontinuity, suggesting complete desiccation of the central basin (Johnson et al., 1996; Scholz et al., 1998). The last desiccation of Lake Victoria is marked by dry, dense or crumbly sediment interpreted as paleo-Vertisol, found in most offshore cores (Johnson et al., 1996). Common features associated with subaerial exposure are vertical cracks, gypsum precipitates and/or degraded and reworked organic material (e.g., Talbot & Livingstone, 1989; Talbot & Lærdal, 2000). Radiocarbon dating on these paleosols indicates that the end of the desiccation is predominantly centered around 16 ka BP (Beverly et al. (2020), Johnson et al. (2000), Stager (1984), and Stager and Johnson (2008); Fig. 3.1A, Chapter 4, Fig. 4.4). The duration of the lake desiccation is estimated from 500 years (Kendall, 1969) to several thousand years (Johnson et al., 1996). It is also conceivable that Lake Victoria experienced multiple low stands during the Latest Pleistocene drought (Stager & Johnson, 2008). However, the onset, duration, and continuity of latest Pleistocene desiccation remain unknown, as only undated seismic profiles are available to interpret the older part of the record (Johnson et al., 1996; Scholz et al., 1998). Between 16.0–16.5 ka, a rapid re-establishment of high lake levels has been proposed (Beuning et al., 2002; Talbot & Lærdal,

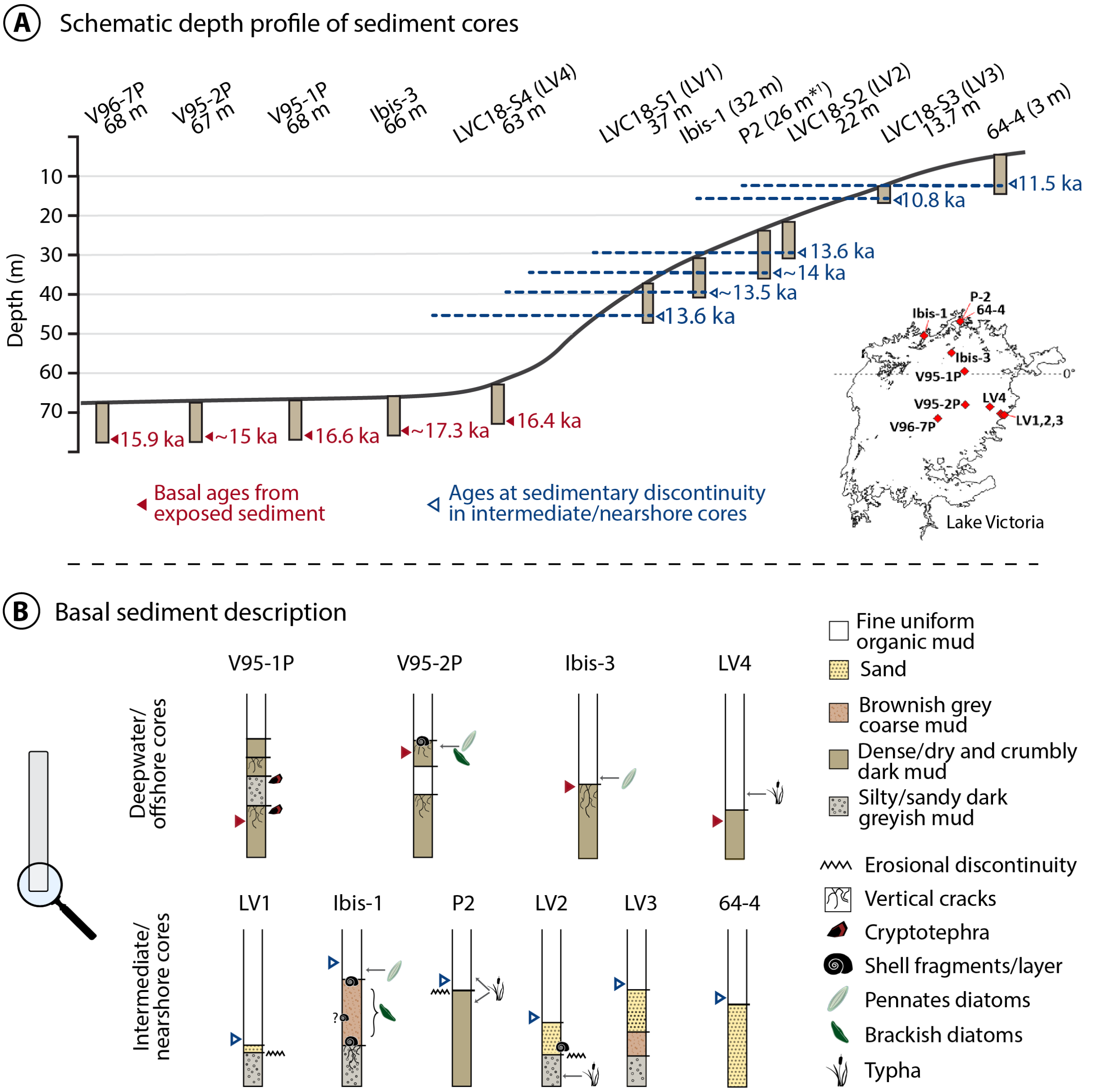

FIGURE 3.1: Schematic overview of sediment cores and their location in Lake Victoria relevant for the contextualization and interpretation of the cores (LV1, 2, 3, and 4) in this thesis. **(A)** Schematic transect of sediment profiles along coring depth with relevant radiocarbon ages (in cal. ka BP). Radiocarbon ages in red are from basal subaerial exposed sediment from the offshore cores providing a temporal range for the last major lake desiccation. Radiocarbon ages in blue indicate sedimentary discontinuities in intermediate/shallow water cores and depict temporal transgression of the lake level in the latest Pleistocene. **(B)** Illustrative depiction of the basal sediment section from the offshore cores with brief sediment descriptions. Triangles indicate the position of the ^{14}C ages presented in the figure above. Please note that the figure is not to scale and does not accurately represent the actual core lengths. A detailed list of references used is provided in Appendix I (Table AI.1 and AI.2)

2000) which contrasts with a proposed second desiccation event around 15 ka (Stager & Johnson, 2008; Stager et al., 2011; Talbot & Lærdal, 2000). However, this second desiccation layer is poorly dated and was not found in other offshore sediment cores (see Fig.3.1B). Contrarily, shallow water/brackish diatom species have been described in sediment sections overlying the exposed paleosol layer (Stager et al. (2002) and Talbot and Livingstone (1989); see Fig. 3.1B) that suggest that shallow water conditions persisted initially. However, this will be discussed in detail in Chapter 4.

Sediment discontinuities, such as shell or sand layers from cores of intermediate to shallow water depth (e.g., Ibis-1 and P2), have previously been correlated to deepwater offshore records or used to infer repeated desiccation events (Stager et al., 2011; Talbot & Livingstone, 1989). However, the basal ages of these cores and the original age-depth models (Kendall, 1969; Stager et al., 1986) appear to be affected by ancient carbon contamination. Stager and Johnson (2000) adjusted the age-depth model for the nearshore cores P2 and 64-4, resulting in more reasonable ages that indicate progressive flooding (~14 and 11.5 ka) of the sites as the lake began to refill. Consistent with this pattern, at ~13.5 ka, a transition of shallow water to pelagic conditions is indicated by a peak and subsequent decline of pennate diatoms in core Ibis-1 (Stager & Johnson, 2008; Stager et al., 2002) (see Fig. 3.1A). Conversely, mollusk shells in core Ibis-1 provide a relatively wide age estimate of 14.2–15.9 ka (Stager et al., 2002).

3.2 Lake-level dynamics and outflow formation

Lake Victoria's post-desiccation history, encompassing its transition from a closed basin to an exoreic lake with the establishment of the Victoria Nile outflow (today, its discharge controls ~80% of the nonflood-season flow along the lower Nile River; Adamson et al. (1980)) has been of interest to various scientific disciplines, including paleoclimatology, aquatic paleoecology, evolutionary biology, and archeology.

Figure 3.2 presents a comprehensive review of inferred lake-levels of Lake Victoria. According to a pronounced phase of diatom decline in an offshore core V95-2P, an outflow from Lake Victoria was suggested to have occurred between 8 and 6.7 ka (Johnson et al., 1998). Oxygen isotopes on sedimentary cellulose suggested that Lake Victoria was a closed basin until about 8 ka (Beuning et al., 1997a; Stager & Johnson, 2000), but was later revised to ~13 ka considering the more reliable V96-7P chronology (Beuning et al., 2002). This time aligns with a study using strontium isotope signatures of upper Nile catchment water bodies proposing a lake overflow no later than 13.5 ka (Talbot & Lærdal, 2000). Additionally, a diatom-inferred lake-level reconstruction of Lake Victoria, derived from core Ibis-1 (see Fig. 3.2), suggests a re-establishment of hydrologically-open conditions following a temporary closure of the outflow around 14 ka ago (Stager et al., 2011). The strontium stratigraphy from Lake Albert, downstream of Lake Victoria and Lake Edward, indicates the arrival of Lake Victoria water between 14.5 and 14 ka (Williams et al., 2006). However, a major constraint remains the age-depth model for the Lake Albert sediment records, which relies on bulk ^{14}C samples and includes erosional discontinuities (Berke et al., 2014; Beuning et al., 1997a).

Further downstream, evidence of remarkably high floods, documented in abandoned channels and ^{14}C-dated former deposits of the White Nile in Sudan, supports a terminal Pleistocene age estimate (14–15 ka) for throughflow from Lakes Victoria and Albert (Adamson et al., 1980; Adamson et al., 1982; Williams et al., 2000). This estimate significantly precedes the timing proposed by Beuning et al. (2002)and Talbot and Lærdal (2000).

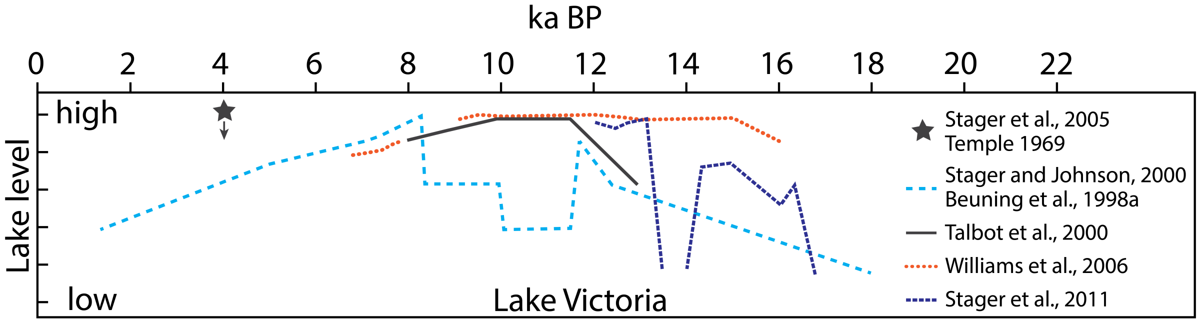

FIGURE 3.2: Summary of inferred lake-levels of Lake Victoria from literature.

Fossil beach deposits located above the modern level of Lake Victoria (Temple, 1963, 1964a, 1964b, 1967; Temple, 1969) suggest that the lake level was once higher, and Lake Victoria once occupied a much larger area. Although their process of formation remains unknown, the tilted strandlines found at significantly higher elevations are thought to have formed during past pluvial periods in the Victoria basin during the middle Pleistocene. However, the horizontal orientation of beach deposits at elevations of 18, 12, and 3 meters suggests that they were formed after the end of tectonic activity in the region (Kendall, 1969; Temple, 1969). The lowest 3-m strandline, dated to be ~4 ka (3720 ^{14}C years BP), marks a Holocene lake stage and the separation of the small Lake Nabugabo from Lake Victoria (Stager et al., 2005; Temple, 1969).

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Chapter 4

4. From Desiccation to wetlands and outflow: Rapid re-filling of Lake Victoria during the Latest Pleistocene 14 – 13 ka

in press in the *Journal of Great Lakes Research*

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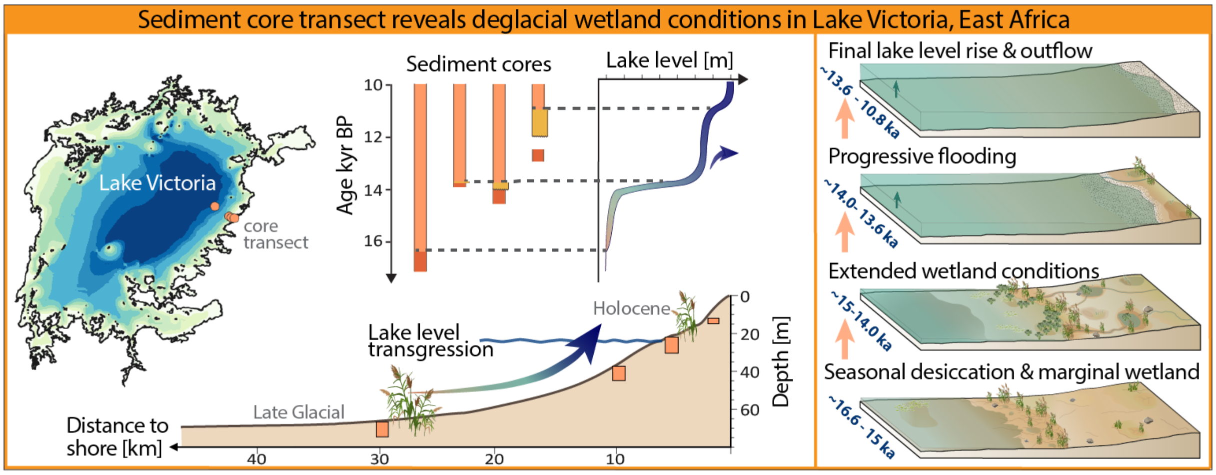
Abstract

Reconstructing hydrological variability is critical for understanding Lake Victoria's (LV) ecosystem history, the evolution of its diverse endemic fish community, the dynamics of vegetation in the catchment, and the dispersal of aquatic and terrestrial fauna in the East African Rift system during Latest Pleistocene and Holocene times. Whereas consensus exists on widespread desiccation of LV ~18 –– 17 ka, the re-filling history (16 – 13 ka) has remained highly controversial. Here, we present data from four new sediment cores along a depth transect. We use lithostratigraphic core correlation, sediment facies, XRF data, wetland vegetation analysis (*Typha* pollen), and ^{14}C chronologies of unprecedented precision to document Latest Pleistocene lake-level variability.

At our coring site in the central basin, local *Typha* wetlands existed >16.7 ka, alternating with periods of desiccation. Moisture increased slightly between ca. 16.7 – 14.5 ka and wetlands with permanent, shallow ponds established simultaneously in the center and the marginal, more elevated parts of the flat lake basin. After ca. 14.0 ka, lake levels increased; wetlands in the central basin were submerged and replaced by lacustrine environments and a >50 m deep lake established ca. 13.5 ka, likely with intermittent overflow most of the time. The lake reached modern or even above-modern levels around 10.8 ka. This lake-level history is consistent with regional terrestrial paleoenvironmental reconstructions, notably the expansion of afromontane and rainforest. Our data suggest a complex picture of paleoclimatic conditions in Eastern Africa and teleconnections to the North-Atlantic and Indian Ocean domains.

Keywords: Climate Change, Late Quaternary, Limnogeology, Paleolimnology, Lake sediments, Eastern Africa



Graphical abstract

4.1 Introduction

Latest Pleistocene refilling had profound impacts on the ecological processes of Lake Victoria (Johnson et al., 1996). The most prominent example is the richness of endemic haplochromine cichlid fish species, which started evolving very rapidly after the refilling of the lake began ~16 ka ago (Stager et al., 2002). This is the fastest vertebrate species radiation known on Earth (McGee et al., 2020; Seehausen, 2002). It has been argued that lake-level variability with desiccation and refilling was a critical environmental constraint and driver for the radiation of cichlid fish species in Lake Victoria (Johnson et al., 1996; Muschick et al., 2018; Seehausen, 2002). Moreover, there is growing evidence that Early Holocene hydroclimatic changes (African Humid Period (AHP)) and related hydrological connectivity played an important dual role as corridors or barriers for fish and mammal dispersal in Eastern Africa. Therefore, comprehensive information on the timing and rate of past lake-level fluctuations of Lake Victoria is imperative to better understand the relation between hydroclimatic change, lake development, and biotic responses in the lake and in the catchment including the cichlid fish adaptive radiation, other evolutionary processes, species dispersal, fire history, and vegetation dynamics (Dommain et al., 2022; McGee et al., 2020; Temoltzin-Loranca et al., 2023), among others.

Sediment-based reconstructions of lake-level fluctuations reveal direct evidence of lake responses to hydroclimatic variability. Earlier studies on sediment cores, predominantly from the northern and central parts of Lake Victoria (Johnson et al., 1996; Kendall, 1969; Stager, 1984; Stager & Johnson, 2008; Stager et al., 2011; Talbot & Livingstone, 1989) provided a complex but still ambiguous and controversial picture of the lake's refilling history after the Latest Pleistocene desiccation. The desiccation period is well established and diagnosed with dry, dense crumbly sediment interpreted as paleo-Vertisol found in the basal strata of sediment cores from the deepest part of the lake (Johnson et al., 1996). According to Stager and Johnson (2008), the lake may have had multiple low stands and "*began to re-fill* ca. *15,000 years ago [. . .] then fell again to virtually complete desiccation some time between 15,900 and 14,200 years ago*". Later, Stager et al. (2011) proposed a substantial lake transgression between 16.0 and 14.5 ka which is, however, not supported by regional $\delta D_{leafwax}$ hydroclimatic data (Berke et al., 2012; Tierney et al., 2008, 2011). Similarly, the short-term desiccation event around 15 ka (14.2 ka Stager et al., 2011) was not found in other sediment cores (e.g., V95-1P, V96-7P; Beuning et al., 2002; Johnson et al., 1996), and the timing of these putative events remained unclear.

Inconsistencies in the interpretation of the Latest Pleistocene lake-level history, particularly between 16 and 14 ka are possibly partly attributable to large distances between the different coring and study sites (Fig. 4.1), different water depths in several sectors of the large lake, disparities in lithologies of the sediment cores and substantial uncertainties in the ^{14}C chronologies (Beuning et al., 2002; Stager et al., 2011; Stager & Johnson, 2000; Talbot & Lærdal, 2000). Some of the published ^{14}C dated sediments were repeatedly reinterpreted and have changed over time along with updated sediment descriptions, different and newly applied the Latest Pleistocene lake-level history, particularly between 16 and 14 ka are possibly partly attributable to large distances between the different coring and study sites (Fig. 4.1), different water depths in several sectors of the large lake, disparities in lithologies of the sediment cores and substantial uncertainties in the ^{14}C chronologies (Beuning et al., 2002; Stager et al., 2011; Stager & Johnson, 2000; Talbot & Lærdal, 2000). Some of the published ^{14}C reservoir corrections and calibration models applied.

Here, we present data from a set of four new sediment cores along an offshore to nearshore transect on the eastern part of the lake (Fig. 4.1; Supplementary Material Table S4.1). The transect is designed to reveal accurate and detailed spatial-temporal documentation of Lake Victoria's Late Quaternary lake-level history and emergence of its modern lacustrine ecosystem. We review the major findings from previous studies in light of our novel chrono-lithostratigraphic approach. We build on sediment core chronologies with unprecedented precision and discuss the paleoclimate conditions that have impacted the Late Quaternary lake-level transgression in the Victoria Basin. Finally, we place our findings into context with the fire history and vegetation dynamics in the catchment of the lake and with East African paleoclimate records.

4.2 Material and methods

4.2.1 Study site and experimental description

Lake Victoria (0.5°N to 3.0°S, 68,800 km^2) is located in a depression between the two branches of the East African Rift (Fig. 4.1). Today, the lake is shallow with a maximum water depth of 68 m (Johnson et al., 1996). Bathymetric surveys reveal a bowl-shaped lake basin without major topographic features and with very gentle slopes (0.035°– 0.15°; Hamilton et al., 2022). The hydrological budget of the lake is positive and controlled by direct precipitation (1790 mm yr^{-1}; >80% of incoming water) and lake surface evaporation (1551 mm yr^{-1}; ~70 % of outgoing water, Yin & Nicholson, 1998)). River runoff from the small catchment area (drainage ratio ~2.67) is limited (runoff coefficient 9%; Crul et al., 1995)) and contributes 338 mm yr^{-1} to the lake's water balance (Yin & Nicholson, 1998). The northern outflow is the primary source of the White Nile River.

Precipitation occurs in two rainy seasons (March to May and October to December) as a

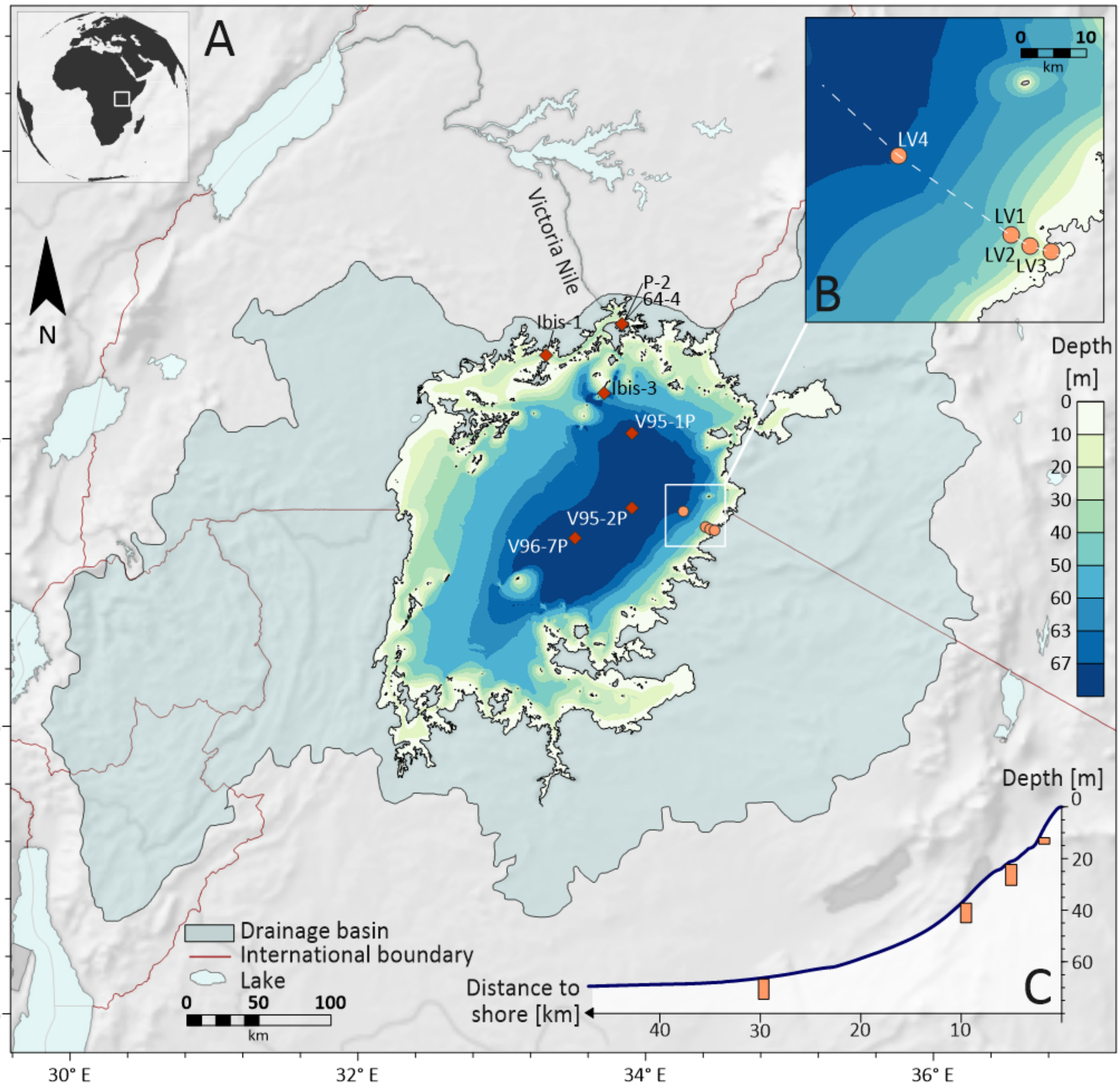


FIGURE 4.1: **(A)** Catchment and bathymetry of Lake Victoria with coring sites: V95-1P (Johnson et al., 1996); V95-2P (Johnson et al., 1996); V96-7P (Johnson et al., 1996); Ibis 3 (Stager et al., 1986); LVC18-S4, LVC18-S1, LVC18-S2 and LVC18-S3 (Temoltzin-Loranca et al., 2023, and this work); Ibis 1/Damba Channel (Stager et al., 1986); P2 and 64-4 (Kendall, 1969) **(B)** Inset map of the coring transect with LVC18-S1 (LV1), LVC18-S2 (LV2), LVC18-S3 (LV3), and LVC18-S4 (LV4); this work; (ESM Table S1). **(C)** Depth profile of the coring transect in distance to the shoreline. Bathymetric data are from Hamilton et al. (2022).

result of the changing position of mesoscale convection (Nicholson, 2018) and is, on long timescales, influenced by the seasonal migration of the Afrotropical rain belt, the position of the Congo Air Boundary and the strength of the Indian and Atlantic monsoons predominantly controlled by orbital, greenhouse gas and North Atlantic forcing (Beverly et al., 2020; Castañeda et al., 2016; Nicholson, 2018; Stager & Johnson, 2000; Verschuren et al., 2009).

In 2018, UWITEC piston cores were taken along a depth transect starting from the eastern shoreline (Fig. 4.1A-B; Table S4.1). Overall, multiple cores were collected at four different coring sites LVC18-S1 to LVC18-S4 (hereafter LV1 to LV4) with water depths ranging from 13.4 to 63 m below modern lake level (m.b.l.l. in October 2018; Fig. 4.1C). A continuous master composite core was established for each coring site. The stratigraphic correlation is based on tie points inferred from XRF data (Fig. S4.1).

4.2.2 Chronology, lithostratigraphy, and analytical methods

The chronologies for cores LV1, LV2, and LV4 were established based on ^{14}C dates from 85 sieved (50 μm mesh) and handpicked terrestrial plant-macrofossils and charcoal pieces (for details see Temoltzin-Loranca et al. (2023). The age model for LV3 is based on ^{14}C dates from 11 sieved (50 μm mesh) and handpicked charcoal pieces (this work: Fig. S4.2, and Tables S4.2 and S4.3). ^{14}C accelerator mass spectrometry (AMS) analysis was performed for all samples with the MICADAS system at the Laboratory for the Analysis of Radiocarbon (LARA) at the University of Bern (Szidat et al., 2014). Calibration was performed with IntCal20 (Reimer et al., 2020). Freeze-dried and homogenized sediment samples from a short gravity core nearby LVC18-S3 (LVC18-S3-SC2) were analyzed for ^{137}Cs and ^{226}Ra directly by gamma-ray spectrometry using a HPGe well-type detector (GCW 2021) at the Faculty of Oceanography and Geography, University of Gdansk, Poland. ^{210}Pb activities were measured indirectly by ^{210}Po using alpha spectrometry (Table S4.3). For details see Tylmann et al. (2016). Unsupported ^{210}Pb was calculated with the level-by-level method. Sediment ages were obtained using a Bayesian statistical approach with the software package rplum (Aquino-López et al., 2018) and with the Constant Flux-Constant Sedimentation (CF-CS) model.

Lithofacies description and interpretation of the sediment across the paleosol-wetland-lake continuum follows the model of Ashley et al. (2013) which was developed for the Loboi Swamp in Kenya. Following Richardson et al. (2022) we use the term ‘wetland’ for an environment inferred from >30 % emergent vegetation (here mainly *Typha* as identified by pollen analysis; Temoltzin-Loranca et al. (2023)) in a mosaic with shallow (<2–3 m) ponds of up to a few ha in size with lentic water. According to Temoltzin-Loranca et al. (2023) this environment was treeless. Pollen samples with >5 % *Typha* pollen are interpreted as representative of local stands of cattail (rational pollen percentage limit, Davis et al. (1991)).

Scanning X-ray fluorescence (XRF) for major elemental composition was carried out on core halves using both a Mo- and Cr-anode X-ray tube and an 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 over 5 mm intervals.

Total organic carbon (TOC) and nitrogen isotope compositions (δ^{15}N) were measured on homogenized and freeze-dried samples 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 N_2 (AIR) and VPDB (Vienna Pee Dee Belemnite) standards, respectively. Analytical reproducibility of the measurements is better than 0.2 ‰. Total sulphur was measured on 10 mg homogenized and freeze-dried samples using a CNS Vario El cube Elemental Analyser.

4.3 Results and discussion

4.3.1 Late Pleistocene lake-level variability

The lithostratigraphy at our deep-water site LV4 (63 m.b.l.l.) reveals (partial) exposure of the lake floor from at least ~20.2 ka (bottom of LV4), until prior to ~16.4 ka, as indicated by a 14 cm section of fine-grained, dry and dense mud below 763 cm sediment depth (Fig. 4.2 and Fig. S4.3). The low water content and high bulk density compared with the overlying sediment (Fig. 4.3) suggest episodically exposed environments (Ashley et al., 2013). At 16.6 ka (777–778 cm sediment depth), *Typha* pollen > 5 % indicate local stands of cattail and wetland environments with shallow ponds. Because of the low-energy aquatic depositional environment (sedimentation rates < 0.1 mm yr^{-1}; Temoltzin-Loranca et al., 2023), wetland sediments are often difficult to distinguish from lacustrine deposits (Ashley et al., 2013). Today, heliophilous *Typha* is growing in ponds and up to tens of meters away from the lake shoreline and at water depth up to 1 m (Grace & Wetzel, 1981). Since *Typha* pollen is unlikely to travel large distances we use it as an indicator for local wetland environments (Temoltzin-Loranca et al., 2023). Basal sediments at LV4 dated between ~20.2 and 16.6–16.4 ka (Fig. 4.4 and Fig. S4.3), lack features of soil formation (paleo-Vertisol), in contrast to what has been observed at other sites in the central basin at this time (Fig. 4.4; Johnson et al., 1996; Talbot & Lærdal, 2000). Instead, our data suggest that wetlands persisted locally at least from ~16.6 ka onwards, similar to wetlands found adjacent to modern savannas in parts of the surrounding landscapes. However, the lack of pollen in several of the basal samples (e.g., between 763 and 776 cm) is interpreted as indicating century-scale drier intervals with lower water tables and oxidation of organic matter, supporting the general view of episodic subaerial exposure of the site. Given the very flat topography of the lake basin, the presence of wetlands with small ponds at LV4 does not refute the existence of a paleo-Vertisol elsewhere in the central basin of the lake at the same time (Fig. 4.5A).

An initial, weak, and limited increase in moisture is inferred to have occurred between 16.4 and 15.0 ka. The continuing presence of abundant *Typha* pollen (>5 %) and sponge spicules at the offshore site (LV4, 63 m.b.l.l.) and the near shore site (LV2, 22.6 m.b.l.l.; >15 % *Typha* pollen; Fig. 4.2) suggest extended and persistent wetland conditions at both sites. Increasing Rb/K values, interpreted as indicating erosional input from the catchment, and chemical weathering of lithogenic material (Burnett et al., 2011; Davies et al., 2015) remained at low levels (Fig. 4.3). This suggests that transport of poorly weathered lithogenic material from the catchment was limited under generally dry conditions. The relatively high δ^{15}N values observed in this part of the core are typical for soil organic matter N sources from a grassland-dominated catchment

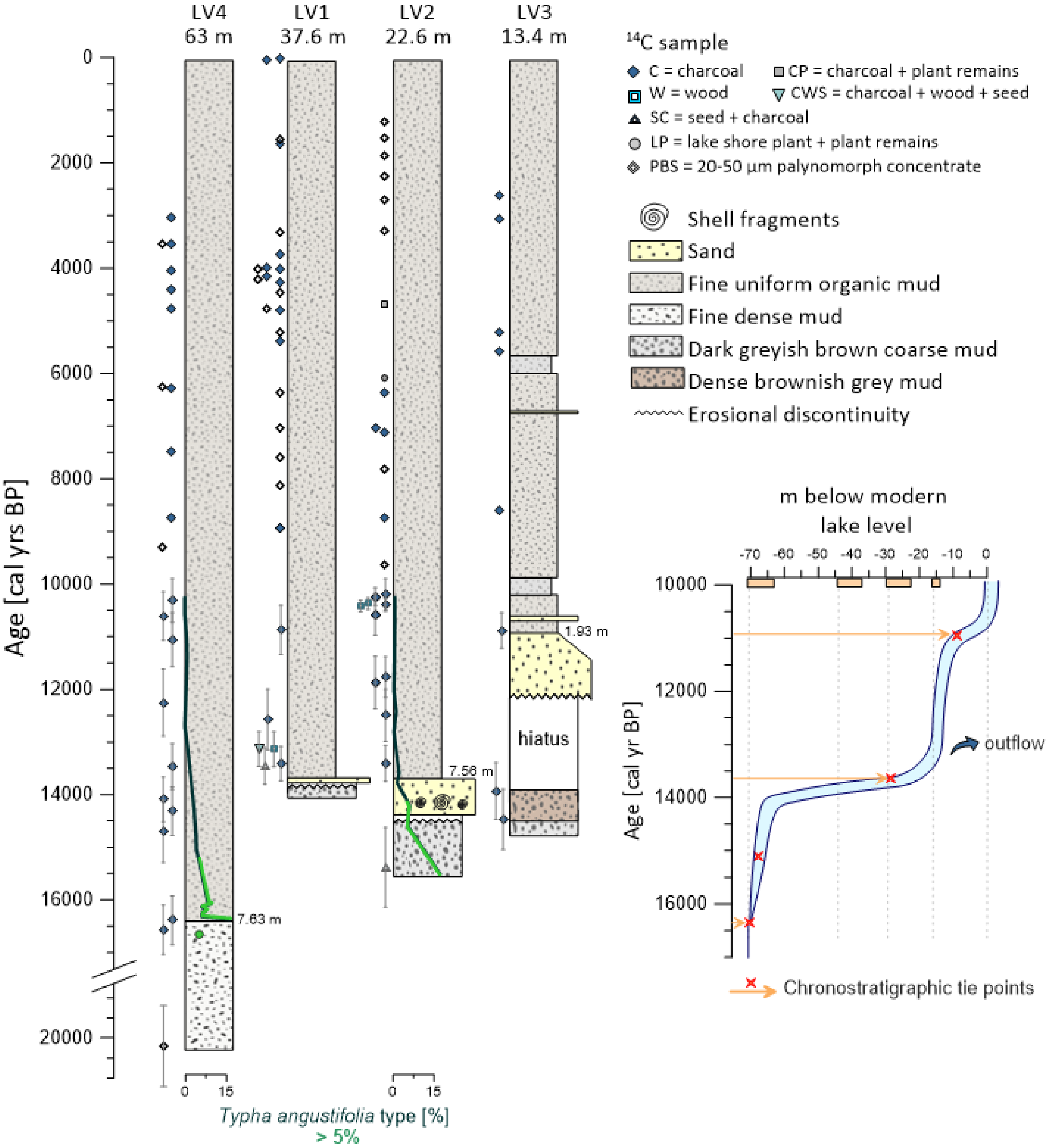


FIGURE 4.2: Chronology and lithostratigraphy of cores LV4, LV1, LV2 and LV3 along the transect and inferred lake-level changes 20.2–10 ka. Typha angustifolia type pollen (>5 % light green) suggest local stands of cattail and wetland environments (Temoltzin-Loranca et al., 2023). The widths of the stratigraphic column indicate grain size differences. Diamonds indicate ^{14}C Bacon model ages (95 % C.I. only for dates within the discussed period > 10 ka) (Temoltzin-Loranca et al., 2023, data for LV3 in ESM Fig. S4.2 and Table S4.2). The inset shows the lake-level reconstruction including stratigraphic tie points (main text) with an uncertainty envelope (±5 m) and the lake overflow event (blue arrow). The four bares along the x-axis indicate the cores. See Fig. S4.3 for detailed geochemical/physical properties.

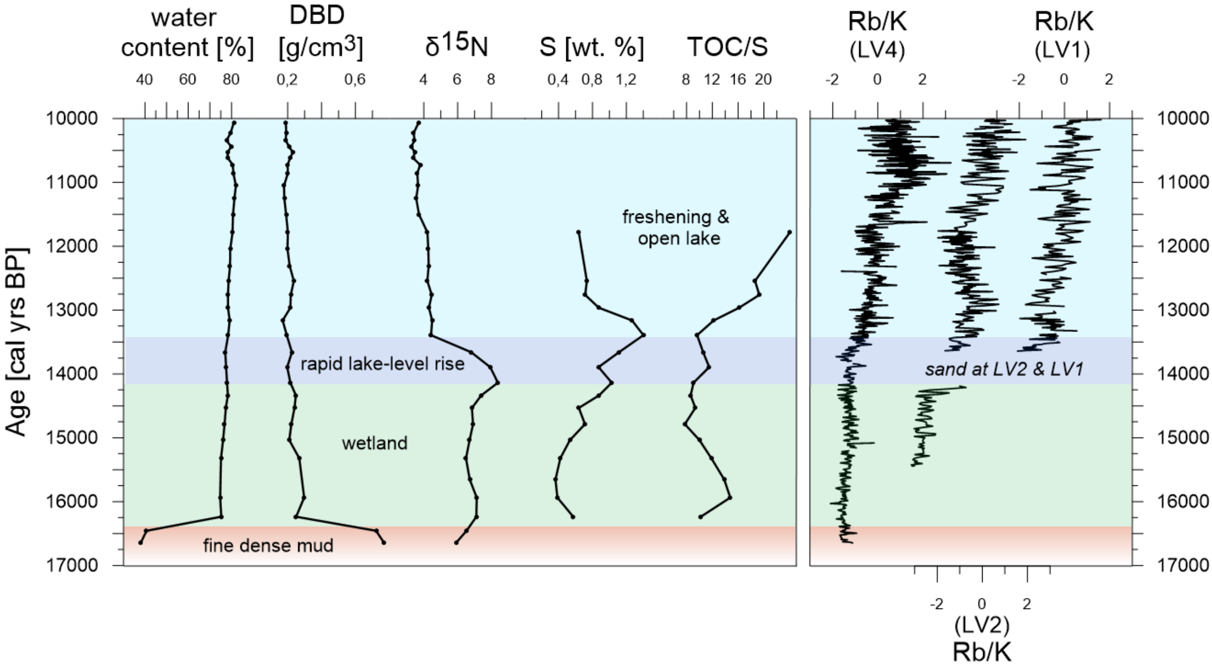


FIGURE 4.3: Water content, dry bulk density (DBD), δ^{15}N, total S and TOC/S ratios from core LV4 indicating the dry conditions prior to 16.4 ka (brown), the wetland period (green), the rapid lake-level rise 14.2–13.6 ka (dark blue) and the freshening and open system of Lake Victoria after 13.5 ka (light blue). The Rb/K ratio is standardized for better comparison between the coring sites (LV4, 1, and 2). Higher Rb/K values indicate erosion and input of poorly weathered lithogenic material from the catchment with increased humidity. The Zr/Ti ratio depicts a very similar trend as Rb/K (not shown).

under still relatively dry conditions and N starvation, or caused by local N limitation in the wetlands (Temoltzin-Loranca et al., 2023; Williams et al., 2006). Our data do not support a major lake transgression for this period as proposed by Stager et al. (2011). Instead, the synchronous presence of permanent wetlands across a large horizontal and vertical gradient in the lake basin (from sites at 63 to 22.6 m.b.l.l.) suggests that shallow water bodies, possibly sustained by near-surface groundwater tables and/or local surface runoff, persisted simultaneously in large parts of the basin with its nearly flat topography. Local geomorphic processes, such as by animal activity, and/or erosion, may have played a role in promoting the formation of wetlands (Tooth & McCarthy, 2007). Nevertheless, steadily decreasing *Typha* pollen at the deep-water site LV4 suggests gently increasing water tables from 16 ka onwards and a growing distance from the local *Typha* stands at the lake shores. Given the nearly flat topography of the lake basin, only a very subtle rise in lake level would create a substantial increase in distance between the *Typha* stands and the core site. A permanent and widespread shallow lake close to the elevation of LV4 would correspond to a very shallow <5 m-deep lake covering roughly < 25 % of the modern surface with an extensive zone of fringing wetlands (Fig. 4.5A). It is conceivable that perennial wetlands with ponds occupied large parts of the basin.

Evidence for a second desiccation event 15.9 – 14.2 ka (Stager & Johnson, 2008; Stager et al., 2011, Fig. 4.4) is absent in LV4. Instead, our record reveals continuous sedimentation of fine sediment with lower bulk density and higher organic matter content 15 – 14 ka (Fig. 4.3

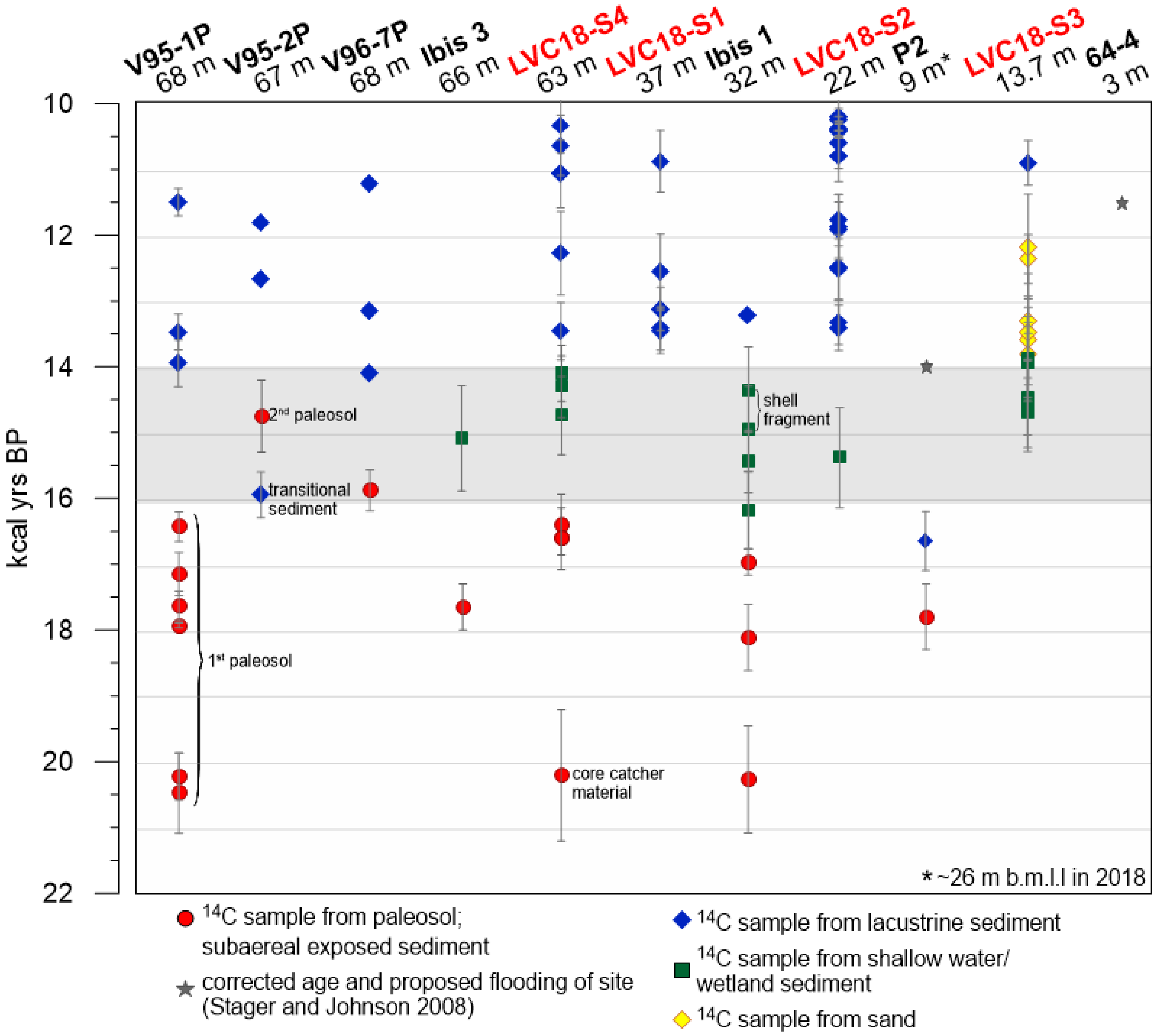


FIGURE 4.4: Compilation of calibrated radiocarbon ages (with uncertainty ranges where available in the literature) and corresponding environmental interpretations from Lake Victoria sediment records sorted by water depth at the coring site: V95-1P (Johnson et al., 1996; Lane et al., 2018); V95-2P (Johnson et al., 1996; Stager et al., 2002; Talbot & Lærdal, 2000, the basal calibrated radiocarbon ages differ between published chronologies)); V96-7P (Beuning et al., 2002; Stager et al., 2002); Ibis 3 (Stager et al., 2002; Talbot & Livingstone, 1989); LVC18-S1-4 (Temoltzin-Loranca et al., 2023, this work marked); Ibis 1/Damba Channel (Stager & Johnson, 2008; Stager et al., 2011); P2 and 64-4 (Kendall, 1969; Stager & Johnson, 2008). Note that coastal cores P2 and 64-4 have much higher sedimentation rates and the lacustrine sediments have a lower topographic position (26 m.b.l.l.). Red circles indicate dated sediments interpreted mostly as subaerial exposed deposits or paleo-Vertisols, possibly with local episodic wetlands, suggesting a consistent picture of very dry conditions prior to 17 ka and ending by 16 ka at latest. Green squares represent sediment interpreted as shallow water and wetland conditions. Diagnostic features include Typha pollen (>5%, Temoltzin-Loranca et al., 2023), low hydrogen index values (Ibis 1 and 3; Talbot & Livingstone, 1989) or abundant brackish water diatoms (Ibis 1; Stager et al., 2011). Blue diamonds indicate sediments deposited in deeper lacustrine conditions and flooding at the coring sites. Yellow diamonds mark ^{14}C dates in littoral sand deposits with significant reworking and age inversions. The grey shading marks the discussed period of heterogenic sediment features and diverging interpretations.

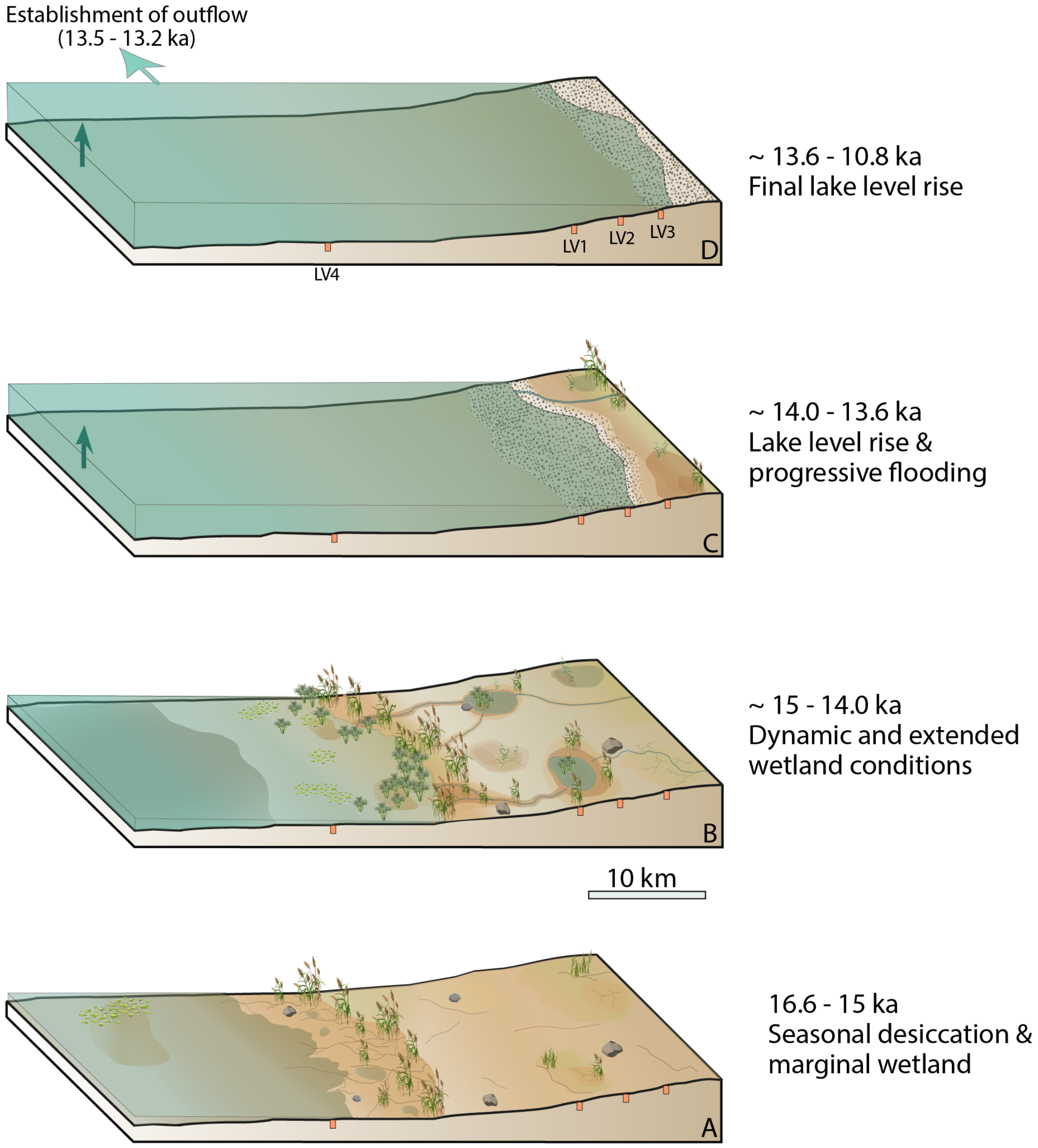


FIGURE 4.5: Lake transgression and wetland formation in the Lake Victoria basin across the transect LV1-4 from 16.6 to 10 ka with coring sites (orange bars).

and Fig. S4.3). Rb/K (at site LV4 and LV2) and δ^{15}N remain at constantly low and high levels, respectively, suggesting that a drastic change in the environment was unlikely during this period. Also, sedimentation rates remained unchanged (5 mm yr^{-1}, Temoltzin-Loranca et al., 2023) suggesting uninterrupted wetland or very shallow lake conditions at that site (Fig. 4.5B) with nearby or local *Typha* stands (around 5 % *Typha* pollen). During this same time period, local *Typha* stands persisted concurrently at high elevation in the lake basin (LV2, 22 m.b.l.l.), where dark greyish, coarse mud formed at that time (Fig. 4.2 and S4.3).

Between 14.0 and 13.6 ka, we observe a phase of very rapid uninterrupted lake-level rise. At site LV2 (22.6 m.b.l.l.), local stands of *Typha* disappeared, and wetland deposits were replaced by lacustrine littoral deposits (sand with mollusk fragments) prior to 13.6 ka. Continuous lacustrine environmental conditions were established at LV2 site (22.6 m.b.l.l.) by ~13.6 ka (Fig. 4.2). At the near-shore site (LV3, 13.4 m.b.l.l.) dense, brownish-grey mud was deposited but partly reworked and eroded possibly due to littoral wave action (hiatus in LV3, Fig. 4.2). The simultaneous replacement of littoral deposits with pelagic deposits at LV1 (37.6 m.b.l.l.) and LV2 around 13.8 – 13.6 ka is chronologically well constrained and suggests a very rapid lake transgression, over a timespan of a few hundreds of years. A 40–50 m deep lake was established by ~13.6 ka (Fig. 4.5C), an inference which is also supported by observations from the coastal cores Ibis-1 and P2 in the northern part of Lake Victoria (Dommain et al., 2022; Stager, 1984; Stager et al., 2002; Talbot & Livingstone, 1989). In the central part of the lake (LV4), Rb/K gradually increased, which is interpreted as indicating enhanced erosional input from the catchment and stronger K leaching from soils under more humid climatic conditions. δ^{15}N values decreased sharply during the lake-level rise at both LV4 and V95-P2 (Talbot et al., 2006), suggesting the rapid lake transgression between 14.0 and 13.6 ka (Fig. 4.5C) was a basin-wide phenomenon. Low δ^{15}N may result from greater N input from the catchment, as has been suggested in Lake Albert (Talbot et al., 2006), and/or increased atmospheric N fixation from cyanobacteria and reduced denitrification in an open basin, as has been suggested for Lake Titicaca (Ballantyne et al., 2011).

Shortly thereafter (13.5–13.2 ka), the lake level reached topographic outflow as suggested by a step change in the S and TOC/S profiles, and a stabilization of δ^{15}N at consistently lower values in LV4 (Fig. 4.3), very similar in the structure and timing (within the chronological uncertainty) as found in V95-2P (Talbot et al., 2006) Rb/K values further increased at both sites LV4 and LV2 (Fig. 4.3). TOC/S ratios, often used as a salinity indicator (Cohen, 2003) increase sharply and indicate freshening due to lake overflow 13.4 ka (Fig. 4.3). Likewise, the decreasing trend of δ^{15}N and the subsequent stabilization at lower values could reflect a combination of (i) a source shift away from the terrestrial soil-derived N towards more aquatic N sources, and/or (ii) a decrease in denitrification rates as the system becomes more hydrologically open (Ballantyne et al., 2011). The lake overflow and freshening at that time is temporally consistent with Sr isotope data from the White Nile domain (Talbot & Lærdal, 2000) and $\delta^{18}O_{cellulose}$ data from core V96-7P (Beuning et al., 2002).

Thereafter, Rb/K and δ^{15}N values in the central part of the lake (LV4) remained constantly high and low, respectively, suggesting sustained erosional influx of lithogenic material and nutrients in a wetter climate and hydrological boundary conditions that support a permanent large lake with an outflow during most of the time. We do not find evidence in the δ^{15}N or TOC/S data for longer periods of closed-basin conditions and prolonged periods with increased aridity, for instance during the Younger Dryas (YD, ca. 12.8 – 11.7 ka). Water levels quickly reached the near-shore site LV3 (13.4 m.b.l.l; Fig. 4.2, Fig. 4.5D). However, sedimentation is discontinuous at that site and the large scatter of ^{14}C dates in the 20 cm sand deposit (Fig. 4.2, Fig. S4.2 and S4.3) suggests sediment reworking under wave action and fluctuating lake levels at high stages. Following this dynamic phase, continuous lacustrine deposition started at the shallow water site LV3 10.8 ka (Fig. 4.2, Fig. 4.5D), marking yet another lake-level increase to modern or even above modern levels (Stager & Johnson, 2008; Stager & Mayewski, 1997). Rb/K values (at LV4) reach maximum levels ca. 11 ka, possibly suggesting maximum humidity (African Humid Period), although a decrease thereafter could have results from landscape stabilization under rainforest expansion (Temoltzin-Loranca et al., 2023, Fig. 4.6).

4.3.2 Latest Pleistocene environmental and regional climatic change

Lake Victoria's refilling history is consistent with dry conditions in the Latest Pleistocene prior to ~15 ka and the transition to much wetter conditions at the onset of the African Humid Period, starting between 15 and 13 ka, is widely observed in equatorial Eastern African paleoclimate records (Fig. 4.6; Castañeda et al., 2016; Gasse, 2000; Junginger & Trauth, 2013; Loakes et al., 2018; Otto-Bliesner et al., 2014; Shanahan et al., 2015; Wolff et al., 2011).

Closed-lake basins, such as Lake Victoria prior to 13.6 ka, are excellent recorders for past hydroclimatic changes, because they respond very sensitively to changes in P-E and adjust lake levels immediately to even subtle climatic changes. Today, the water budget of the lake is mainly controlled by direct precipitation and evaporation (Yin & Nicholson, 1998). A climate-water-budget model for Lake Victoria (Beverly et al., 2020) suggests that, depending on paleoclimate scenarios including temperature, precipitation, and orbital forcing, Lake Victoria can completely dry out and re-fill to modern levels within centuries to a few millennia. Importantly, in the flat lake basin, small changes in water depth translate into large changes in lake surface area (Olaka et al., 2010). This has three important implications which that act as positive feedbacks to the lake's water balance: (i) changes in the fraction of lake surface versus land strongly influence the water balance of the lake (runoff coefficient today 9 %, Crul et al., 1995), (ii) a large lake has higher cloudiness which reduces evaporation (Yin & Nicholson, 1998) and, (iii) the size of the lake controls precipitation in the catchment; today ca. 80 % of the inflow in Lake Victoria is recycled moisture from the large lake itself (Beverly et al., 2020; Yin & Nicholson, 2002). Accordingly, Lake Victoria would dry out within centuries if precipitation rates fell below 75 % of modern values (Beverly et al., 2020). Conversely, and depending on the temperatures, the Latest Pleistocene dry lake basin would fill up to modern levels within a few centuries if precipitation rates are close to modern and runoff is generated in the catchment (Beverly et al., 2020), implying that there is only a narrow hydroclimatic range that keeps the lake between desiccation and overflow. This paleoclimatic scenario and hydrological response of Lake Victoria (Beverly et al., 2020) could well explain the rapid lake-level increase inferred

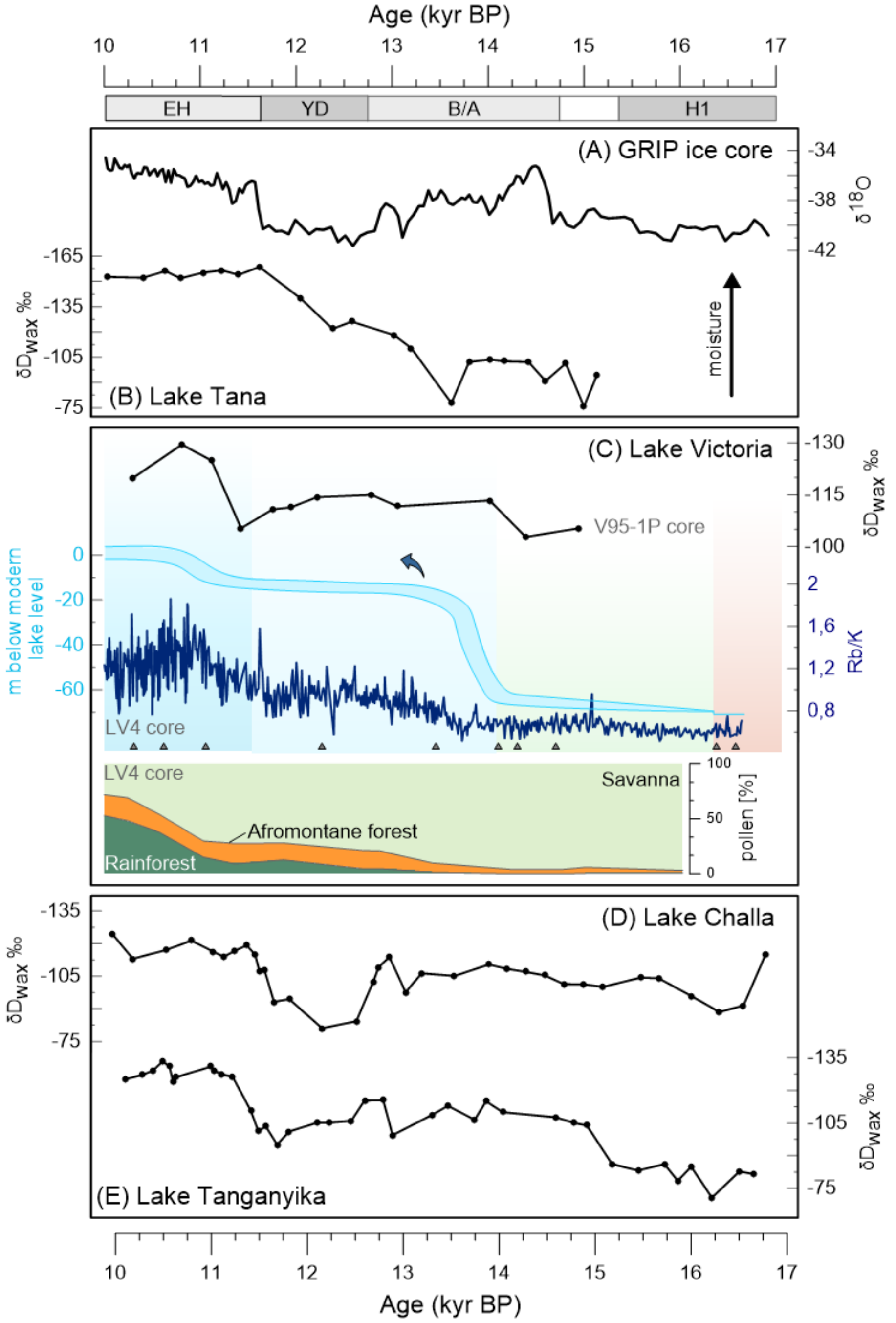


FIGURE 4.6: The Lake Victoria record (this study) in the context of regional and global paleoclimate records 17–10 ka including the Oldest Dryas/H1 Event, the Bølling–Allerød B/A, the Younger Dryas YD, and the Early Holocene EH. $\delta D_{leafwax}$ indicates hydroclimate variability (amount and source effects). **A)** δ^{18}O from NGRIP (Grootes et al., 1993), **B)** $\delta D_{leafwax}$ of Lake Tana (Costa et al., 2014),**C)** Lake levels from Lake Victoria and Rb/K of LVC18-S4 (this study); catchment vegetation (Temoltzin-Loranca et al., 2023); $\delta D_{leafwax}$ of Lake Victoria (Berke et al., 2012), The colored background highlights the periods of seasonal desiccation, extended wetland conditions and high lake levels in Lake Victoria, the blue arrow indicates the outflow event (Beuning et al., 2002; Talbot & Lærdal, 2000). Grey triangles indicate ^{14}C ages for LV4 (Temoltzin-Loranca et al. (2023)). **D)** $\delta D_{leafwax}$ of Lake Challa (Tierney et al., 2011), **E)** $\delta D_{leafwax}$ of Lake Tanganyika (Tierney et al., 2008)

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from our data between 14 and 13.5 ka.

Hydroclimate also directly influences terrestrial vegetation and fire regimes in the catchment of Lake Victoria (Karp et al., 2023; Temoltzin-Loranca et al., 2023). Therefore, information on past vegetation dynamics and fire regimes serves as an independent validation of the lake level reconstruction's implications for paleoprecipitation. Pollen analysis on LV4 (Temoltzin-Loranca et al. (2023)) shows that, prior to 13.5 ka, the area was dominated by savanna grasslands with only very small traces of mesophilous Afromontane vegetation (e.g., *Olea, Podocarpus*). Flammable biomass and fire activity was persistently low but increased slightly between 15 and 14 ka (Temoltzin-Loranca et al. (2023)). This corresponds well with generally dry conditions and only weakly increased moisture after 15 ka as inferred from the lake level reconstruction (Fig. 4.4, Fig. 4.5, Fig. 4.6). The rapid lake-level rise after 14 ka is largely synchronous with a substantial increase in Afromontane vegetation after 13.5 ka; local stands of *Olea* and *Podocarpus* established after 13.5 ka (Temoltzin-Loranca et al. (2023)). Rainforest expands continuously after 10.7 ka, synchronously with the shift in $\delta D_{leafwax}$ (Fig. 4.6, Berke et al. (2012)) and the final lake-level rise to modern or above modern levels. Rb/K values reach their maximum and decrease with the expansion of the rainforest after 11 ka.

The temporal link between Lake Victoria's low lake levels and Heinrich Event H1 at ~16 ka and shifts in the monsoon and Congo Air Boundary is well described and emphasizes the orbital and greenhouse gas forcings as well as teleconnections with North Atlantic meltwater/SST and Indian Ocean forcings (Castañeda et al., 2016; Otto-Bliesner et al., 2014; Stager et al., 2002). Similar observations have been made for other lakes in the East African Rift (Junginger & Trauth, 2013; Loakes et al., 2018, among others). Relative aridity has been documented in multiple records from tropical Africa and the Nile Basin between 18 and 16 ka, followed by an increase in humidity until 14–13 ka and a marked drying during the Younger Dryas (YD) ~12 ka (Fig. 4.6; Berke et al., 2012; Castañeda et al., 2016; Loakes et al., 2018). Our findings are consistent with this picture, although the moisture increase in Lake Victoria after 16 ka was rather weakly expressed and delayed compared with lipid-biomarker records from Lake Tanganyika (Fig. 4.6) and the northern Nile Basin (Castañeda et al., 2016). But the timing in Lake Victoria goes along with most records in tropical West and Eastern Africa 0-5°N that do not show the significant and abrupt hydroclimatic change before 14 ka (Loakes et al., 2018; Shanahan et al., 2015). Aside of chronological disparities, it is most conceivable that, depending on (i) the paleoclimatic proxy used and (ii) the type of site-specific (eco)-hydrological linkage between water in precipitation and plants (Bodé et al., 2020), the timing of the reconstructed hydroclimatic change differs from site to site. Additionally, orographic effects might determine regional, and site-specific atmospheric hydroclimate conditions. Given the flat topography of the Lake Victoria lake basin, the role of runoff from the catchment, positive cloud-evaporation feedbacks and the overflow at the level of the sill, the lake level variability of Lake Victoria was mostly driven by non-linear processes and thresholds (of surface runoff and/or overflow). As a consequence, the response would be expected to be somewhat different from other sites in tropical Eastern Africa. This may also explain why, compared with other records from lakes Challa and Albert and model simulations (Fig. 4.6; Otto-Bliesner et al., 2014; Tierney et al., 2011), the Younger

Dryas (YD) drying is poorly expressed in our records, possibly with the exception of the sediment hiatus and sand layer in LV3 (Fig. 4.2) and a plateau or even a local minimum in the general Rb/K increase in LV2 and LV4 between 13 and 12 ka (Fig. 4.3). The YD drying was apparently not long and/or strong enough to convert the open lake system into a closed lake system, which would be clearly detectable in our proxies from the more profundal sites.

In general, the two periods of rapid lake-level rise in Lake Victoria (14.0-–13.5 ka and 11 ka) align with major northern hemisphere warming events: the onset of the Bølling–Allerød (here mostly the Allerød) and the onset of the Holocene. Both events are associated with abrupt intensification of the East African monsoon system (Overpeck et al., 1996; Shanahan et al., 2015). Paleoclimate model simulations suggest that these abrupt increases in precipitation in tropical and subtropical Africa are attributable to a combination of orbital and greenhouse gas forcings, North Atlantic meltwater forcings and western Indian Ocean sea surface temperatures (Otto-Bliesner et al., 2014), possibly enhanced by land surface – climate feedbacks (Shanahan et al., 2015).

However, when examined in detail, Latest Pleistocene hydroclimatic variability in Eastern Africa between 14 and 13 ka seems to show a spatially and temporally heterogeneous pattern that is still not fully understood (Berke et al., 2014; Loakes et al., 2018). This seems particularly to be the case for $\delta D_{leafwax}$ proxies which are not only related to the 'amount effect' (effective moisture) but also to the 'source effect' (Costa et al., 2014, Atlantic versus Indian Ocean moisture sources). Accordingly, shifts in $\delta D_{leafwax}$ may also be modulated by topographic features and/or displacements of the Congo Air Boundary which further complicates a convergence of different single-site interpretations into a consistent paleoclimatic picture (Fig. 4.6; Berke et al., 2014; Castañeda et al., 2016; Costa et al., 2014; Junginger & Trauth, 2013; Loakes et al., 2018).

4.4 Conclusions

We conclude from our data that Lake Victoria experienced widespread desiccation with localized seasonal wetlands between ~20.2 and 16.7 ka. A first moisture increase 16.7-–15.0 ka established permanent wetlands with very shallow ponds in the center of the Lake Victoria basin surrounded by a savanna landscape with predominance of grasses. Subsequently, moisture levels further increased; a shallow permanent lake was formed and wetlands extended across most of the lake basin around 14.5 ka. A final lake-level increase occurred between ~14.0 ka until 13.5 ka, when the lake reached outflow levels with concurrent expansion of Afromontane and rainforest vegetation. The beginning of the Holocene (after 11.5 ka) is marked by a second significant increase to modern, or even above-modern lake levels and a landscape dominated by rainforest vegetation. This revised history of the Lake Victoria drainage basin hydroclimate variability may serve, among others, as a basis to further test ecosystem responses to hydroclimate change. It can also help to assess to which extent the desiccation and refilling history and subsequent lake-level changes, as well as emerging hydrological connectivity of river systems in Eastern Africa were constraining and driving pacemakers for the evolution of the lake's endemic species richness and the species dispersal and range dynamics of terrestrial species.

Declaration of contribution: Author contributions to the article are as follows: GW, MG, and HV conceptualized the study for this manuscript. OS, MG and BM led the design of the project. GW, YTL, WoT, SB, and MJ collected the data. MK coordinated the necessary permits. MK, SM, and MM coordinated the fieldwork for core collection. GW, HV, and MG led the interpretation of data and wrote the manuscript. All co-authors contributed to the data interpretation, commented on drafts, and gave final approval to the manuscript.

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.

4.5 Acknowledgments

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4.7 Supplementary Material

Sediment cores and ^{14}C chronologies from Lake Victoria

The information about the coring sites for the piston cores LVC18-S1 to LVC18-S4 and the short gravity core LVC18-S3-SC2 (^{210}Pb dating; this study) is shown in Table S4.1.

TABLE S4.1: Sediment cores from Lake Victoria 2018

Core ID	Location		Water depth	Core length	Chronology
	Lat (°S)	Long (°E)	(m b.m.l.l.)*	(m)	
LVC18-S4 (LV4)	1.049433°	33.796133°	63	7.78	Temoltzin-Loranca et al. (2023)
LVC18-S1 (LV1)	1.115230°	33.9191°	37	7.22	Temoltzin-Loranca et al. (2023)
LVC18-S2 (LV2)	1.130833°	33.946333°	22.6	8.01	Temoltzin-Loranca et al. (2023)
LVC18-S3 (LV3)	1.139067°	33.97655°	13.4	2.51	This work
LVC18-S3-SC2	1.13910°	33.97655°	10	0.40	This work

Fresh sediment of LVC18-S3 was sieved (50 μm mesh) continuously at 2 cm intervals; charcoal fragments (> 50 μm) were handpicked and immediately frozen following the procedure of Temoltzin-Loranca et al. (2023). A total of 26 samples (23 of charcoal, 3 bulk sediment) were selected for ^{14}C dating (Table S4.2). The dates on bulk sediments are parallel dates to charcoal dates; they were taken for a different purpose (assessing ^{14}C reservoir effects in LV) and are excluded from the chronology (Fig. S4.2). Samples with small mass (< 300 μgC) were measured with the direct gas measurement, larger samples were measured from graphite targets. ^{14}C AMS analysis was performed for all samples with the MICADAS system at the Laboratory for the Analysis of Radiocarbon (LARA) at the University of Bern (Szidat et al., 2014). Calibration was performed with IntCal20 (Reimer et al., 2020). Freeze-dried and homogenized sediment from a short gravity core nearby LVC18-S3 (LVC18-S3-SC2) were analyzed for ^{137}Cs and ^{226}Ra directly by gamma-ray spectrometry using a HPGe well-type detector (GCW 2021) at the Faculty of Oceanography and Geography, University of Gdansk, Poland. ^{210}Pb activities were measured indirectly by ^{210}Po using alpha spectrometry (Table S4.3). For details see Tylmann et al. (2016). Unsupported ^{210}Pb was calculated with the level-by-level method. Sediment ages were obtained using a Bayesian statistical approach with the software package rplum (Aquino-López et al., 2018) and with the Constant Flux-Constant Sedimentation (CF-CS) model corrected for the missing inventory (Tylmann et al., 2016). The ^{137}Cs activity profile data was inconclusive and was not used in the final age model The ^{210}Pb chronology of the short core suggests that the surface sediment at the coring site LVC18-S3 is recent and that, today, sediment erosion, reworking and focusing are all insignificant.

The final age-depth model for LVC18-S3 (Fig. S4.1) was established by combining the ^{210}Pb and 10 ^{14}C dates, using the rBacon software (version 2.5.8) (Blaauw & Christen, 2011), with the rplum ^{210}Pb ages constraining the top of the core. Radiocarbon ages from the sand layer are reworked and were not included in the final model. In order to build the age-depth model, the core LVC18-S3 was split into three intervals based on lithology using the boundary function in rbacon.

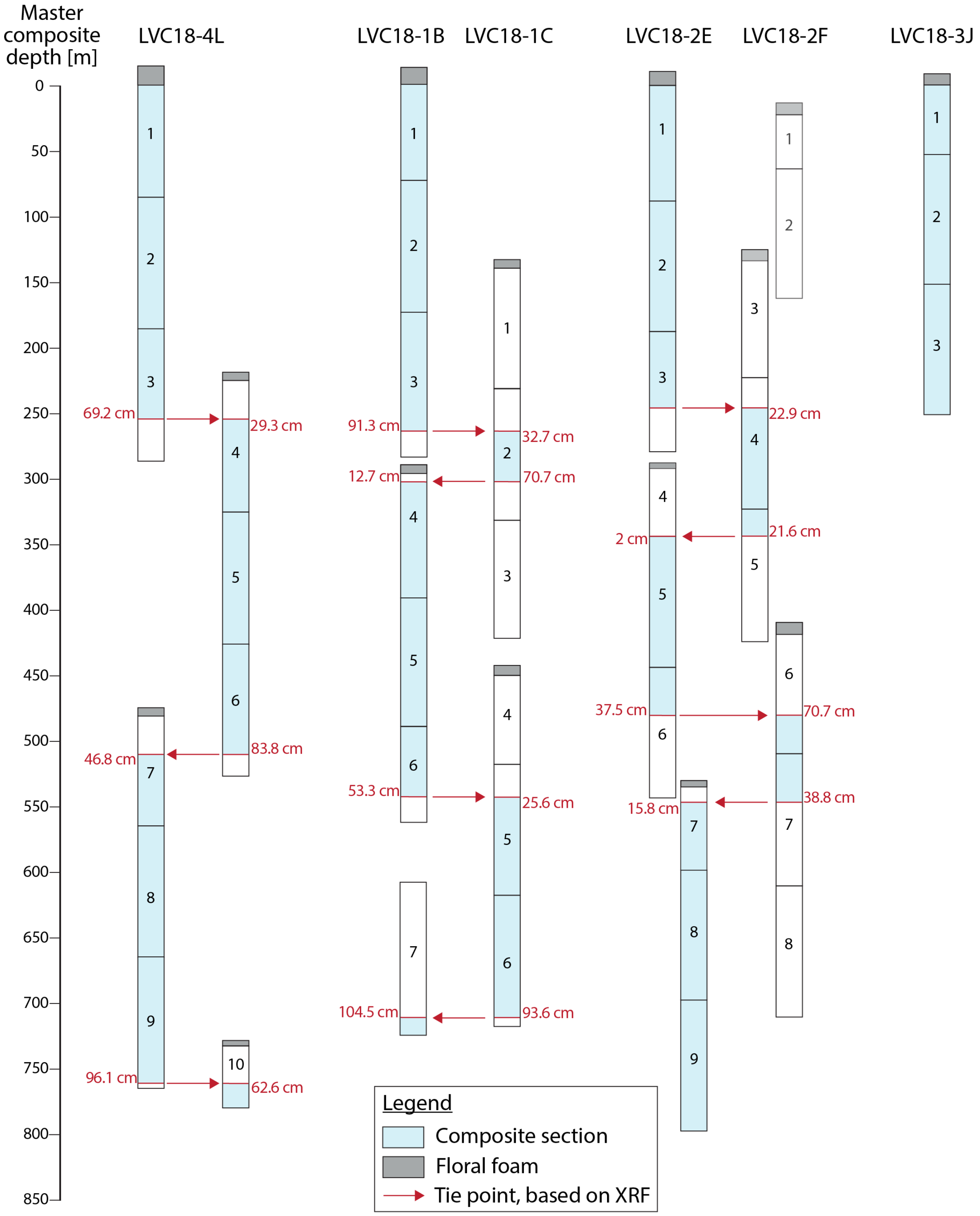

FIGURE S4.1: Core segments and master composite cores for the coring sites LV1 – LV4. The stratigraphic correlation is based on tie points inferred from XRF data.

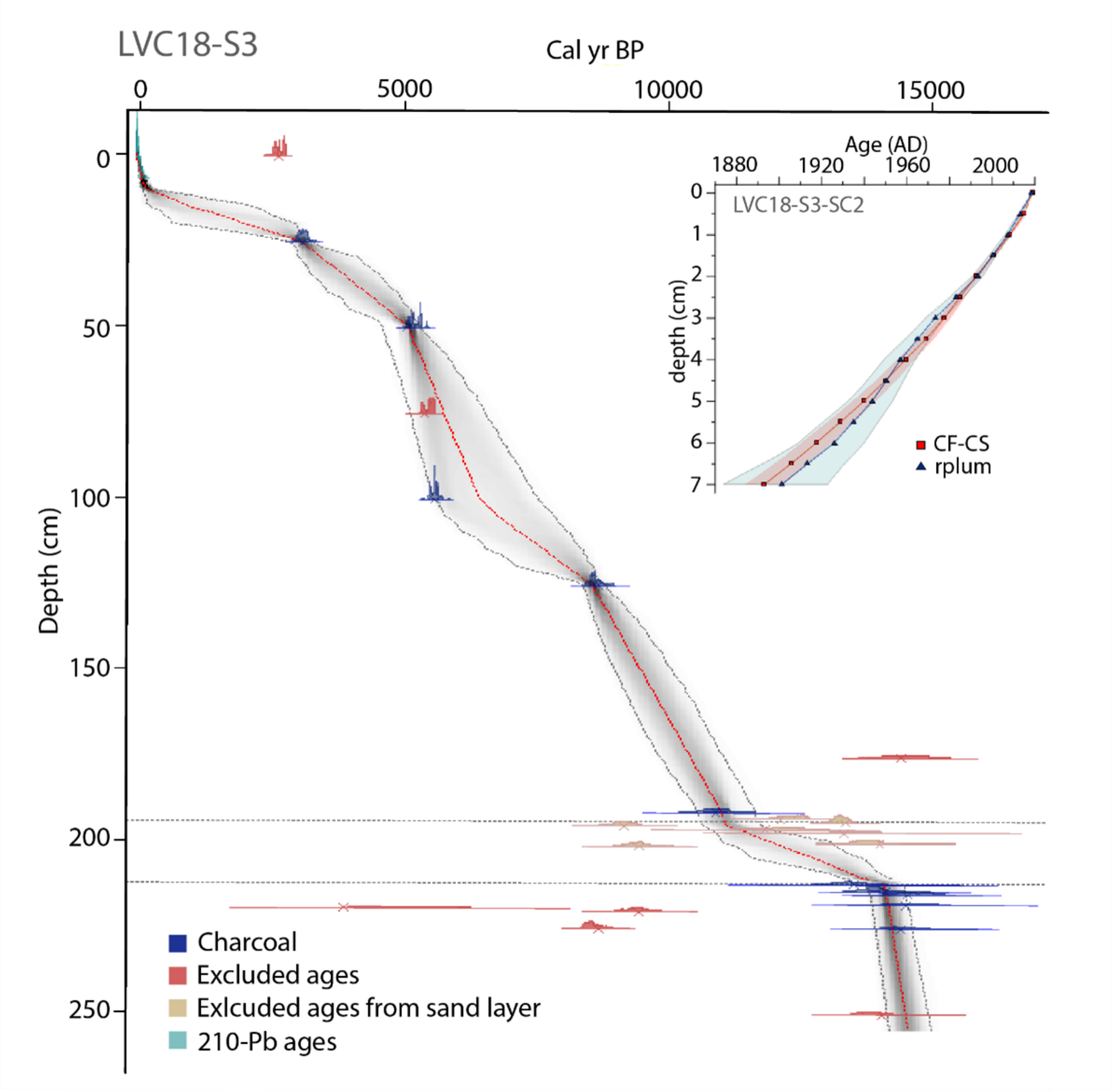

FIGURE S4.2: Age-depth model of core LVC18-S3 including radiocarbon and ^{210}Pb rplum dates (Aquino-López et al., 2018) with the weighted mean (red dashed line) and 95% confidence interval (grey stippled line). The ^{210}Pb chronologies (CF-CS and rplum) of the surface core LVC18-S3-SC2 are shown in the inset.

Table S4.2: AMS ^{14}C ages and calibrated ^{14}C ages of the sediment core LVC18-S3.

Laboratory Code	Core and Sample ID	Sediment depth (cm)	Material*	Carbon mass μgC	Measurement	^{14}C yr BP (cal yr BP)	Error ages ($\pm 1\sigma$)	Median	95 % C.I.	Lithology	Included in model (Yes/No)
BE-17652.1.1	LVC3J1_9-10	0.5	c	660	graphite	2549	39	2626	2744–2497	homogenous fine mud	N (contaminated)
BE-17653.1.1	LVC3J1_34-35	25.5	c	527	graphite	2927	43	3077	3204–2950	homogenous fine mud	Y
BE-17654.1.1	LVC3J1_59-60	50.5	c	449	graphite	4562	31	5214.5	5425–5063	homogenous fine mud	Y
BE-17655.1.1	LVC3J2_22.5-23.5_bulk	75.5	b	395	graphite	4745	44	5492	5578–5332	homogenous fine mud	N (bulk)
BE-17656.1.1	LVC3J2_47.5-48.5	100.5	c	318	graphite	4858	42	5589	5696–5483	homogenous fine mud	Y
BE-17657.1.2	LVC3J2_72.5-73.5	125.5	c	986	graphite	7828	53	8612	8927–8464	homogenous fine mud	Y
BE-17678.1.1	LVC3J3_23.5-24.5_char	175.5	c	5.8	gas	12347	161	14478.5	15068–13937	homogenous fine mud	N (reworked)
BE-17663.1.1	LVC3J3_39.5-41.5	191.5	c	8.9	gas	9562	131	10894.5	11195–10520	homogenous fine mud	Y
BE-17664.1.1	LVC3J3_41.5-42.5	193.5	c	65.3	gas	10475	117	12356	12683–11940	sand	N (potentially reworked)
BE-17665.1.1	LVC3J3_42.5-43.5	194.5	c	33.1	gas	11405	123	13283	13499–13102	sand	
BE-17666.1.1	LVC3J3_43.5-44.5	195.5	c	58.3	gas	8218	144	9183	9475–8722	sand	

* Material dated: c = charcoal, b = bulk

Continued on next page

Table S4.2: AMS ^{14}C ages and calibrated ^{14}C ages of the sediment core LVC18-S3. (Continued)

Laboratory Code	Core and Sample ID	Sediment depth (cm)	Material*	Carbon mass μgC	Measurement	^{14}C yr BP (cal yr BP)	Error ages ($\pm1\sigma$)	Median	95 % C.I.	Lithology	Included in model (Yes/No)
BE-17667.1.1	LVC3J3_44.5-45.5	196.5	c	122.4	gas	10416	311	12162.5	12869–11275	sand	
BE-17668.1.1	LVC3J3_45.5-46.5	197.5	c	330.5	gas	11629	404	13576	14839–12842	sand	
BE-17669.1.1	LVC3J3_48.5-49.5	200.5	c	42.1	gas	11907	186	13788	14350–13397	sand	
BE-17660.1.1	LVC3J3_49.5-50.5_bulk	201.5	b	435	graphite	7582	458	8465	9496–7607	sand	
BE-17679.1.1	LVC3J3_49.5-50.5_char	201.5	c	30.9	gas	8471	161	9448	9949–9051	sand	
BE-17670.1.1	LVC3J3_60.5-61.5	212.5	c	18.3	gas	11578	269	13466	14040–12949	sand/sed. interface	Y
BE-17671.1.1	LVC3J3_62.5-63.5	214.5	c	15.2	gas	12047	148	13936	14680–13604	brownish sediment	Y
BE-17672.1.1	LVC3J3_63.5-64.5	215.5	c	37.1	gas	12513	141	14701	15232–14176	brownish sediment	Y
BE-17673.1.1	LVC3J3_64.5-65.5	216.5	c	23	gas	12304	578	14531	16159–13226	brownish sediment	N (large error)
BE-17674.1.1	LVC3J3_66.5-67.5	218.5	c	76	gas	12430	215	14602	15300–13922	brownish sediment	Y
BE-17675.1.1	LVC3J3_67.5-68.5	219.5	c	72.2	gas	4588	510	5188	6349–3901	brownish sediment	N (large error)
BE-17676.1.1	LVC3J3_68.5-69.5	220.5	c	11.2	gas	8471	161	9454	9933–9045	brownish sediment	N (low C)
BE-17661	LVC3J3_73.5-74.5_bulk	225.5	b	44	graphite	7776	102	8571	8949–8399	brownish sediment	N (bulk)
BE-17681.1.1	LVC3J3_73.5-74.5_char	225.5	c	48	gas	12347	161	14466	15057–13909	brownish sediment	Y

* Material dated: c = charcoal, b = bulk

Continued on next page

Table S4.2: AMS ^{14}C ages and calibrated ^{14}C ages of the sediment core LVC18-S3. (Continued)

Laboratory Code	Core and Sample ID	Sediment depth (cm)	Material*	Carbon mass μgC	Measurement	^{14}C yr BP (cal yr BP)	Error ages ($\pm 1\sigma$)	Median	95 % C.I.	Lithology	Included in model (Yes/No)
BE-17662	LVC3J3_98.5-99.5	250.5	c	19	graphite	11975	204	13883	14749–13464	greyish sediment	N (low C)

* Material dated: c = charcoal, b = bulk

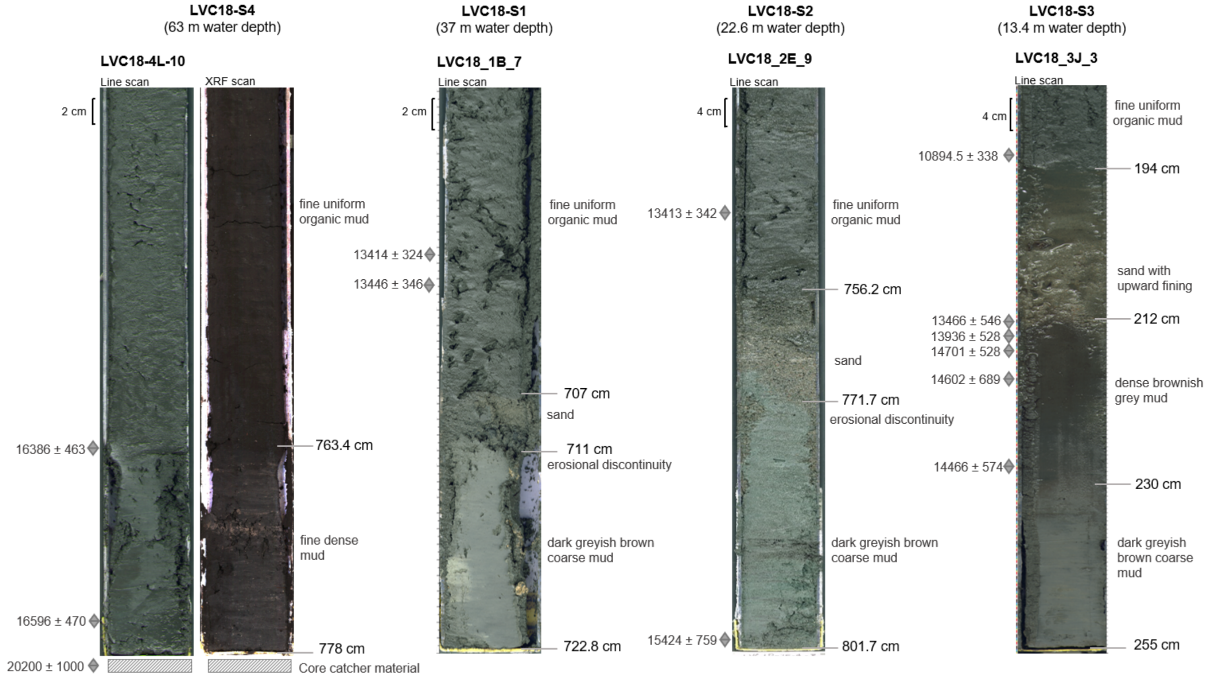

FIGURE S4.3: Core description and line scan images of the basal part of the sediment cores LVC18-S4, LVC18-S1, LVC18-S2, and LVC18-3. The composite sediment depths (master core) and the radiocarbon ages (cal yr BP) are noted at the side.

TABLE S4.3: ^{210}Pb and ^{137}Cs data from the sediment core LVC18-S3-SC2

Laboratory Code	Mid-depth	cum. dry mass	^{210}Pb unsupported	Error	Total ^{137}Cs activity	Error	Age CF-CS*	Age rplum
Coring year	0.000						2018.83	2018.80
LVC18_3_SC2_B_01	0.375	0.038	340.1	12.9	21.5	4.4	2016.00	2013.10
LVC18_3_SC2_B_02	1.000	0.128	175.3	8.6	16.3	5.8	2009.31	2007.40
LVC18_3_SC2_B_03	1.500	0.233	125.2	7.5	26.8	7.0	2001.51	2000.30
LVC18_3_SC2_B_04	2.000	0.340	116.7	7.4	24.6	6.0	1993.48	1993.20
LVC18_3_SC2_B_05	2.500	0.444	119.0	7.4	31.5	5.8	1985.74	1983.20
LVC18_3_SC2_B_06	3.000	0.542	83.1	6.5	20.1	5.3	1978.46	1973.30
LVC18_3_SC2_B_07	3.500	0.655	36.7	5.5			1970.01	1965.20
LVC18_3_SC2_B_08	4.000	0.783	29.9	5.4			1960.47	1957.20
LVC18_3_SC2_B_09	4.500	0.911	17.6	5.1			1950.95	1950.40
LVC18_3_SC2_B_10	5.000	1.048	17.1	5.1			1940.79	1943.70
LVC18_3_SC2_B_11	5.500	1.195	12.2	4.9			1929.81	1934.80
LVC18_3_SC2_B_12	6.000	1.347	16.2	5.1			1918.50	1925.90
LVC18_3_SC2_B_13	6.500	1.506	8.0	5.0			1906.64	1913.50
LVC18_3_SC2_B_14	7.000	1.676	6.7	4.8			1893.95	1901.20

* Inventory correction 22.1 Bq/g; mean MAR 0.013 ± 0.001; mean SR 0.053 ± 0.003.

Chapter 5

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

accepted for publication in *Quaternary Science Reviews*

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Abstract

Lake Victoria is an ideal site to investigate Late Quaternary hydroclimatic variability and related ecosystem responses. 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 la BP), PP_{aq} levels remained generally low, while chromophytes and chlorophytes dominated the algal community. Following the rapid lake level rise (~14.2 ka) 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, 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.

Keywords: Quaternary, climate change, paleolimnology, limnogeology, sedimentary pigments, eutrophication

5.1 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 & 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., accepted). 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 & Smol, 2024; Michelutti & Smol, 2016). Several methods exist to reconstruct long-term (centennial to multi-millennial) variability of aquatic primary paleo-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 & 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 & 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 nearshore (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; Temoltzin-Loranca et al., 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., accepted, 2023). 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 by delivering new insights into potential first-order effects of internal changes in the lake's biogeochemical conditions.

5.2 Material and methods

5.2.1 Study area

Lake Victoria (0.5 °N to 3.0 °S; 68,800 km^2, 1135 m.a.s.l) is located in equatorial eastern Africa between two branches of the East African Rift Valley (Fig. 5.1). 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 & Nicholson, 1998). The hydrological budget is controlled by direct precipitation (>80% of incoming water) and lake surface evaporation (~70% of outgoing water) (Yin & Nicholson, 1998). River runoff makes only a limited contribution to the water input (Crul et al., 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

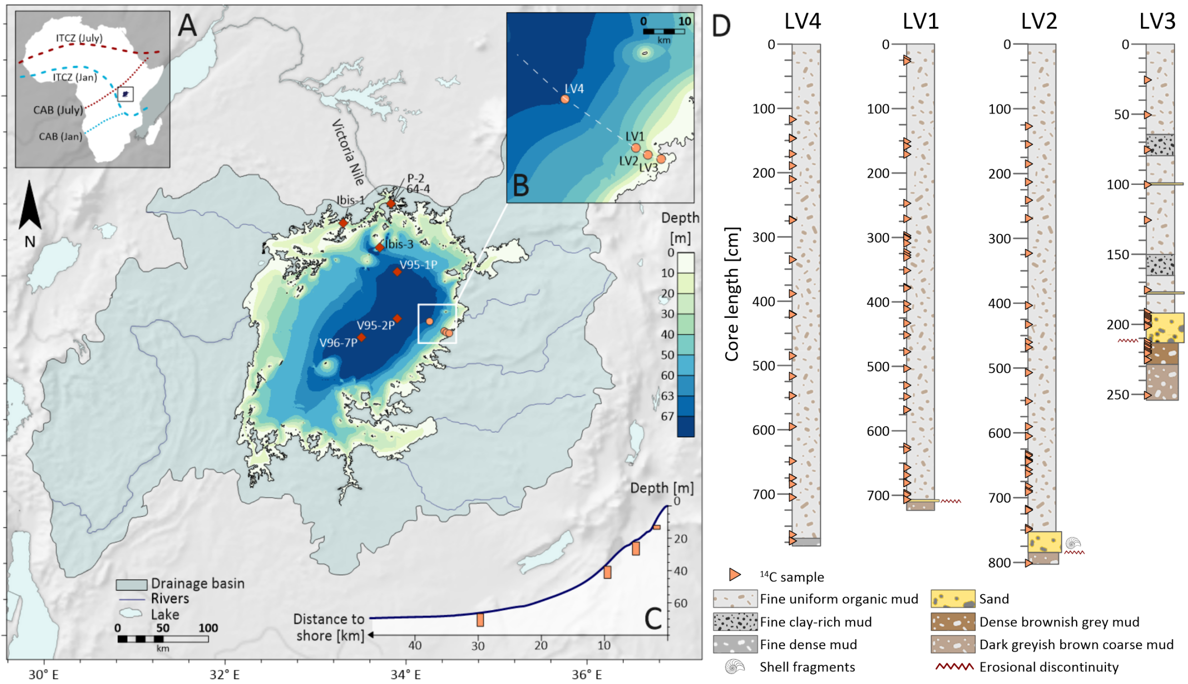

FIGURE 5.1: Catchment and bathymetry of Lake Victoria with sediment cores (LVC18-S1 to LVC18-S4; hereafter referred to as LV1 to LV4, this study, orange circles) and previously collected cores (red diamonds) **(A)** Inset map of the African continent with the location of Lake Victoria and the position 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)

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 (Hecky et al., 1994; Mugidde, 1993; Ngoepe et al., accepted; Stager et al., 2009).

5.2.2 Sediment chronologies

A series of UWITEC piston cores were obtained in October 2018 along a depth transect off the eastern shoreline (Fig. 5.1A-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 13.4–63 meters below the modern lake level (m.b.l.l.) (Fig. 5.1C-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 ^{14}C AMS MICADAS dating and Bacon age modeling (Blaauw & 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. 5.1D.

5.2.3 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 cm^3; Table S5.1).

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 seconds 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 coloured degradation products) and is interpreted as total algal abundance and a proxy for aquatic paleo-productivity (Michelutti & Smol, 2016). Further methodological details are described in Butz et al. (2015) and Zander et al. (2022).

Total carbon (TC), $\delta^{13}C$ and $\delta^{15}N$ 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 N_2 (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 H_2O_2 prior to leaching (Mortlock & 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. S5.4).

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 & Zibilske, 1991; Tu et al., 2021).

Analytical efficiency was controlled with the certified reference sediment material (CRM) BCR-684 and showed good agreement (Table S5.2).

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).

5.2.4 Statistical analyses

All statistical analyses were performed using R v4.1.2 (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 vegan::rda() function (Oksanen et al., 2019). Unconstrained cluster analysis was done using the ward.D2 clustering method with the Euclidean distance (Murtagh & 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).

5.3 Results and interpretation

5.3.1 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. 5.2).

The basal sedimentary Unit I in LV4 (16.7 – 14.5 cal ka BP; 778 – 692 cm; Fig. 4.2; 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 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 – 13 cal ka BP and the subsequent establishment of the modern lake with an overflow towards the Nile (Wienhues et al., in press).

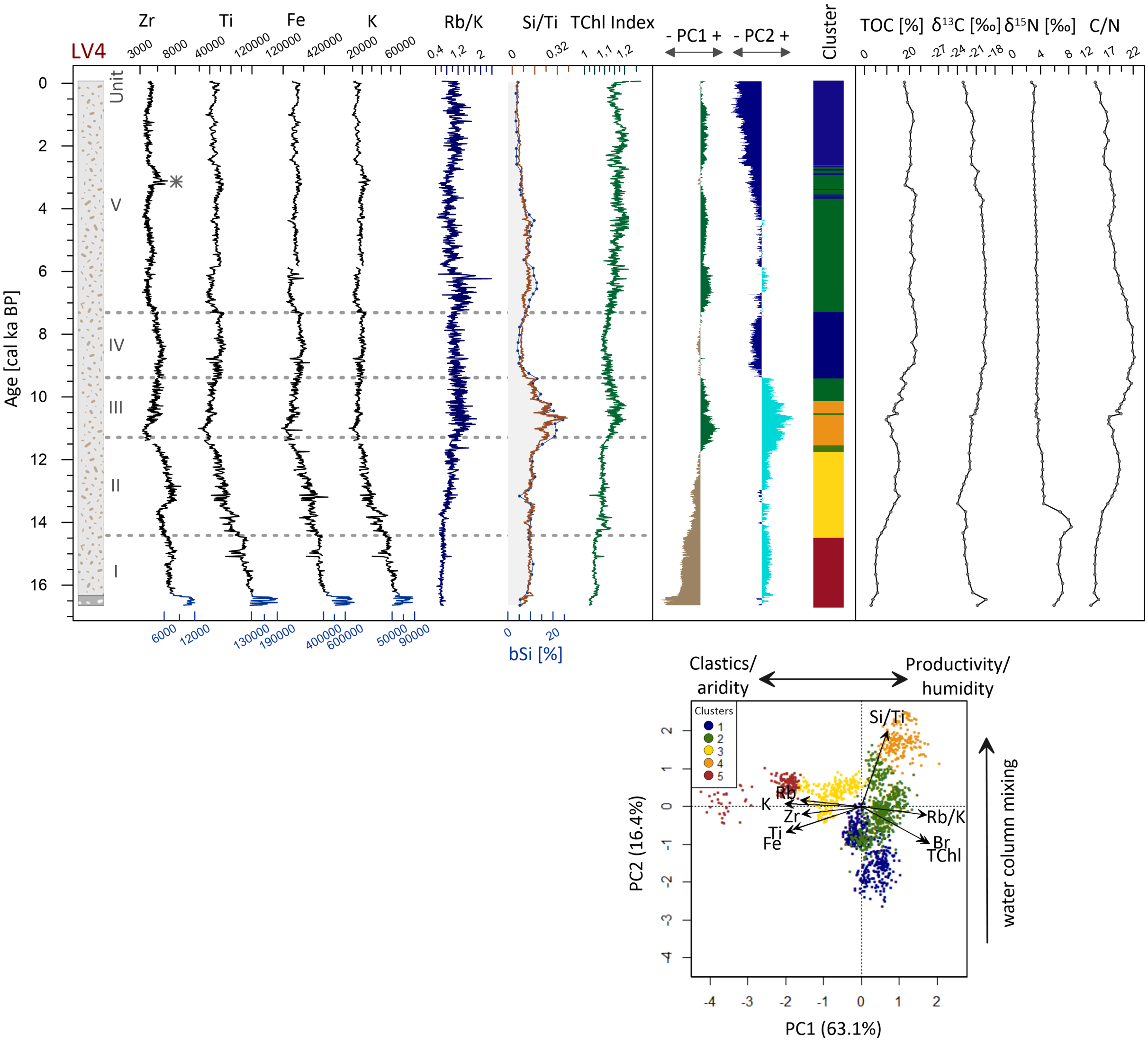

Figure 5.2: Selected bio-geochemical variables (XRF, HSI, bSi, TOC, δ^{13}C, δ^{15}N, and atomic C/N ratio) and PCA scores plotted by age for LV4. For Zr, Ti, Fe, and K, the blue color refers to the scale at the bottom. The colored bar shows the lithotypes identified by unconstrained cluster analysis. 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 the Supplementary Material (Figs S5.1, S5.2, S5.3)

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., 1997; Stager et al., 2003; Stager & Johnson, 2000). 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 – 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. 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. 5.2) 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 – 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 & Johnson, 2000). Accordingly, positive PC2 scores suggest well-mixed conditions between 16.5 and 9 cal ka BP, in particular between 12–9 cal ka BP, and around 6 cal ka BP whereas periods with higher water column stability are found between 9–7 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. S5.1, S5.2, S5.3. 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 colours in Figs. S5.1, S5.2, S5.3 represent similar lithotypes as in LV4, Fig. 5.2). 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 cal ka BP 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 10.7–9.5 cal ka BP and between 6.5–5.5 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.

5.3.2 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. 5.2). 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. S5.1, S5.2).

In LV1, LV2 and LV4 cores, δ^{13}C values span from -24 to -19 ‰ (Figs. 5.1 and S5.1, S5.2). Prior to 13.5 cal ka BP, more negative δ^{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 δ^{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 & 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 δ^{15}N values are relatively high with values up to +8.3 ‰(LV4) notably in the lower parts of the cores (Figs. 5.2, S5.1 and S5.2) when shallow pond and wetland environments prevailed. In all cores, δ^{15}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, δ^{15}N values remained remarkably stable within a very narrow range (mean values LV1, LV2 and LV4 between 1.9 ‰and 3.4 ‰ ±0.5‰). LV1 and LV2 show stable δ^{15}N values in the early Holocene and slightly negative trends between 8 cal ka BP 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 δ^{15}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. 5.2). Similar trends are reproduced in LV1 and LV2, albeit with generally lower values (C/N = 10 – 16; Figs. S5.1 and S5.2). 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 & Hendzel, 1980; Hecky et al., 1994) and proposed adjusted C/N thresholds for aquatic organic matter sources in the lake (Fig. 5.3A). 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. 5.3A). 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 & Hall, 2023; Guildford et al., 2003).

Additionally, Fig. 5.3B 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.

5.3.3 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

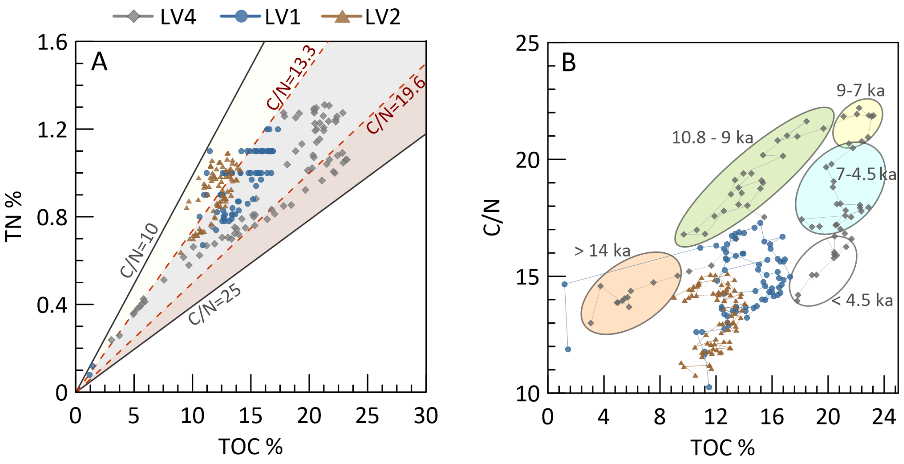

FIGURE 5.3: **(A)** TOC vs. TN for the cores LV4, LV1, and LV2. C/N boundaries for endmembers (aquatic or terrestrial organic matter; Meyers, 1997)). Dashed lines indicate algal C/N composition under moderate and severe nitrogen deficiency (Talbot & Lærdal, 2000). **(B)** TOC vs C/N for the cores LV4, LV1, and LV2. The LV4 data is subdivided into distinct diatom productivity periods in Lake Victoria presented in Fig. 5.7.

a, and β,β-carotene are indicators for total phytoplankton biomass and are used as proxies for paleo-productivity (Michelutti & 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). Dinoxanthin 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 S5.1.

The CONISS analysis on sedimentary pigments in LV4 revealed four pigment zones (PZ) (Fig. 5.4A):

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).

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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 & 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* (Figs. 5.4A and 5.5) 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 BP with peak relative abundances between 11–10 cal ka BP followed by a relative decline ca. 9 cal ka BP and stable conditions until 5.3 cal ka BP (Fig. 5.2). 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 & 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, 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 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 – 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 cal ka BP (Fig. 5.4B):

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 phase, colonial cyanobacteria (myxoxanthophyll, canthaxanthin and

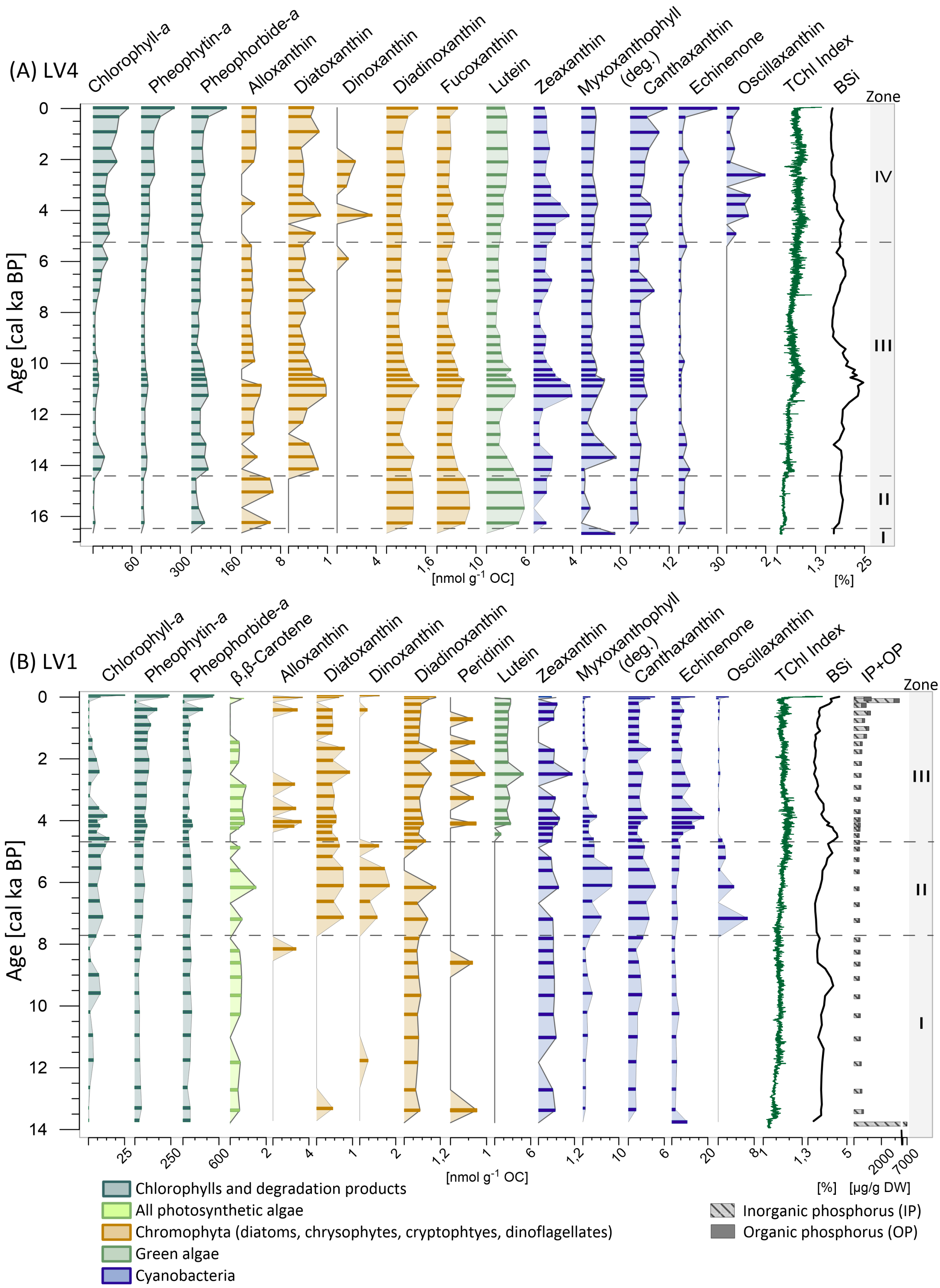

FIGURE 5.4: HPLC sedimentary pigment stratigraphy for **(A)** LV4 and **(B)** LV1. Pigment zones were defined by CONISS analyses (far right). TChl Index, BSi, IP, and OP were not included in the cluster analyses.

oscillaxanthin) dominate under better stratified water column conditions (low bSi values between 7.7 and 6 cal ka BP; Fig 5.6). 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 – 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 5.4B, S5.5) gradually increase.

5.3.4 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 & Canuel, 2011). In Lake Victoria overall, the chlorophyll degradation products pheophytin *a* and pheophorbide *a* are the most abundant sedimentary pigments (Fig. 5.5B) suggesting substantial cellular senescence and/or zooplankton grazing in the water column. Other chlorophyll degradation products such as pyropheopytin, 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. 5.5A and B). This trend could be attributed to the gradual increase of hypolimnetic hypoxia as a result of enhanced stratification (low bSi, Fig. 5.2) and, hence, better pigment preservation at the deep-water site LV4 compared to LV1. Chl *a* is especially sensitive to dissolved oxygen (Leavitt & Hodgson, 2001).

In both cores, the ratio between pheophytin *a* (general cell senescence) and pheophorbide *a* (cell destruction by grazing; Bianchi & Canuel, 2011) increases from older to younger ages (Fig. 5.5B) 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 & Catalan, 2008) and reveals substantial fluctuations at both sites through time (Fig. 5.5A). 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 cal ka BP and between 8 – 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.

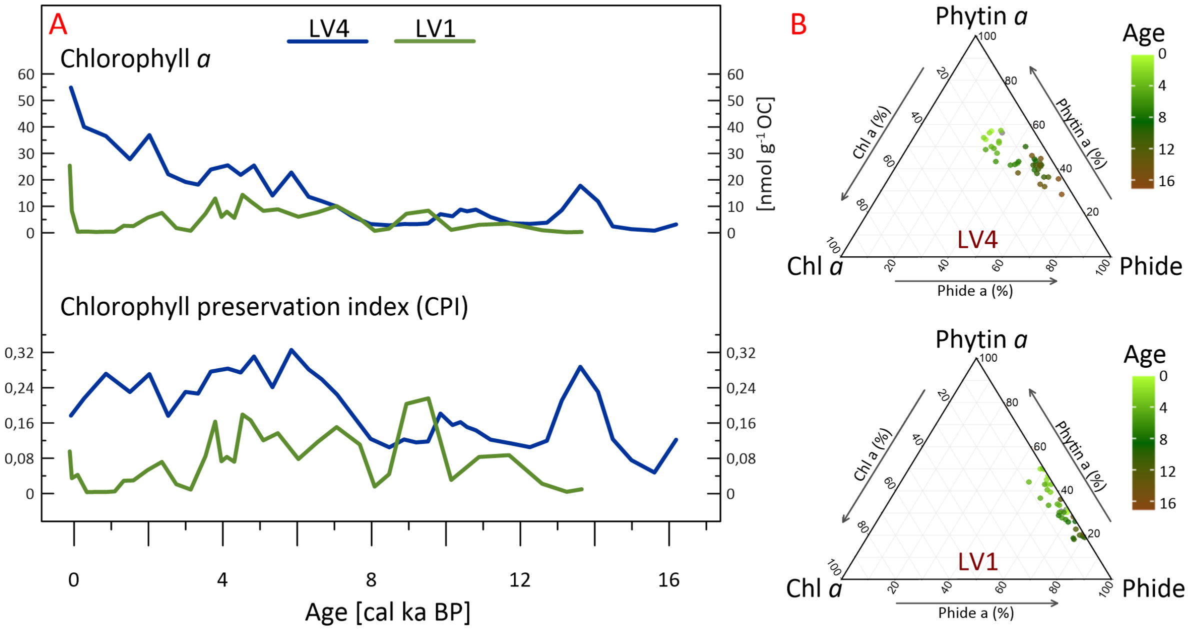

FIGURE 5.5: **(A)** Time series of Chl *a* and CPI (Chlorophyll Preservation Index) for LV4 and LV1. **(B)** Ternary diagram for Chl *a* and its degradation products (pheophytin *a* and pheophorbide *a*). Colors indicate the age of the data points (cal. ka BP).

5.4 Discussion

Overall, our results suggest that it is possible to quantify spatio-temporal variability of PP_{aq} in a tropical lake based on bio-geochemical 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.

5.4.1 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. 5.5). 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 & 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 to 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. 5.4B) 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 & Hamilton, 2024). 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. 5.4) which is known to degrade quickly (Hurley & 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 & 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.

5.4.2 The transition from wetlands to an exorheic lake

Prior to the rapid and massive lake level rise 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 cal ka BP, sedimentary pigments indicate the presence of a chlorophyte and chromophyte algal assemblage, which includes cryptophytes, during this phase of shallow water conditions (Zone$_{\mathrm{LV4}}$ II; Fig. 5.4) 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 δ^{13}C values, and predominance of clastic sediments: overall an environment with low PP$_{\mathrm{aq}}$ and poor pigment preservation in shallow water conditions with light and oxygen exposure and possible sediment reworking. The low δ^{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 & 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 & Bicudo, 2010).

With the major lake-level rise and establishment of the outflow to the Nile river between 14.1 and 13.6 cal ka BP Wienhues et al., in press, a gradual decrease in chlorophytes and chromophytes was observed, accompanied by a rise in PP$_{\mathrm{aq}}$, 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 *Nitzschia fonticola* (Stager

& Johnson, 2000).

5.4.3 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., Sarmento 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 favored by stable water column conditions (Reynolds, 1987, 2006). Today, the lake-wide convection over the water body is seasonally driven by southeastern and northwestern 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-productivity (bSi; Fig. 5.7), 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. 5.2), in the PC2 loadings (positive during mixing phases) and K/Rb ratios (enhanced precipitation and erosion during periods with strong mixing; Fig. 5.2). Although water column temperature is generally positively correlated to the lake's water column stability, this pattern is not reflected in the TEX_{86} water temperature record (Berke et al., 2012).

The isochronic alignment of all existing bSi records from Lake Victoria (Fig. 5.7; 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 biomarker 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 (Berke et al., 2012; Stager & Mayewski, 1997; Wienhues et al., in press). 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. 5.4). 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 & Johnson, 2000; Stager & Mayewski, 1997).

In contrast, the decline in bSi across offshore sediment cores between 9 and 7 cal ka BP (Fig. 5.7) would reflect increased lake stratification. During this period, diatom frustules are absent in the core V95-2P (Stager & Johnson, 2000); TChl concentrations were relatively low and clastic input reduced (LV4; Figs. 5.2 and 5.5A). 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. 5.5B) 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 & 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 & Hecky, 2000; Guildford et al., 2003). Indeed, offshore N limitation around 9–7 cal ka BP is supported by very high C/N ratios (Fig. 5.3B). 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 - ~4 cal ka BP (Fig. 5.4B). 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. 5.7) 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 & 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 & Johnson, 2000). This is evident in the second bSi maximum during the mid-Holocene offshore around 7 cal ka BP (Fig. 5.7), and it began with respect to diatom assemblages in nearshore cores ~8 cal ka BP (Stager et al., 2003; Stager & 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. 5.7). Increased diatom productivity during that time is not reflected in the phytoplankton biomarker stratigraphy at LV4 (Fig. 5.4); this could be related to the labile nature of diatom pigments and the enhanced degree of pigment degradation (Fig. 5.5). 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. 5.4 and 5.5), showing enhanced cyanobacteria, less severe N limitation (lower C/N ratios, Fig. 5.3B) and better pigment preservation. Maxima in δ^{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. 5.6), marking the gradual decrease of δ^{13}C in all cores whereas PP_{aq} (TChl) remains relatively high. Subsequently, diatom productivity decreased systematically (Fig. 5.7) 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.

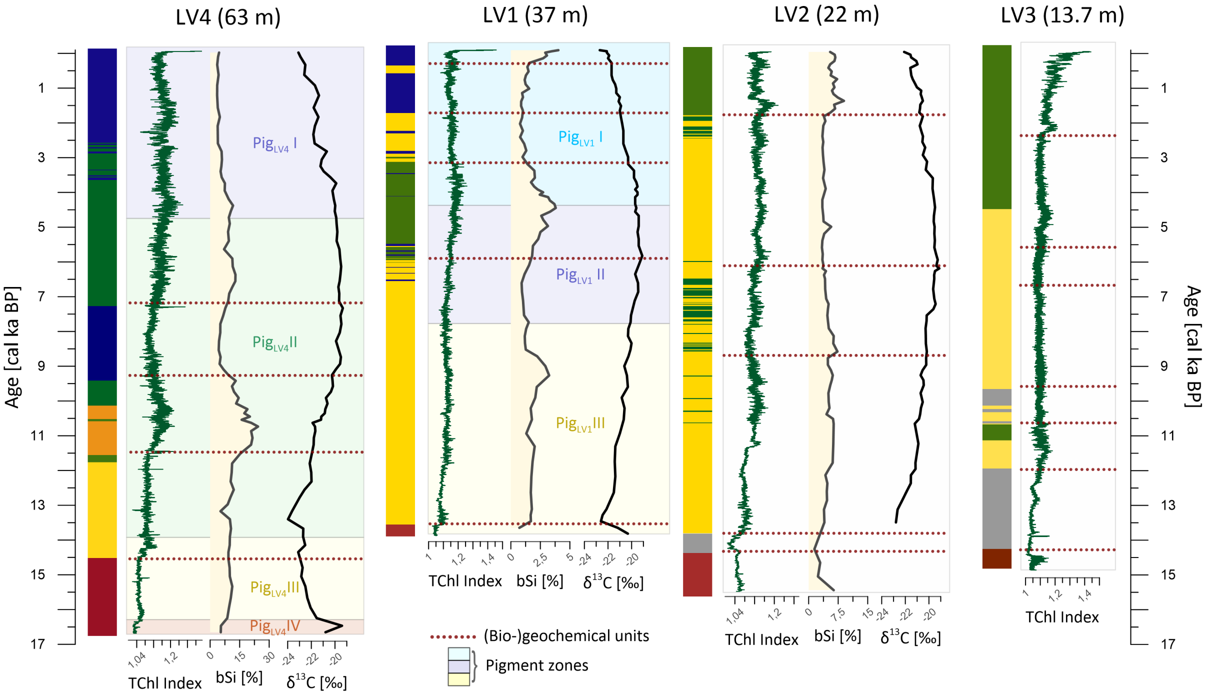

FIGURE 5.6: Compilation of lithotypes, TChl, bSi, δ^{13}C, sedimentary units (Figs 5.2, S5.1. S5.2, S5.3) and pigments zones (Fig. 5.4 across the transect with the four sediment cores (LV1 to LV4).

5.4.4 Primary production and regional hyydroclimate 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. 5.8). 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. 5.8; 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 Afromontane forests (Kendall, 1969; Temoltzin-Loranca et al., 2023a; Van Zinderen Bakker & Coetzee, 1988) and affecting aquatic primary producers and lake ecology. 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. 5.8C).

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

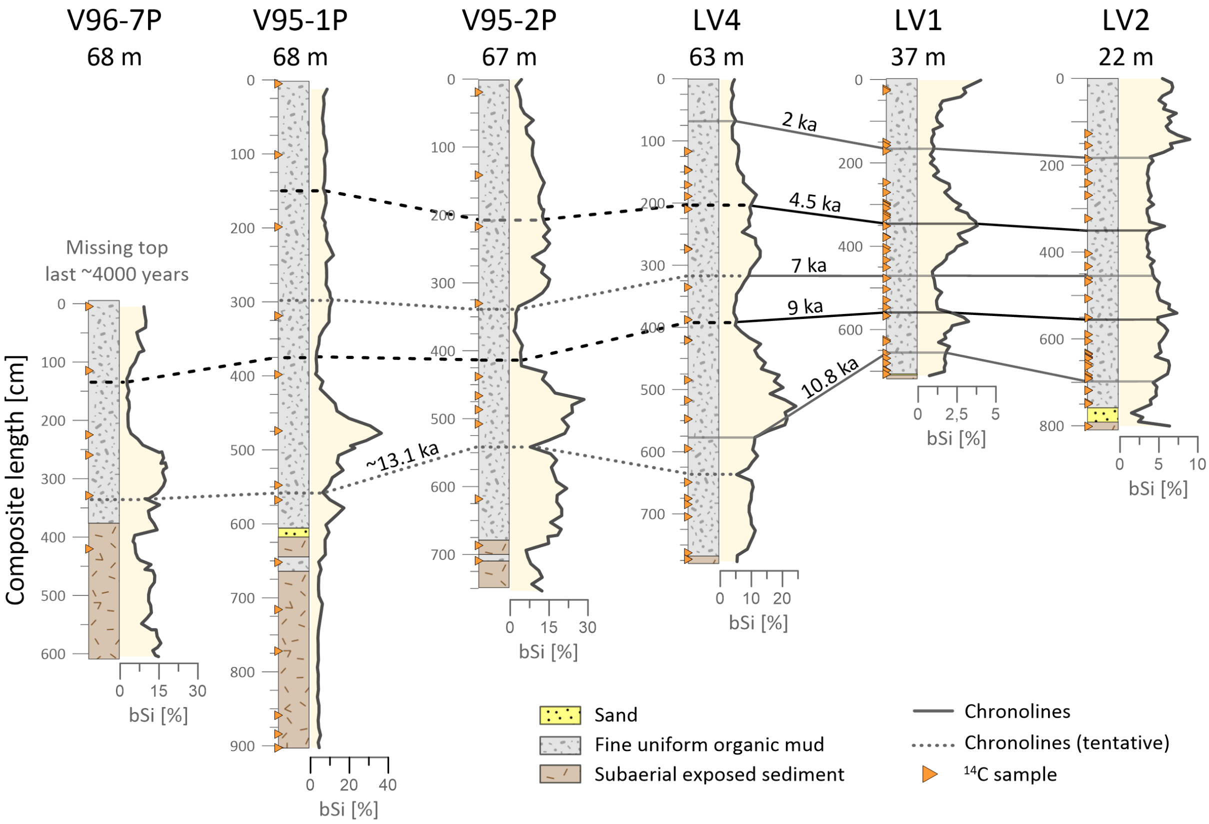

FIGURE 5.7: Compilation of bSi records across Lake Victoria displayed in composite core lengths (Beuning et al., 2002; Talbot and Lærdal, 2000; Verschuren et al., 1998, and three LV cores from this study) and isochrones of phases with high (low) bSi values. Schematic core lithologies were derived from sediment descriptions in the literature (Beuning et al., 2002; Talbot & Lærdal, 2000; Verschuren et al., 1998; Wienhues et al., in press). Orange triangles mark ^{14}C dates. The bSi records from V95-3P and V95-6P have only one ^{14}C date and were omitted but display distinctly different bSi profiles (see full figure is provided in the Supplementary Material; Fig. S5.6) Note the different scales of the x-axis.

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. 5.2) and, more specifically, of the profile records in LV4 (Fig. 5.8C) 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., 2012, 2015). 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, around 9 cal ka BP, between 7.8 – 7.2 cal ka BP, around 4 cal ka BP and between 3.2 – 3.0 cal ka BP (red shading in Fig. 5.8C).

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 ka; Berke et al., 2012; Costa et al., 2014; Tierney et al., 2008, 2011) and rainforest expanded in the Victoria catchment (Temoltzin-Loranca et al., 2023a, Fig. 5.8C). 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. 5.8C). 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 – 8 cal ka BP towards the mid Holocene occurred in the region, likely causing a reduction of tropical rainforests and moderate expansion of subtropical Afromontane 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 (EMHT; Stager et al., 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. 5.8D). 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 5.6, and 5.8). 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. 5.3B).

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 cal ka BP ago (Stager et al., 2005a) 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. Foerster et al., 2012; Tierney et al., 2011). Droughts around that time are also found in the Rb/K and K records of LV4 (Fig. 5.8C) 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. 5.6) and the mid Holocene chromophyte and cyanobacteria-dominated communities were more prominently represented by cyanobacteria (Fig. 5.8).

5.5 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

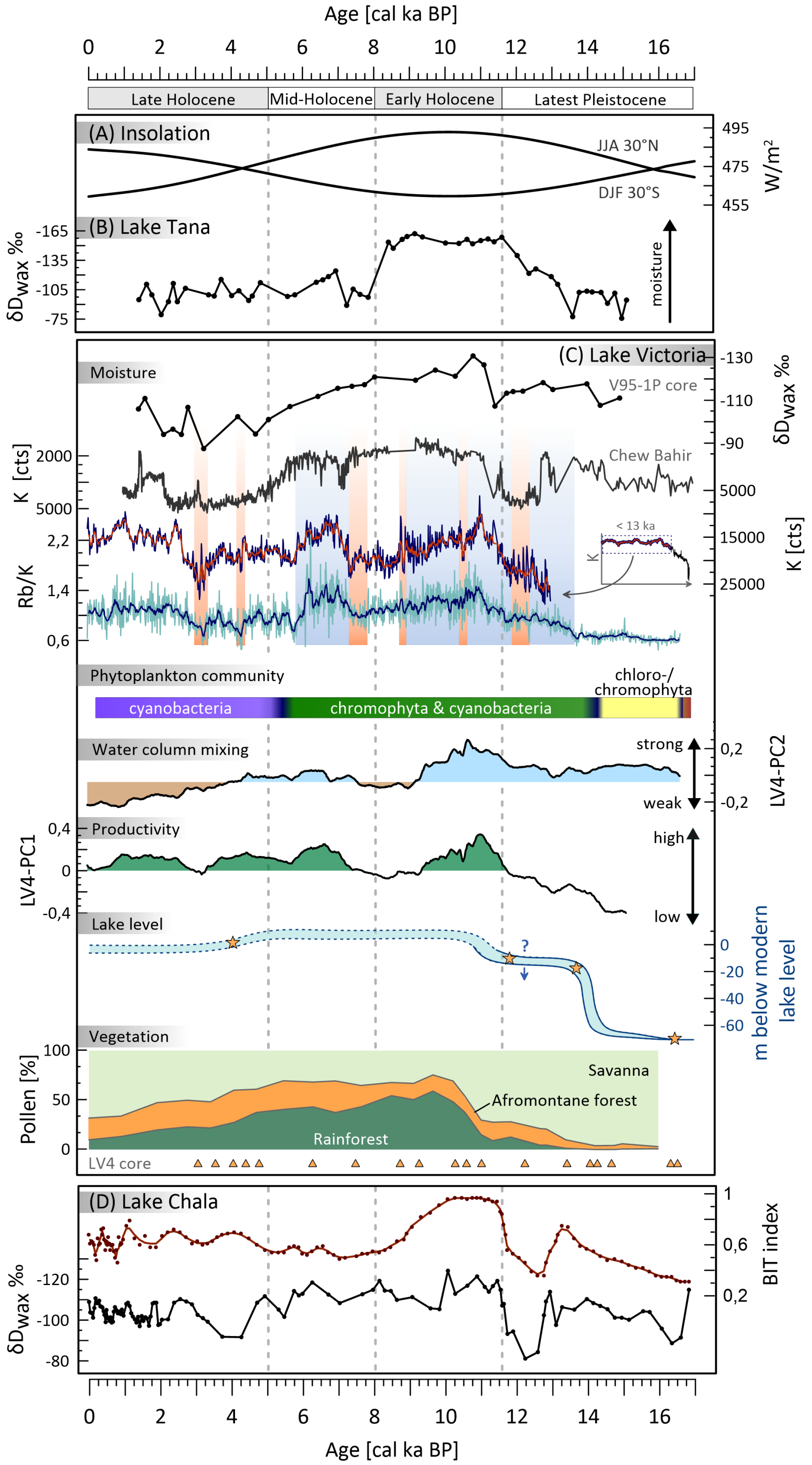

FIGURE 5.8: The Lake Victoria record in the context of regional paleoclimate records. $\delta D_{\text{leaf wax}}$ indicates hydroclimate variability (amount and source effects). **(A)** Summer (JJA) and winter (DJF) insolation (Berger & Loutre, 1991). **(B)** $\delta D_{\text{leaf wax}}$ of Lake Tana (Costa et al., 2014). **(C)** $\delta D_{\text{leaf wax}}$ 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; Stager et al., 2005b; Wienhues et al., in press), catchment vegetation (Temoltzin-Loranca et al., 2023a), LV4). **(D)** Chala BIT (branched and isoprenoid tetraether) index (Verschuren et al., 2009) and $\delta D_{\text{leaf wax}}$ of Lake Chala (Tierney et al., 2011).

covering the last 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 period 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.

Declaration of contribution: Author contributions of the article are as follows: GW, MG, and HV conceptualized the study. AL performed pigment measurement and chromatographic evaluation. MAM assessed the scanning XRF data. SB and MJ conducted the isotopic analysis. GW did the sample preparation, laboratory analyses, numerical investigations, the data visualisation and wrote the draft of the manuscript. OS, BM, MM, and MG acquired the funding. All authors discussed the results, commented on the manuscript, and agreed on the science and the style of the manuscript. We thank the two reviewers, Curt Stager and Inka Meyer, for very constructive comments.

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5.7 Supplementary Material

TABLE S5.1: Overview of analysed cores and applied methods including the sample resolution

Cores	Applied method and sample resolution		
	≤1 cm	10 cm - discrete	20 cm - discrete
LV4	HSI^a, XRF^b	TC, δ^{13}C, δ^{15}N, bSi, Grain size	Pigments
LV1	HSI^a, XRF^b	TC, δ^{13}C, δ^{15}N, bSi, Grain size	Pigments, P fractions
LV2	HSI^a, XRF^b	TC, δ^{13}C, δ^{15}N, bSi, Grain size	
LV3	HSI^a, XRF^c		
Sampling resolution: ^{a}0.069 mm ^{b}5 mm ^{c}10 mm			

TABLE S5.2: Recoveries of extractable phosphorus in certified reference material (BCR®-684) following the five-step extraction procedure including the average recovery and relative standard deviation (SD) (n=3). **NAIP** = Non-Apatite Inorganic Phosphorus; **AP**= Apatite Phosphorus; **IP** = Inorganic Phosphorus; **OP** = Organic Phosphorus; **TP** = Total Phosphorus.

	NAIP	AP	IP	OP	TP
Average recovery in % (n =3)	89.4	107.0	75.9	91.3	89.2
Standard deviation	±7.0	±4.5	±12.0	±4.5	±6.9

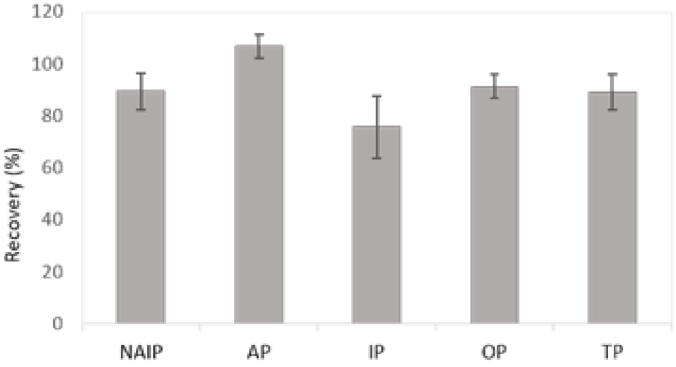

TABLE S5.3: List of analysed pigments in the sediment of LV4 and LV1

Pigment	Abbreviation	LV4	LV1	Taxonomical affinity
Chlorophyll *a* (sum of all isomers)	ChlaT	x	x	All primary producers
Pheophytin *a* (sum of all isomers)	PhphT	x	x	Chlorophyll *a* derivative (senescence)
Pheophorbide *a* (sum of all isomers)	PhideT	x	x	Chlorophyll *a* derivative (grazing)
β,β-carotene	β,β-Car	-	x	All primary producers
Alloxanthin	Allo	x	x	Cryptophyta
Peridinin	Peri	-	x	Dinophyta
Fucoxanthin	Fuco	x	-	Dinophyta, Bacillariophyta, Chrysophyta
Diadinoxanthin	Diadi	x	x	Dinophyta, Bacillariophyta, Chrysophyta, Cryptophyta
Diatoxanthin	Diato	x	x	Bacillariophyta, Dinophyta, Chrysophyta
Dinoxanthin	Dinox	x	x	Dinophyta and Chrysophytes
Lutein	Lute	x	x	Chlorophyta (green algae)
Echinenone	Echi	x	x	Cyanobacteria
Zeaxanthin	Zea	x	x	Cyanobacteria
Myxoxanthophyll (deg.)	Myxodeg	x	x	Colonial Cyanobacteria
Oscillaxanthin	Oscillax	x	x	Cyanobacteria (Oscillatoria)
Canthaxanthin	Cantha	x	x	Cyanobacteria
(x) detected; (-) not detected; degr. = degradation product				

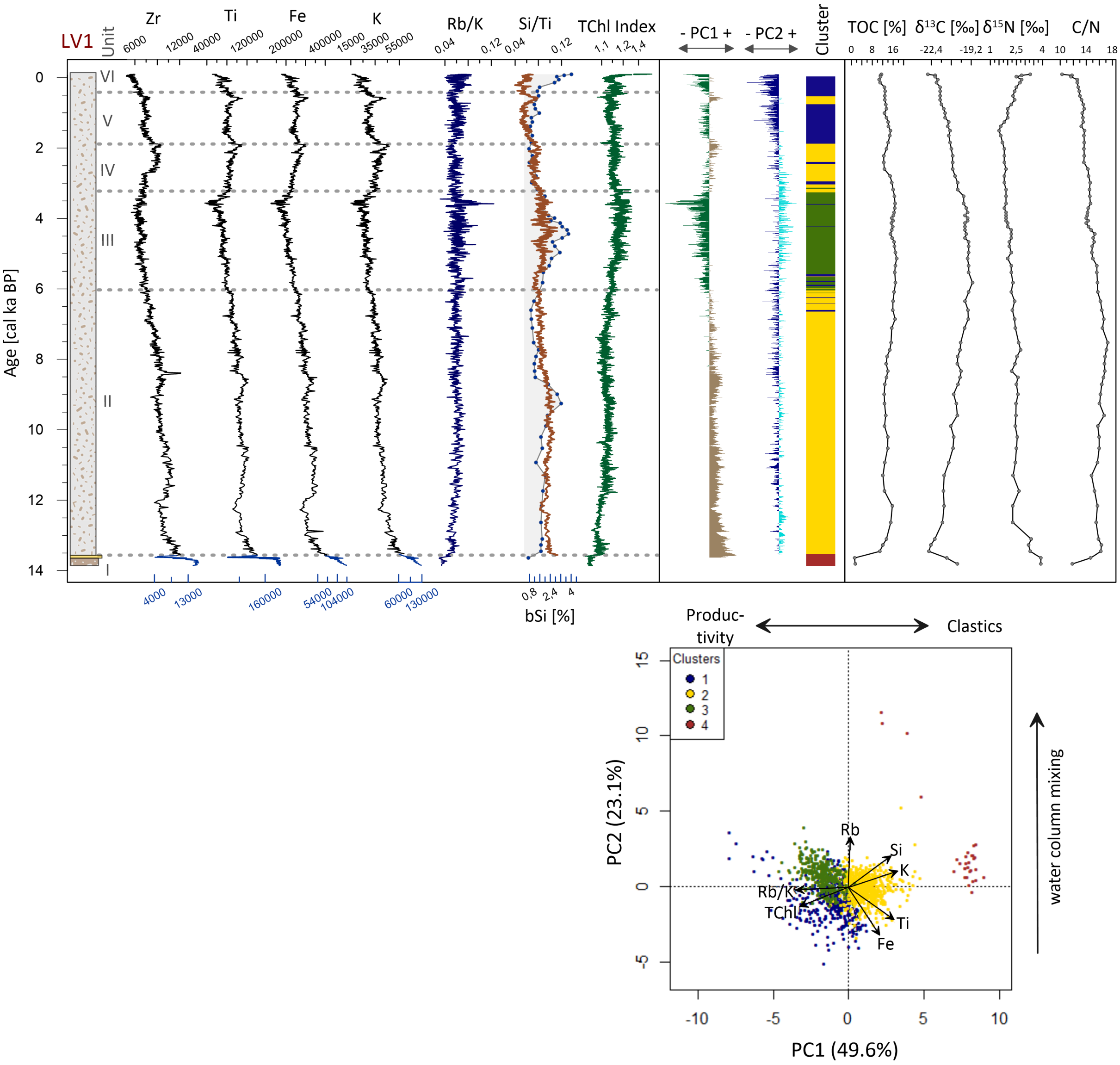

FIGURE S5.1: Selected bio-geochemical variables (XRF, HSI, bSi, TOC, δ^{13}C, δ^{15}N, and C/N) plotted by age for core LV1. For Zr, Ti, Fe, and K, the blue color refers to the scale at the bottom. The colored bar shows the lithotypes identified by unconstrained cluster analysis. The constrained cluster boundaries (Units I-VI) are shown as horizontal dashed grey lines. The principal component biplot shows the first two principal components with loadings of each variable depicted as black arrows. Data points are grouped by cluster/lithotype and indicated by different colors.

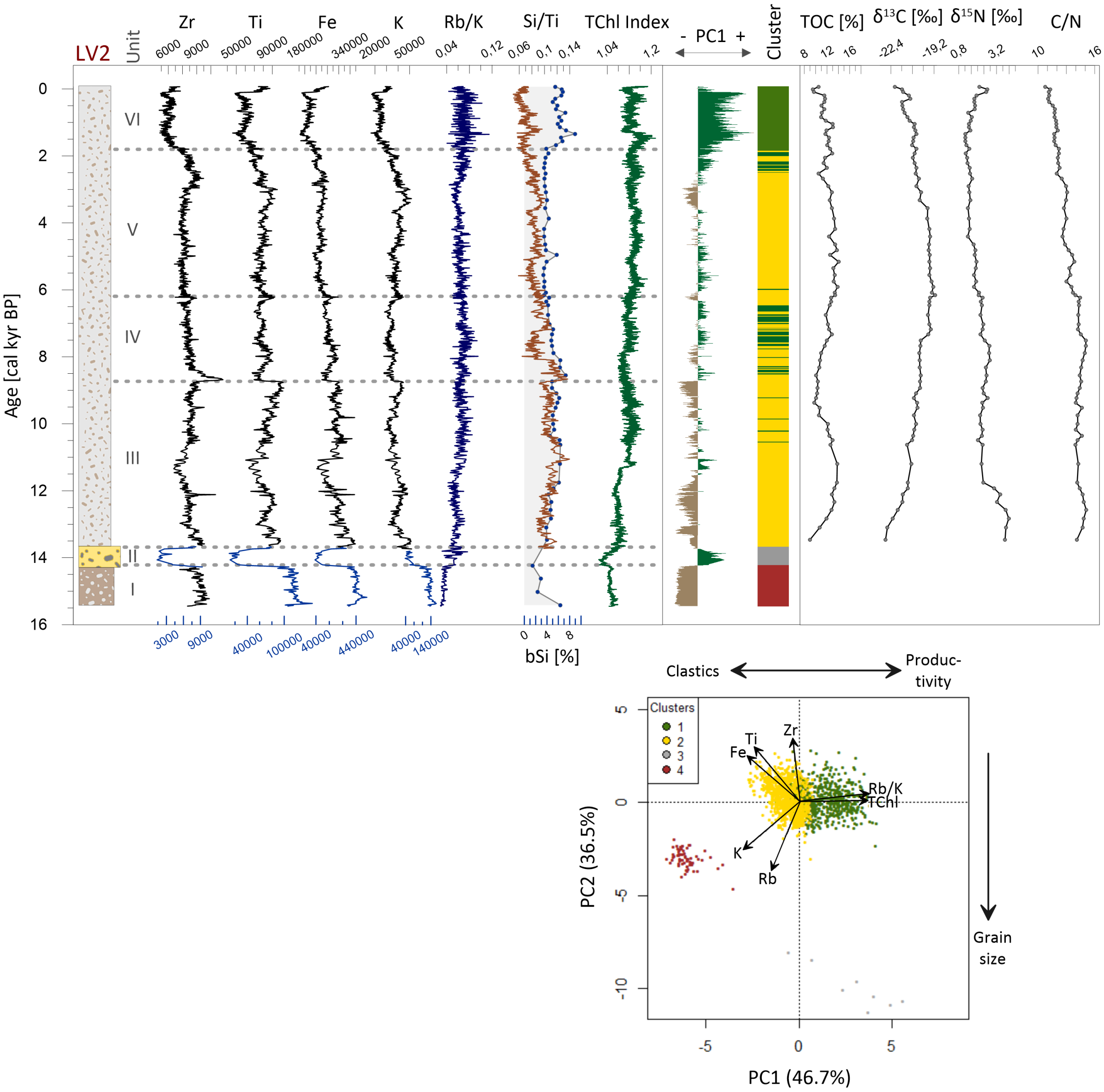

FIGURE S5.2: Selected bio-geochemical variables (XRF, HSI, bSi, TOC, δ^{13}C, δ^{15}N, and C/N) plotted by age for core LV2. For Zr, Ti, Fe, and K, the blue color refers to the scale at the bottom. The colored bar shows the lithotypes identified by unconstrained cluster analysis. The constrained cluster boundaries (Units I-VI) are shown as horizontal dashed grey lines. The principal component biplot shows the first two principal components with loadings of each variable depicted as black arrows. Data points are grouped by cluster/lithotype and indicated by different colors.

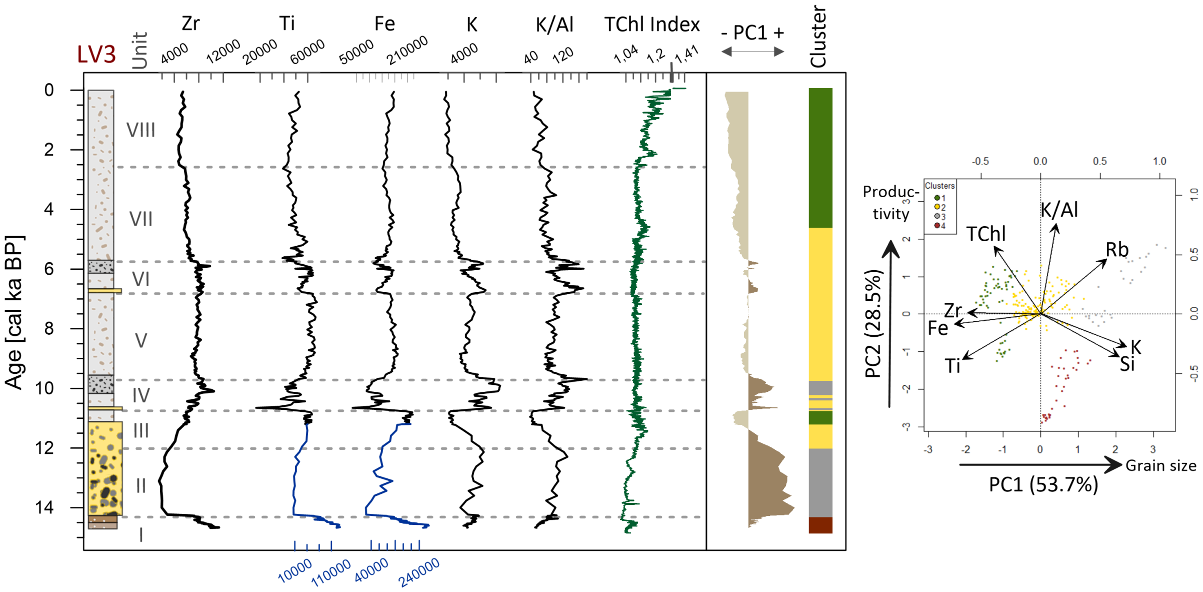

FIGURE S5.3: Selected (bio)-geochemical variables (XRF, HSI) plotted by age for core LV3. For, Ti and Fe, the blue color refers to the scale at the bottom. The colored bar shows the lithotypes identified by unconstrained cluster analysis. The constrained cluster boundaries (Units I-VIII) are shown as horizontal dashed grey lines. The principal component biplot shows the first two principal components with loadings of each variable depicted as black arrows. Data points are grouped by cluster/lithotype and indicated by different colors.

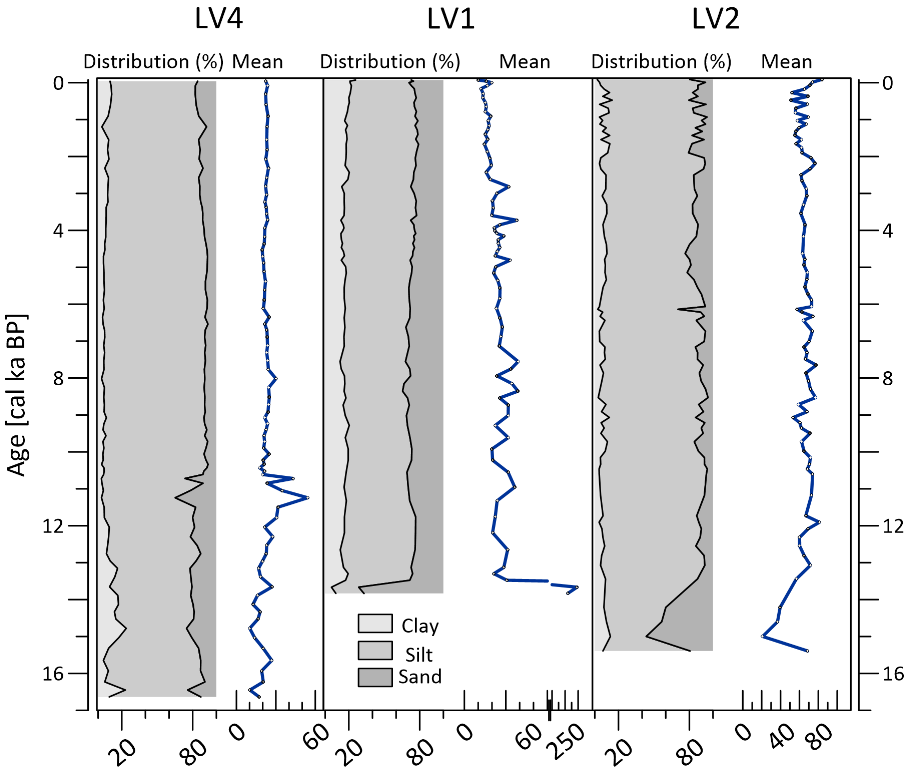

FIGURE S5.4: Particle size fractions (in %) and mean particle size in blue for the sediment cores LV4, 1, and 2.

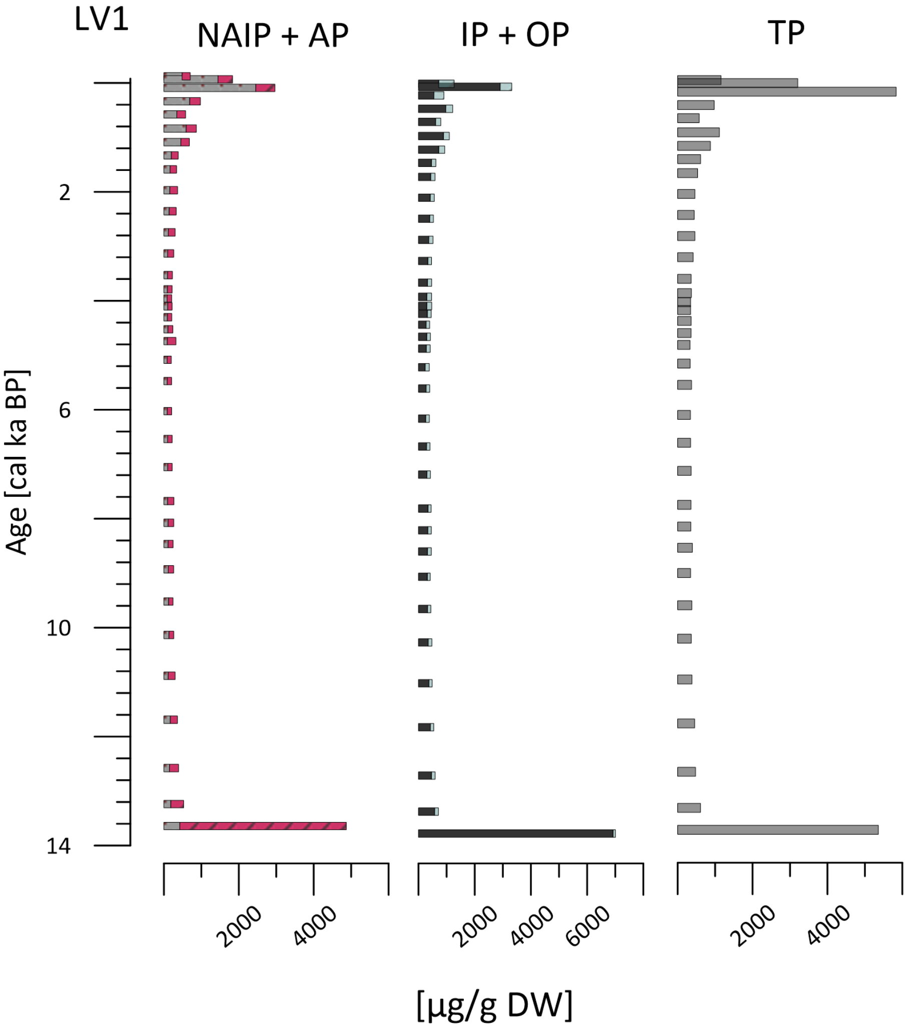

FIGURE S5.5: Phosphorus fractions from sediment core LV1. **NAIP** = Non-Apatite Inorganic Phosphorus; **AP**= Apatite Phosphorus; **IP** = Inorganic Phosphorus; **OP** = Organic Phosphorus; **TP** = Total Phosphorus.

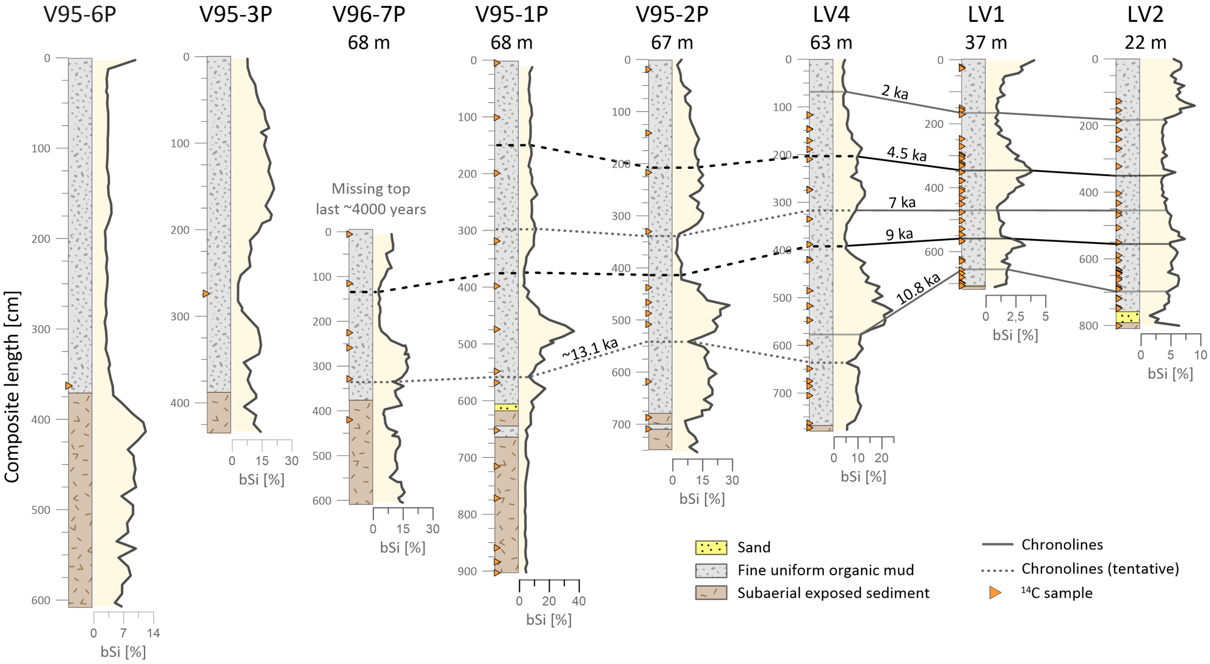

FIGURE S5.6: Compilation of bSi records across Lake Victoria displayed in composite core lengths (Beuning et al., 2002; Talbot and Lærdal, 2000; Verschuren et al., 2000, and three LV cores from this study) and isochrones of phases with high (low) bSi values. Orange triangles mark ^{14}C dates. The bSi records from V95-3P and V95-6P have only one ^{14}C date and were not correlated.

Chapter 6

6. Anthropogenic eutrophication drives major food web changes in Mwanza Gulf, Lake Victoria

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Keywords: Cladocera, eutrophication, food web, paleolimnology, photosynthetic pigments, tropical lake

Higlights

- Anthropogenic eutrophication of Mwanza Gulf began around 1920.
- Increased primary production linked to nutrient enrichment, not food web changes.
- Cladoceran decline driven by lake-level rise and predation pressures in the Gulf.

Abstract

Discerning ecosystem change and food web dynamics underlying anthropogenic eutrophication and introduction of non-native taxa is necessary for ensuring the long-term sustainability of fisheries and lake biodiversity. Previous studies of eutrophication in Lake Victoria, eastern Africa, have focused on the loss of much of the endemic fish biodiversity, but changes in the plankton communities remain unclear. We examined sediment cores from a eutrophic embayment, Mwanza Gulf, to determine the timing and magnitude of changes in the phytoplankton and zooplankton assemblages in relation to changes in fish community structure. Biogeochemical proxies indicate nutrient enrichment began ~ 1920 CE and led to rapid increases in primary production, and our analysis of photosynthetic pigments revealed three zones: pre-eutrophication (prior to 1920 CE), onset of eutrophication with increases of all pigments (1920–1990 CE), and sustained eutrophication with cyanobacterial dominance (1990 CE–present). Cladoceran remains indicate an abrupt decline in biomass in the 1960s, following a substantial lake-level rise and preceding the collapse of haplochromine cichlids in the 1980s. *Alona* and *Chydorus*, typically benthic littoral taxa, have remained at relatively low abundances since the 1960s, whereas the abundance of *Bosmina*, typically a planktonic taxon, increased in the 1990s concurrently with the biomass recovery

of haplochromine cichlid fishes. Overall, our results demonstrate substantial changes in the biomass structure and taxonomic composition of Mwanza Gulf phytoplankton and zooplankton communities over the past century, providing a historical food web perspective that can help understand the recent changes and inform future resource management decisions in the Lake Victoria ecosystem.

6.1 Introduction

Situated in one of Africa's most densely populated regions, Lake Victoria's vast resource potential has contributed to consistently higher population growth compared to the rest of the continent (Odada et al., 2009). Lake Victoria (Fig. 6.1) plays a vital role in providing ecosystem services to the local population, most notably by supporting the world's largest inland fishery (Sterner et al., 2020). The lake has experienced rapid ecological change in the past century driven by various climatic and anthropogenic pressures (Fig. 3.2), with inshore areas being particularly affected. Although long term biological datasets are crucial for documenting such ecosystem variability, existing time series rarely span more than a few decades (Gilarranz et al., 2022) and are particularly rare in tropical regions (Plisnier et al., 2023). Thus, paleolimnological records serve as a complementary source of long-term data, offering insights into past environmental changes and food web dynamics in lakes (Davidson & Jeppesen, 2013).

Anthropogenic eutrophication (Smith & Schindler, 2009) of Lake Victoria began as early as the 1920s in response to land use change within the catchment (Hecky et al., 2010; Njagi et al., 2022; Verschuren et al., 2002). Further complicating the observed ecological changes, higher than average rainfall and outflow damming at Jinja in the early 1960s led to a sustained 2m increase in water level (Fig. 6.2A). Accelerated population growth (Fig. 3.2B) led to increased agriculture, urbanization, and deforestation, which culminated in substantial nutrient enrichment to the lake (Fig. 6.2C–D; Hecky et al., 1993). Subsequently, phytoplankton production increased and shifted to greater cyanobacterial dominance (Hecky et al., 1993; Verschuren et al., 2002). Increased productivity led to decreased water transparency and decreased bottom water oxygenation, which in turn impacted habitat suitability for many fish species (Hecky et al., 1994; Kaufman, 1992; Seehausen et al., 1997).

There have been several significant changes in Lake Victoria's fish community that have been documented over the past century, most notably of which are the decline in the species diversity and biomass of haplochromine cichlid fishes (Fig. 6.2E) and the introduction and population expansion of Nile perch (Fig. 6.2F). Fisheries records from the 1960s (compiled in Fig. 6.1E), suggest that endemic haplochromine cichlids constituted >80% of total fish biomass in Mwanza Gulf (Kudhongania & Cordone, 1974), and this biomass constituted more than 120 different species in the Mwanza Gulf alone (Witte et al., 1992). However, there was a major decrease in haplochromine biomass and diversity in the 1980-90s, that has several possible underlying causes, including i) reduced habitat availability, particularly in the shallower inshore gulfs where the effects of eutrophication have been more intense (Mugidde, 1993), ii) intensive fishing pressures (van Zwieten et al., 2016; Witte et al., 1992), and iii) the introduction and later population explosion of Nile perch (*Lates niloticus*; a large piscivorous predator) along with the early loss of piscivorous haplochromines that feed on juvenile Nile perch (Witte et al., 2007).

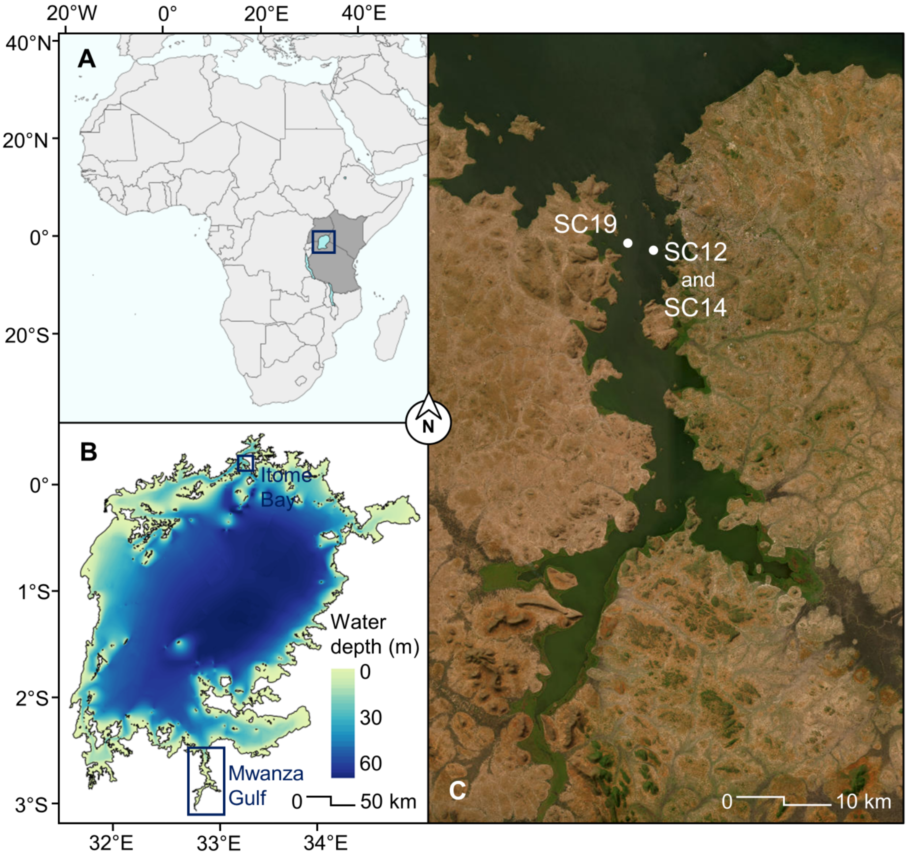

FIGURE 6.1: **(A)** The African continent with Lake Victoria. **(B)** Bathymetry of Lake Victoria and location of the Mwanza Gulf estuary. **(C)** Satellite imagery (2018–2023) of the Mwanza Gulf (ESRI, Maxar, Earthstar Geographics, and the GIS User Community) with coring locations marked with white circles.

Another major change in the fish community starting in the 1980s was the population increase of the native cyprinid, dagaa (*Rastrineobola argentea*, a small zooplanktivore), which may have occurred in response to reduced competition from the declining haplochromine cichlid biomass and the loss of predatory haplochromines (Goldschmidt & Witte, 1992; Wanink, 1999). Some recovery of the haplochromine cichlid biomass has been observed in the past decades (Fig. 6.2E), but much of the species diversity remains lost (Kishe-Machumu et al., 2015; Witte et al., 2000).

Despite intensive research on Lake Victoria's fish community in the past few decades (Kolding et al., 2014; van Zwieten et al., 2016), there is limited empirical data to provide insight into changes in the phytoplankton and zooplankton communities over the past century. In the absence of lake monitoring data, analysis of lake sediments using photosynthetic pigment biomarker concentrations (Leavitt & Hodgson, 2001) and subfossil remains of Cladocera and *Chaoborus* aquatic insect larvae (Korhola & Rautio, 2001; Verschuren et al., 2002) can provide insights into past phytoplankton and zooplankton community structure (i.e. abundance and taxonomic composition). For example, such reconstructions can be useful for identifying how the timing of changes in plankton community structure relate to changes in lake productivity and fish community structure (Skov et al., 2010).

In order to elucidate the impact of anthropogenic eutrophication on food web dynamics of Lake Victoria, we examined a wide range of paleolimnological indicators from two coring sites located in the Mwanza Gulf (Fig. 6.1). We used multiple biogeochemical proxies to provide insight into potential changes in nutrient availability. Sedimentary photosynthetic pigments were measured as an indicator of past phytoplankton community composition and total algal biomass. Lastly, plankton community structure was explored using sedimentary cladoceran microfossils, and related to survey records of fish abundance. Our main objectives were to: **(1)** investigate the onset of anthropogenic eutrophication and associated ecological changes in the Mwanza Gulf over the past century, and **(2)** examine the temporal changes in the zooplankton and zoobenthos assemblage in relation to changes in primary production and fish community structure (Fig. 6.2E,F).

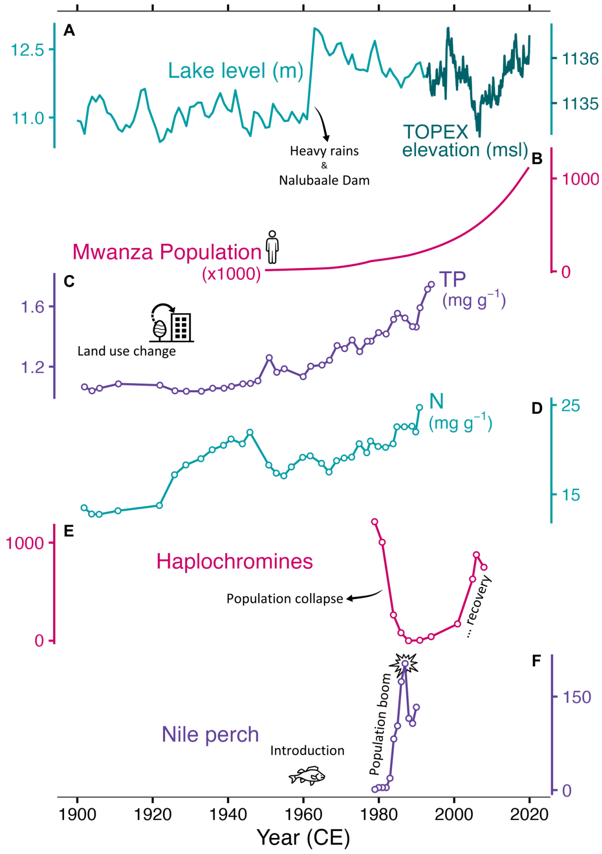

FIGURE 6.2: Time series data collected for Lake Victoria, including lake level monitoring (**A**; 1900–2023), the population of Mwanza City (**B**; 1950–2023), weight concentrations of nutrients (**C–D**; 1900–2000), and mean number of key fish taxa caught in fish trawls in Mwanza Gulf (**E–F**; 1979–2008). Lake levels were adapted from Levêque (2017) (m above Nalubaale Dam gauge; light teal line) and TOPEX satellite lake elevation observations (m above sea level, dark teal line). Population estimates of Mwanza were obtained from the United Nations World Urbanization Prospects (DESA, 2018). Sediment extracted nutrient concentrations (TP, total phosphorus; N, total fixed nitrogen) were adapted from Hecky et al. (2010) and measured from a nearshore sediment core collected from Itome Bay (Uganda). Fish survey data was obtained from Natugonza et al. (2021).

6.2 Materials and methods

6.2.1 Study site description

Located in equatorial eastern Africa, Lake Victoria (Fig. 6.1) is the world's largest tropical lake (surface area = 68,800 km², mean depth = 40 m). The lake is well-known as a biodiversity hotspot, featuring a prolific fish community of over 500 haplochromine cichlid species (Genner et al., 2004). Previous paleolimnological research has investigated eutrophication in northern Lake Victoria (Hecky et al., 2010; Njagi et al., 2022; Verschuren et al., 2002) but its impact in southern inshore areas of Lake Victoria remains understudied. Specifically, the Mwanza Gulf (Fig. 6.1; 60 km long, 2.5–11 km wide) currently receives the highest daily municipal water pollution within Tanzania (Juma et al., 2014). The composition and abundance of phytoplankton in Mwanza Gulf varies from that observed in the open water and northern gulfs (Frank et al., 2023). The surrounding land is primarily agricultural (>60%) and urban (~16%), with less than ~5% remaining as unconverted wetlands and woodland (Cornelissen et al., 2014). Non-native Nile perch and water hyacinth (*Eichhornia crassipes*, a free-floating macrophyte) were first reported in the Mwanza Gulf in 1961 (Pringle, 2005) and 1990 (Witte et al., 1995), respectively. However, the Nile perch population remained low until the early 1980s when the population increased exponentially (Witte et al., 1992).

6.2.2 Sediment core collection and subsampling

Sediment cores were collected in 2018 from two sites in the Mwanza Gulf using a UWITEC gravity corer (60 mm internal diameter; Fig. 6.1C). Two of the cores were collected as a paired set (SC12 and SC14, lengths = 37 cm and 28 cm, respectively) at the same coring location (2°33.473′ S, 32°52.470′ E) with a water depth of 14.5 m, whereas the third core (SC19, length = 47 cm) was collected on the opposite side of the gulf (2°33.015′ S, 32°51.023′ E) at a water depth of 10.5 m. Cores were split lengthwise and the core face was scanned using hyperspectral imaging (HSI) and x-ray fluorescence (XRF) techniques. Core halves were wet subsampled contiguously in 1–2 cm intervals depending on the required sediment volume for the analysis.

6.2.3 Geochronological dating

Sediment samples from the cores SC12 and SC19 were analyzed for ^{137}Cs and ^{226}Ra using γ-spectrometry and for ^{210}Pb (via ^{210}Po) by alpha-spectrometry. ^{226}Ra measurements were difficult due to small sample mass (0.4–0.8 g) and provided unstable results; thus, constant supported ^{210}Pb activities were calculated from the mean for the lowermost parts of the core profiles. Sediment ages were modeled using the Bayesian plum model (Tables S6.1, S6.2; Aquino-López et al., 2018). Additionally, we tested the sensitivity of the age-depth model choice by comparing the plum ages with the Constant Flux Constant Sedimentation (CFCS) and Constant Rate of Supply (CRS) age models (Fig. S6.1; Appleby & Oldfield, 1978). SC14 was stratigraphically correlated with the SC12 chronology based on hyperspectral-inferred total chloropigment (TChl) profiles, with linear interpolation used to assign dates between correlation points (Fig. S6.2).

6.2.4 Biogeochemical indicators

Biogeochemical methods included scanning the surface of split core halves with HSI and XRF techniques. HSI was used to examine changes in total chloropigments in the sediment (TChl: Chlorophyll *a*, *b*, and derivatives; Butz et al., 2015). All cores were scanned with a Specim Single Core Scanner system (Spectral Imaging Ltd., Oulu, Finland) equipped with a Specim PFD-xx-V10E camera (400–1000 nm). Relative absorption band depth index ($RABD_{655\text{-}680}$) was used to quantify total chlorophylls and colored derivatives.

X-ray fluorescence (XRF) was carried out to assess changes in the elemental composition of sediments indicative of major shifts in the lake environment. Scans were performed using an ITRAX (Cox Ltd., Sweden) with a chromium anode at 50 mA, 30 kV, and 30 seconds integration time over 0.5 cm intervals.

Sequential phosphorus (P) extraction protocol for SC12 and SC19 followed the protocol developed by the Standards, Measurements, and Testing (SMT) program (Ruban et al., 2001) with modifications following Tu et al. (2021). Three independent extractions using NaOH and HCl were completed to measure five P fractions: non-apatite inorganic P (hereafter referred to as Fe–P), calcium phosphate apatite (AP), inorganic P (IP), organic P (OP), and total P (TP). P concentrations in unfiltered samples were measured spectrophotometrically (Shimadzu UV-1800) with the malachite green method at an absorbance of 610 nm (Ohno & Zibilske, 1991).

Total carbon and nitrogen isotope analyses (TC%, TN %, $\delta^{13}C$, $\delta^{15}N$) were undertaken to evaluate shifts in trophic state conditions through time. Sediment subsamples were freeze-dried, homogenized, and weighed into tin capsules. Samples were then measured via combustion using a ThermoFisher Flash-EA 1112 coupled with a Conflo IV interface to a ThermoFisher DeltaV isotope ratio mass spectrometer. Isotopic compositions are reported in conventional delta notation relative to the international standards (Vienna Pee Dee Belemnite (V-PDB) and atmospheric N_2 (AIR). Signatures of $\delta^{13}C$ were corrected for the Suess effect (Fig. S6.3) following Verburg (2007). TC corresponds to total organic carbon as prior tests indicated inorganic carbon was absent in sediment samples.

6.2.5 Photosynthetic pigments

Sedimentary pigments were extracted from ~200 mg dry homogenized sediment following Sanchini and Grosjean (2020). Extracts were quantified using the methodology of Lami et al. (2000, 1994) by high performance liquid chromatography (HPLC). Analysis was restricted to taxonomically diagnostic pigments (Table 6.1). The chlorophyll *a* preservation index (CPI) was calculated as the ratio of Chl *a* to the sum of Chl *a* and derivatives, with low values indicating poor preservation (Buchaca & Catalan, 2008).

6.2.6 Zooplankton microfossils

The concentration of zooplankton microfossils (calculated as the number of individuals per volume of wet sediment) was determined from SC14 subsamples. The volume of sediment for each subsample was measured and subsamples were then wet sieved through a 38-μm mesh.

Lycopodium clavatum marker spores (mean number of spores = 9666, σ = 671; Lund University, Batch 3862) were dissolved in each subsample to assess the proportion of sediment examined. While ensuring the sample was adequately mixed, the solution was permanently mounted on glass slides and each slide was examined across its entirety using bright-field illumination on a compound microscope at 200–400x. Cladoceran remains were identified to the most detailed taxonomic level possible and counted separately (King et al., 2024b; Szeroczyńska & Sarmaja-Korjonen, 2007). The minimum number of individuals was determined by the most abundant body part of each taxon (Zharov et al., 2022).

TABLE 6.1: List of indicators and their taxonomic affiliation and/or interpretation

Trophic level	Indicator	Taxonomic affiliation and ecological interpretation
Phytoplankton (photosynthetic pigments)	β,β-carotene	All primary producers
	Chlorophyll *a*	All primary producers (sum of isomers)
	Pheophytin *a*	Chl *a* derivative (sum of isomers)
	Pheophorbide *a*	Chl *a* derivative (sum of isomers)
	Alloxanthin	Cryptophytes
	Diatoxanthin	Diatoms
	Diadinoxanthin	Diatoms, dinoflagellates, chrysophytes
	Dinoxanthin	Dinoflagellates & chrysophytes
	Peridinin	Dinoflagellates
	Lutein	Chlorophytes
	Echinenone	Total cyanobacteria
	Canthaxanthin	Colonial cyanobacteria
	Myxoxanthophyll*	Cyanobacteria
	Oscillaxanthin	Cyanobacteria (Oscillatoria)
	Zeaxanthin	Carotenoid characteristic of cyanobacteria
Zooplankton (macrofossils)	Cladocera: *Alona*	Littoral, scraper feeders (Fryer, 1968)
	Chydorus	Littoral, scraper feeders (Fryer, 1968)
	Bosmina	Planktonic, selective feeders (Korhola & Rautio, 2001)
	Diptera: *Chaoborus*	Planktonic larvae with diel vertical migration, predatory (Dawidowicz et al., 1990)

6.2.7 Statistical analyses

Stratigraphically constrained cluster analysis (CONISS; Grimm, 1987) on the SC12 pigment dataset identified the timing of shifts between distinct primary producer assemblages. Prior to clustering, pigment concentrations were log-transformed and scaled to a mean of 0. Zone determination used a broken-stick model (Bennett, 1996). SC19 pigments were not clustered due to deeper sediment mixing. Randomized intervention analysis (RIA; Carpenter et al., 1988) of the pigment and zooplankton assessed changes in the mean associated with the onset of eutrophication determined from pigment clustering. Intervention points at 14 cm, 18 cm, or 26 cm for SC14, SC12, and SC19, respectively, were based on the geochronological layers for 1920 CE (Common Era). The analysis performed one thousand random permutations of each time series and calculated the distribution of the mean difference before and after 1920 for each metric (R Core Team 2022, version 4.2.2). Significance levels (p-values) were calculated as the proportion of randomized mean differences equal to or exceeding the observed intervention effect in absolute value.

6.3 Results

6.3.1 Geochronology

Exponential decline of excess ^{210}Pb was observed in both cores and reach supported ^{210}Pb at 25 cm (SC12) and 35 cm (SC19), respectively (Fig. 6.3). Sediment disturbance and/or bioturbation was inferred from declining ^{210}Pb concentrations in the uppermost 4 cm of SC12 and 5 cm of SC19. Additionally, the section from 5 to 15 cm in SC19 shows significant variations in excess ^{210}Pb activities indicating deeper sediment disturbances, which could be explained by shallower water depth. Most of our subsequent analyses focused on SC12 due to the lesser degree of sediment disturbance. Age-depth models extended back to ~1900 CE (± 9 years), with age estimates prior to this year having large uncertainties (Fig. 6.3). Given the relative agreement between modeling approaches (Fig. S6.1), we proceeded using the Bayesian *plum* model. This model aligns well with the range of the most likely age-depth distribution. Concentrations of ^{137}Cs in the sediments were not sufficient to constrain either core chronology, which is typical for tropical African lakes (Walling & He, 2000). Thus, downcore ^{137}Cs concentrations (Fig. 6.3) were attributed to post-depositional diffusion through pore waters (Klaminder et al., 2012) or sediment mixing.

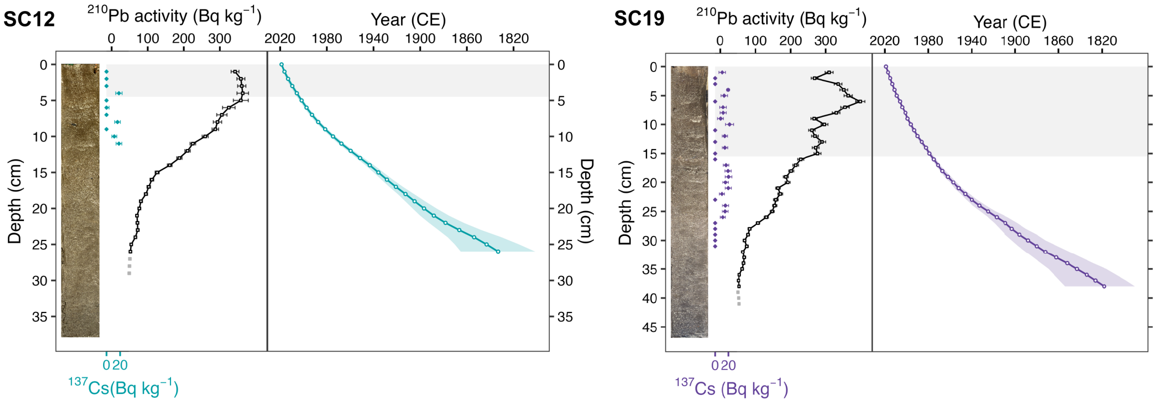

FIGURE 6.3: Activity profiles of total ^{210}Pb with error bars (black open squares) and ^{137}Cs (diamonds), measured throughout SC12 (teal) and SC19 (purple). The lowermost parts of the profiles indicate the supported ^{210}Pb (gray filled squares). Age-depth models were calculated for SC12 and SC19 based on the Bayesian *plum* model (Aquino-López et al., 2020); 95% confidence interval indicated by shaded ribbon). Gray shading indicates core layers with turbated sediment.

6.3.2 Biogeochemical and isotopic sediment composition over time

Mwanza Gulf cores showed a consistent pattern of nutrient enrichment and increased productivity over the past century. TChl index values remained low until the 1920s, followed by a rapid increase until peaking around 1985 and subsequently stabilizing (Fig.6.4). Values of lithogenic material (Ti, Zr, K, Fe, Si) remained relatively stable over the past century, while organic material (Br) increased after 1920 CE (Fig. 6.5). Atomic ratios of TC:TN (range = 9.3–11.0) exhibited decreasing trends in both cores over the past century (Fig. 6.5). Value of δ^{15}N displayed contrasting patterns between cores, increasing in SC12 (range = 0.8–1.8‰) and decreasing in SC19 (range = 0.4–1.3‰). Similarly, Suess-corrected δ^{13}C values decreased gradually until the early-1960s in both cores, and subsequently exhibited differing trends with further decreases observed in SC19 and increased values in SC12 (Fig. 5.5). All P fractions exhibited increasing trends over time. Among these fractions, OP and Fe–P demonstrated the most substantial rises, significantly contributing to the overall TP increase. TP concentrations in the sediments ranged from 538.2 to 1395.9 $\mu g/g_{d.s.}$ and 340.8 to 2225.5 $\mu g/g_{d.s}$ in SC12 and SC19, respectively.

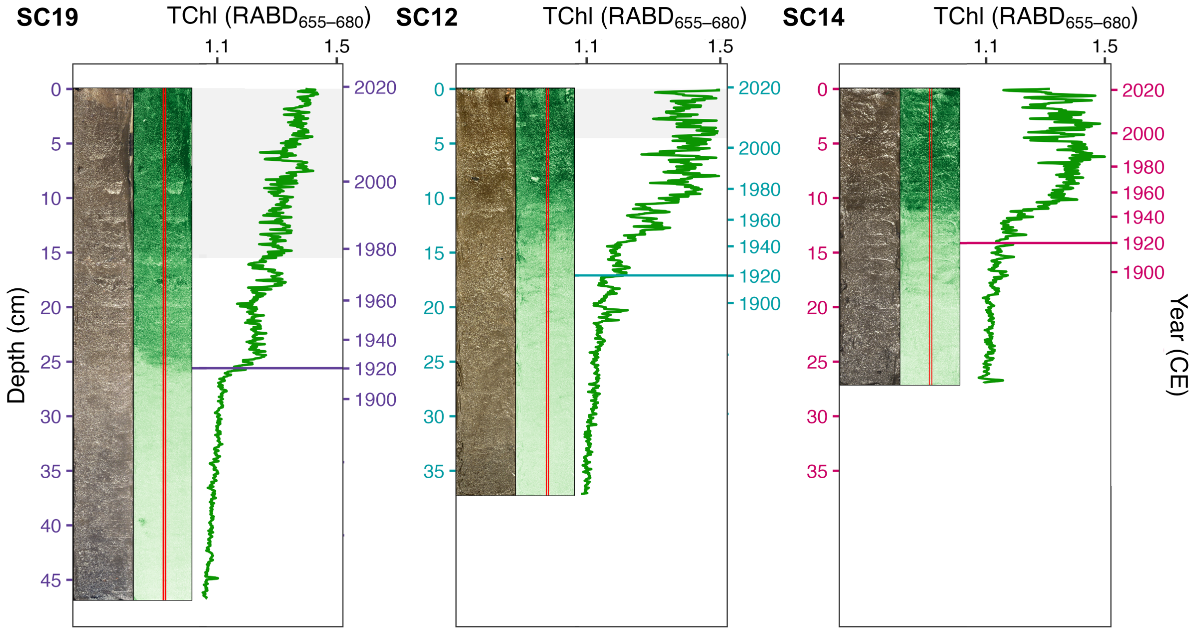

FIGURE 6.4: Color photographs of split core faces, colorized image for chloropigment stratigraphy and total chloropigment (TChl) moving average (k = 13 samples) profiles of SC19 (purple), SC12 (teal), and SC14 (pink). Solid horizontal lines indicate the year 1920 CE (± 7 yrs, 95% CI) based on the chronology of each core, and gray shading indicates core parts with turbated sediment.

6.3.3 Food web responses to eutrophication (photosynthetic pigments and zooplankton)

Photosynthetic pigments displayed a trend of increasingly elevated relative concentrations following the onset of eutrophication, regardless of increasing flux after ~1986 CE (Figs. 6.6; S6.4). Most pigments were detected in both SC12 and SC19, with the exception of β,β-carotene and peridin in SC12, and alloxanthin in SC19. CONISS revealed three zones consisting of distinct pigment assemblages: pre-eutrophication (prior to 1920 CE), onset of eutrophication with increases of most pigments (1920–1990 CE), and sustained eutrophication with cyanobacterial dominance (1990 CE–present). RIA indicated mean concentrations increased to values ~2–10x times higher than the low stable concentrations observed prior to 1920 (Figs. S6.5, S6.6, and Table S6.3).

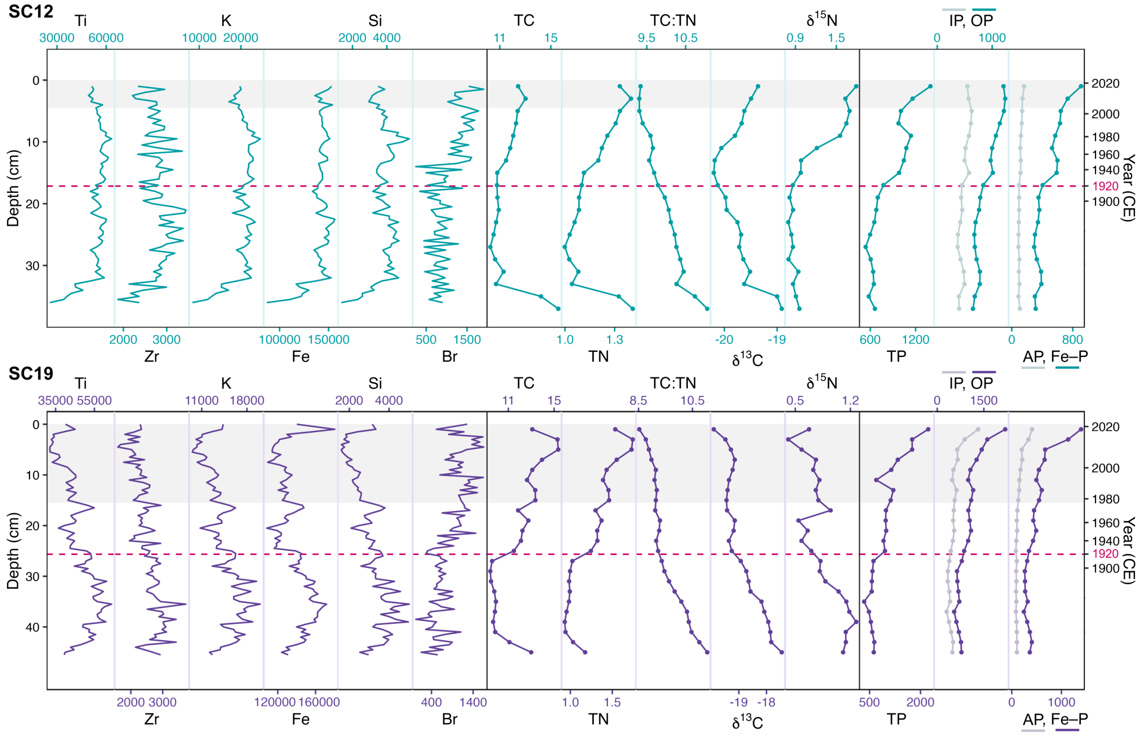

FIGURE 6.5: Biogeochemical proxies analyzed in SC12 (teal) and SC19 (purple), including: XRF (Ti, Zr, K, Si, Br; total counts), carbon and nitrogen isotope geochemistry (TC, %; TN, %; C:N; Suess-corrected δ^{13}C, ‰; δ^{15}N, ‰), and phosphorus concentrations (TP, IP, OP, AP, Fe–P; µg P g^{-1} $_{\text{d.s.}}$). Dashed horizontal lines indicate the year 1920 (± 7 yrs, 95% CI), and gray shading indicates core parts with turbated sediment.

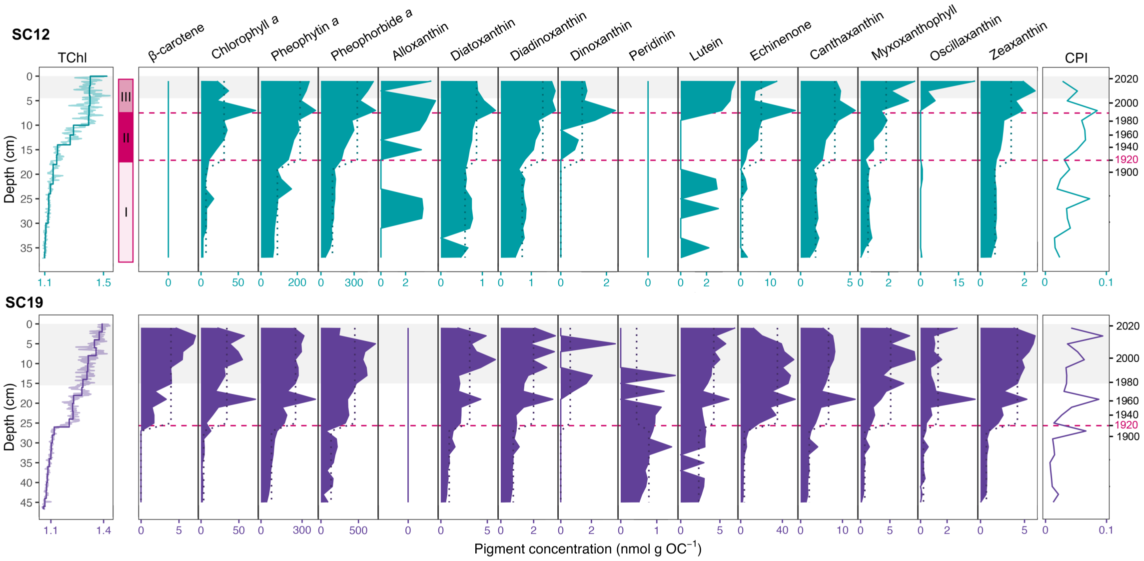

FIGURE 6.6: Binned (2 cm intervals) hyperspectral total chloropigments (TChl) and relative concentrations of photosynthetic pigments (nmol g OC^{-1}), and chlorophyll preservation index (CPI) measured throughout SC12 and SC19. Zone (I-III) differentiation was based on cluster analysis. Dashed horizontal lines indicate 1920 (± 7 yrs, 95% CI) and 1990 (± 2 yrs), and gray shading indicates core parts with turbated sediment. Dotted lines indicate significant differences between means before and after 1920. Pigment associations are listed in Table 6.1

The zooplankton of SC14 consisted of three genera of cladoceran taxa, including benthic chydorids (*Alona* and *Chydorus*) and planktonic *Bosmina*, as well as *Chaoborus* mandibles (Fig. 6.7). All cladoceran taxa exhibited steadily high concentrations until the early-1900s followed by a major decrease around ~1960 (± 5 yrs, 95% CI) despite consistent sampling effort (Fig. S6.7) and changes in sedimentation rates (Fig. S6.8). RIA suggests a significant change in the cladoceran assemblage after 1920, exhibiting decreased mean concentrations by ~15–40% (Fig. S6.9; Table S6.4). Notably, *Bosmina* remains were consistently present and a subsequent increase, whereas *Alona* and *Chydorus* remain at low abundances. *Chaoborus* mandibles were rarely encountered, with at most one individual being found per subsample (Fig. S6.7); thus, no significant change was detected by RIA.

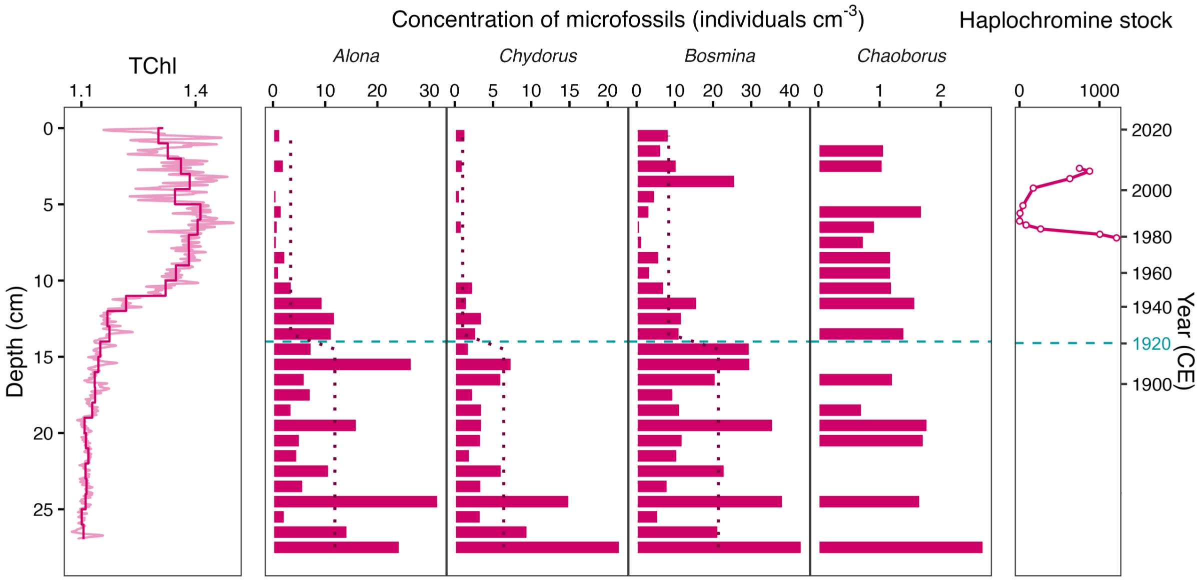

FIGURE 6.7: Binned (1-cm intervals) hyperspectral total chloropigments (TChl) and concentration of zooplankton microfossils counted throughout SC14, as well as mean haplochromine stock from trawling surveys (Natugonza et al., 2021). Dashed horizontal line indicates 1920 CE (± 7 yrs, 95% CI). Dotted lines indicate significant differences between means before and after 1920

6.4 Discussion

Our results suggest that anthropogenic eutrophication of Lake Victoria and the increase in lake level (Fig. 6.2) have had major impacts in the plankton communities of Mwanza Gulf. Nutrient enrichment (P and N) began ~1920 CE at Mwanza Gulf and rapidly caused increased primary production. Analysis of photosynthetic pigments revealed three stratigraphic zones, including pre-eutrophication (prior to 1920), the onset of eutrophication (1920–1990), and sustained eutrophication (1990–present), that featured increasingly higher pigment concentrations. In the 1960s, the cladoceran assemblage, particularly the benthic groups, collapsed at the site of SC14 concurrent with the 2 m increase in water level, and then partially recovered following the recovery of the haplochromine cichlid population in the 1990s.

6.4.1 Reconstructing anthropogenic eutrophication

Nutrient enrichment and excessive algal growth were evident in Mwanza Gulf, marked by a rapid increase of nutrients (P) and productivity (TChl) around the core depths representative of ~1920 (Fig. 6.4). Biostratigraphical analysis of SC12 photosynthetic pigments identified a discernible shift in assemblage at ~16–18 cm, corresponding with ~1920 (±15 yrs). While the 1920 timing of N enrichment is consistent with previous observations of surface cores, enhanced P deposition began earlier in Mwanza Gulf compared to northern inshore areas in which it only began to increase in the 1940s (Hecky et al., 2010). TP and bioavailable P (OP and Fe–P) concentrations exhibited an increasing trend since ~1920, contrasting with low stable values of AP (Fig. 6.5). Further increases in TP until present are consistent with estimates indicating a >100% increase in surface water TP concentrations between the 1960s and 1990s (Hecky et al., 2010). Stability of AP (non-bioavailable in sediments; Tu et al., 2021) and lithogenic material (Ti, Zr, K, Fe) suggests that changes in organic sediment components (e.g., OP and Br) are likely driven by increased primary productivity and autochthonous organic matter deposition rather than detrital input. Altogether, this indicates an earlier onset of eutrophication in Mwanza Gulf compared to northern Lake Victoria and highlights the contextual nature of spatial and temporal lake ecosystem responses to anthropogenic eutrophication.

Concurrent with rising TN content in Mwanza Gulf, δ^{15}N in SC12 increased following the onset of eutrophication and further accelerated after the >2 m lake level rise in the 1960s (Fig. 6.2). The rise of δ^{15}N can be attributed to increased runoff of isotopically heavy nitrogen from sewage and waste material (Leavitt et al., 2006; Machiwa, 2010), which in turn promoted enhanced algal abundance (Bunting et al., 2007). Intensified use of the N pool from abundant phytoplankton, alongside the preferential use of isotopically lighter ^{14}N, would have led to lower fractionation and increased sedimentary δ^{15}N (Talbot, 2001). The magnitude of observed δ^{15}N increase (<1‰) may have been mitigated by proliferation of diazotrophic cyanobacteria (indicated by canthaxanthin; Fig. 6.6), which typically have δ^{15}N signatures of 0 ± 2‰(Talbot, 2001), similar to other tropical lakes (Rosenmeier et al., 2004). The contrasting δ^{15}N trend in SC19 remains puzzling and exemplifies the need for multiple cores to thoroughly ascertain the spatial variability of ecosystem dynamics.

Primary production in the Mwanza Gulf reached unprecedented levels in the history of the modern lake in the ~1980-90s and subsequently stabilized (Frank et al., 2023). Analysis of bulk organic matter using TC:TN ratios revealed steady declines (Fig. 6.5) consistent with increasing algal dominance. High ratios (>20) are typically indicative of vascular land plants, while lower ratios (5–8) represent plankton dominance (Finlay & Kendall, 2007; Meyers, 1994). Thus, declining ratios are typical of lakes experiencing shifts to turbid, phytoplankton-dominated conditions (e.g., King et al., 2024a). Despite its high cellulose content and rapid growth rate, the expansion of water hyacinth cover in 1990 is not reflected in the TC:TN ratio, which attests to the success of the rapid application of biological control agents and awareness campaigns (*Neochetina* weevils; Wilson et al., 2007). TC:TN ratios of Mwanza Gulf were well within the range (typically 8.3–14.6) indicative of moderate N-limitation (Hecky et al., 1993), which is consistent with previous reports of Lake Victoria (Talbot & Lærdal, 2000). At SC12, the reversal of the Suess-corrected δ^{13}C trend (Fig. 6.4) can also be attributed to increased primary production. Due to the preferential utilization of ^{12}C by phytoplankton, periods of low primary productivity will result in relatively low δ^{13}C (Wu et al., 2006). Conversely, periods of high primary productivity will lead to a depletion of ^{12}C in the C pool, and thus increased uptake of ^{13}C (Meyers & Teranes, 2001). Lastly, the obtained δ^{13}C values (Fig. 6.5) are typical of autotrophic lakes (>-27‰) and consistent with expectations for Lake Victoria (Verburg, 2007). The lack of increasing δ^{13}C in SC19 (Fig. 6.5) may result from higher sediment mixing compared to SC12 due to the shallower water depth, which may have stimulated selective preservation of specific fractions of organic matter (Lehmann et al., 2002).

6.4.2 Food web responses to eutrophication

Anthropogenic eutrophication led to major shifts in the algal (Fig. 6.6) and cladoceran (Fig. 6.7) assemblages of Mwanza Gulf. Despite low pigment preservation in tropical lakes (Buchaca et al., 2019), pigments have been used to successfully reconstruct major shifts in primary production in Lake Victoria (Wienhues et al., accepted). In Mwanza Gulf, pigment degradation remained relatively stable across the cores (CPI <0.1; Fig. 6.6). Thus, increased pigment deposition upcore likely reflects increased production rather than degradation.

Initial increases in total primary production around ~1920 (TChl) occurred gradually alongside increased nutrient loading (TP and TN). A doubling of phytoplankton production was similarly observed in northern inshore waters during this period (Mugidde, 1993).The majority of sedimentary pigments increased gradually starting around ~1920, suggesting that all analyzed taxonomic groups benefited from increased nutrient availability. Furthermore, the high-resolution TChl values effectively captured the fluctuations in total primary production over time in more detail (Fig. 6.4) than the pigment data. The phytoplankton assemblage remained dominated by diatoms as indicated by the continuous abundance of diatom-related pigments (diatoxanthin and diadinoxanthin), while the abundance of cyanobacteria-pigment canthaxanthin indicates that cyanobacteria were at least seasonally abundant.

The subsequent assemblage shift around ~1990 CE (± 2 years) indicates increasing dominance of cyanobacteria-related pigments, whereas diatom- and dinoflagellate-related pigments remained stable or decreased (diatoxanthin, diadinoxanthin, dinoxanthin) and remained most likely abundant at low levels (Fig. 6.6). The timing of this shift is consistent with phytoplankton monitoring data that indicates stabilization of phytoplankton abundance since the 1990s in the Mwanza Gulf (Frank et al., 2023). Accordingly, diatoms and cyanobacteria have been the main phytoplankton groups in the Mwanza Gulf, whereas chlorophytes have remained very low or absent. Shifts in primary production did not coincide with major changes in the cladoceran assemblage (Fig. 6.7). Some zooplankton taxa (e.g., copepods) are not preserved in lake sediments; thus, reductions in cladoceran abundances does not necessarily imply a reduction in overall zooplankton biomass. Despite the significant decline in cladocerans, the phytoplankton community did not exhibit a corresponding increase in biomass or productivity, suggesting increasing phytoplankton abundance was not the result of reduced cladoceran grazing pressure.

Abundances of all cladoceran taxa in Mwanza Gulf decreased substantially in the 1960s, possibly due to the cumulative impacts of lake-level rise and anthropogenic eutrophication. The parallel decline of both benthic chydorids and *Bosmina* (Fig. 6.7) suggests that depth-associated changes in habitat conditions, such as a shift of the littoral zone or loss of macrophyte habitat, could have contributed to the observed collapse of the cladoceran community. Changes in lake water depth can strongly influence cladoceran assemblages by altering the extent of littoral and pelagic habitats (Nevalainen et al., 2011). Benthic chydorids (e.g. *Alona* and *Chydorus*), although capable of open water migration, commonly inhabit clear, shallow waters with high macrophyte cover in other eastern African lakes (Verschuren et al., 2000). Comparatively, rising lake levels may have made planktonic *Bosmina* more vulnerable to predation by reducing refuge afforded by submerged open-water macrophytes (Iglesias et al., 2007). Together with the higher water levels, enhanced algal production in the Mwanza Gulf (Fig. 6.6) could have led to decreased water transparency (Verschuren et al., 2002) and light availability for littoral macrophytes (Natugonza et al., 2021). Turbid waters likely inhibited macrophyte establishment due to reduced light penetration and reduced suitable chydorid habitat (Whiteside & Swindoll, 1988). Alternatively, benthic chydorids may have moved into the newly established and inundated littoral environment and not been recovered at the core site due to spatial heterogeneity of cladoceran assemblages (e.g., Nevalainen, 2011). Interestingly, this cladoceran response preceded the collapse of haplochromine cichlids in the 1980s (Fig. 6.1) and is consistent with previous studies indicating higher nearshore and offshore abundances of cladocerans in the early 20th century compared to present (Mwebaza-Ndawula, 1994).

In addition to lake-level rise and eutrophication, interspecific competition as well as invertebrate and fish predation may have led to changes in the zooplankton assemblages of Lake Victoria over the past century (Black & Hairston, 1988; Branstrator et al., 2003). Discontinuous monitoring indicates that decreased cladoceran abundances in Mwanza Gulf were accompanied by increased cyclopoid copepod abundances, which are cladoceran predators (Wanink et al., 2002). Copepods, which make up high fractions of the contemporary zooplankton biomass in Lake Victoria, may have outcompeted small cladocerans as lake conditions changed, possibly due to greater hypoxia tolerance (Vanderploeg et al., 2009) or better predator avoidance (Semyalo et al., 2009). Furthermore, previous cores from northern Lake Victoria displayed a substantial post-1960s increase in *Chaoborus* abundances that occurred alongside decreasing cladoceran abundances (Bridgeman, 2001). We did not observe this pattern in our samples, which had relatively few *Chaoborus* remains due to the limited amount of sediment that we screened relative to other studies (Fig. S6.7; Quinlan & Smol, 2010). Therefore, further efforts are necessary to elucidate the temporal patterns of *Chaoborus* abundance and the predation pressure exerted on Cladocera and copepods in Mwanza Gulf.

Following the surge in Nile perch abundance, the replacement of zooplanktivorous haplochromines by dagaa as the dominant pelagic zooplanktivore in the 1980s (Gophen et al., 1995) could also have affected the zooplankton communities. Despite increased dagaa abundances, the overall biomass of zooplanktivores decreased, suggesting that overall predation pressures also decreased (Wanink et al., 2002). Whereas some studies have speculated that the shift in zooplankton assemblage is attributable to increased dagaa abundances (van Zwieten et al., 2016), our time series demonstrate that the collapse of cladocerans clearly predates changes in the fish community in Mwanza Gulf (Fig. 6.7). However, as nearshore turbidity improved in the 1990s (Sitoki et al., 2010), ongoing fishing pressures contributed to declines in Nile perch population and the recovery of haplochromines in the Mwanza Gulf (Witte et al., 2000). Zooplanktivores made up only ~10–20% of the haplochromine community prior to their decline, but were one of the dominant trophic guilds to rapidly resurge in the 1990s, constituting ~80% of the community (Witte et al., 2007). The concurrent increases in *Bosmina* (Fig. 6.7) suggest that the recovery of haplochromines may have released some of the controls (e.g., *Chaoborus* predation) limiting *Bosmina* abundance.

6.5 Conclusions

This study demonstrates that anthropogenic eutrophication profoundly altered planktonic community structure of Mwanza Gulf. Nutrient increases beginning in ~1920 promoted higher algal abundance but rising lake-levels in the ~1960s might have led to habitat alterations that triggered the decline of both benthic and pelagic cladocerans. The collapse of biomass and species diversity of endemic haplochromines and subsequent recovery of their biomass may have further impacted planktonic *Bosmina* through changes in predation pressure. The lack of a compensatory response in the phytoplankton community, whereby algal biomass increases with decreasing cladoceran abundance, suggests weak top-down control of the algal biomass by cladoceran grazing pressure. Altogether, this study helps unravel additional insights to the food web dynamics underlying anthropogenic eutrophication and the loss of fish stocks in Lake Victoria.

6.6 Acknowlegments

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Conflict of Interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available in Zenodo.

Declaration of contribution: LK and GW are equal contributors to this work and designated as co-first authors. Study conceptualization and design was led by LK, GW, BM, and MG. LK, GW, WT, and AL contributed to data collection. LK, GW, BM, and MG led the data analysis, interpretation and writing of the manuscript. All co-authors contributed to the data interpretation and writing process and approved the manuscript for submission.

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6.8 Supplementary Material

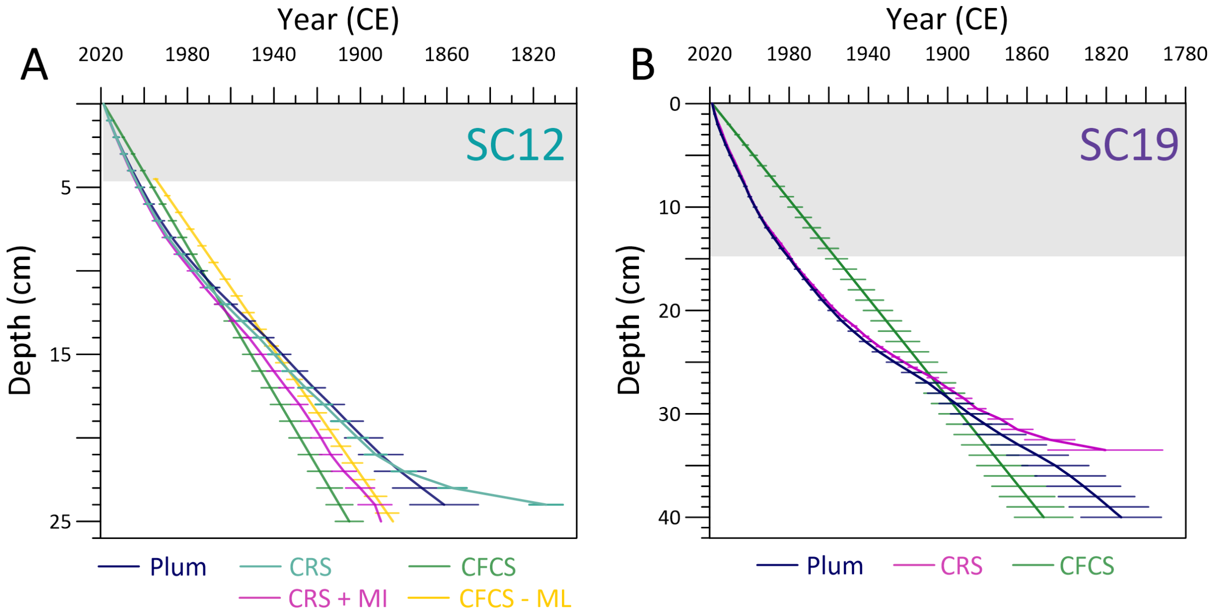

FIGURE S6.1: Alternative age-depth models considered for SC12 (A) and SC19 (B), including the Constant Rate of Supply (CRS), missing inventory corrected Constant Rate of Supply (CRS + MI), Constant Flux:Constant Sedimentation (CFCS), Constant Flux:Constant Sedimentation excluding the turbated layer (CFCS - ML), and Bayesian *plum* models. Gray areas indicate core layers with turbated sediment.

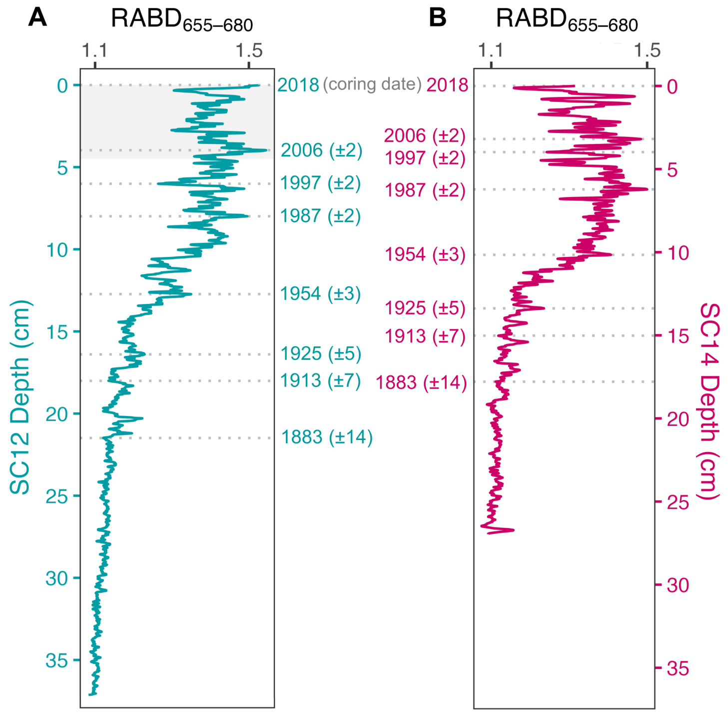

FIGURE S6.2: Correlation points between hyperspectral-inferred $RABD_{655\text{-}680}$ profiles used to apply the SC12 (A) chronology to its paired core, SC14 (B), with ages linearly interpolated between correlation points.

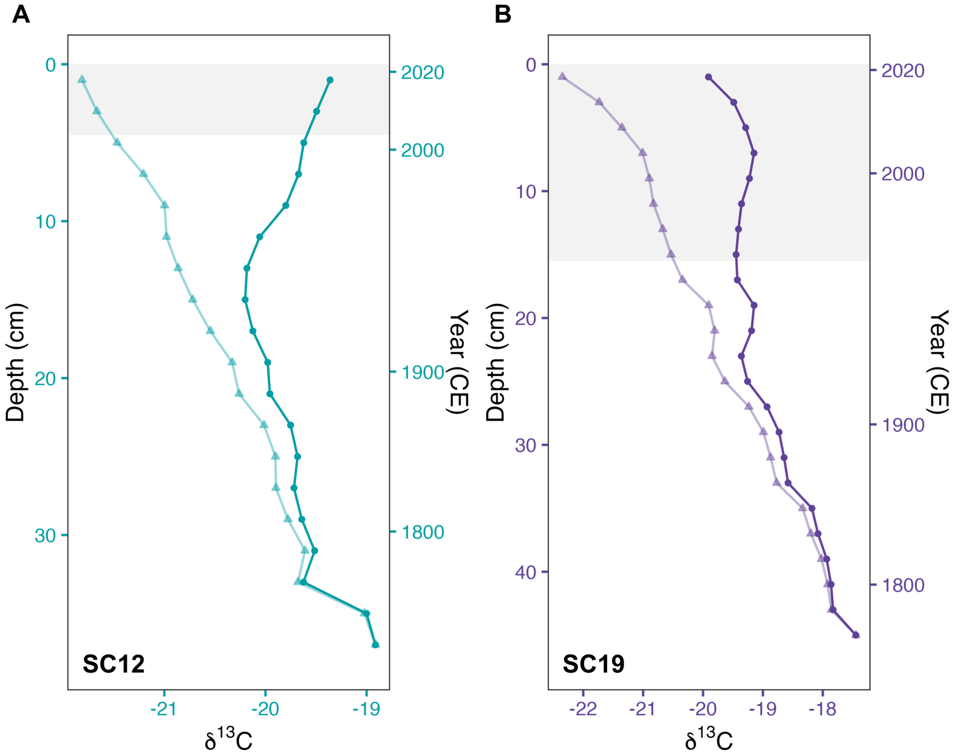

FIGURE S6.3: Suess-corrected δ^{13}C values (dark circles), following Verburg (2007), compared with original δ^{13}C signatures (light triangles) of SC12 (A) and SC19 (B).

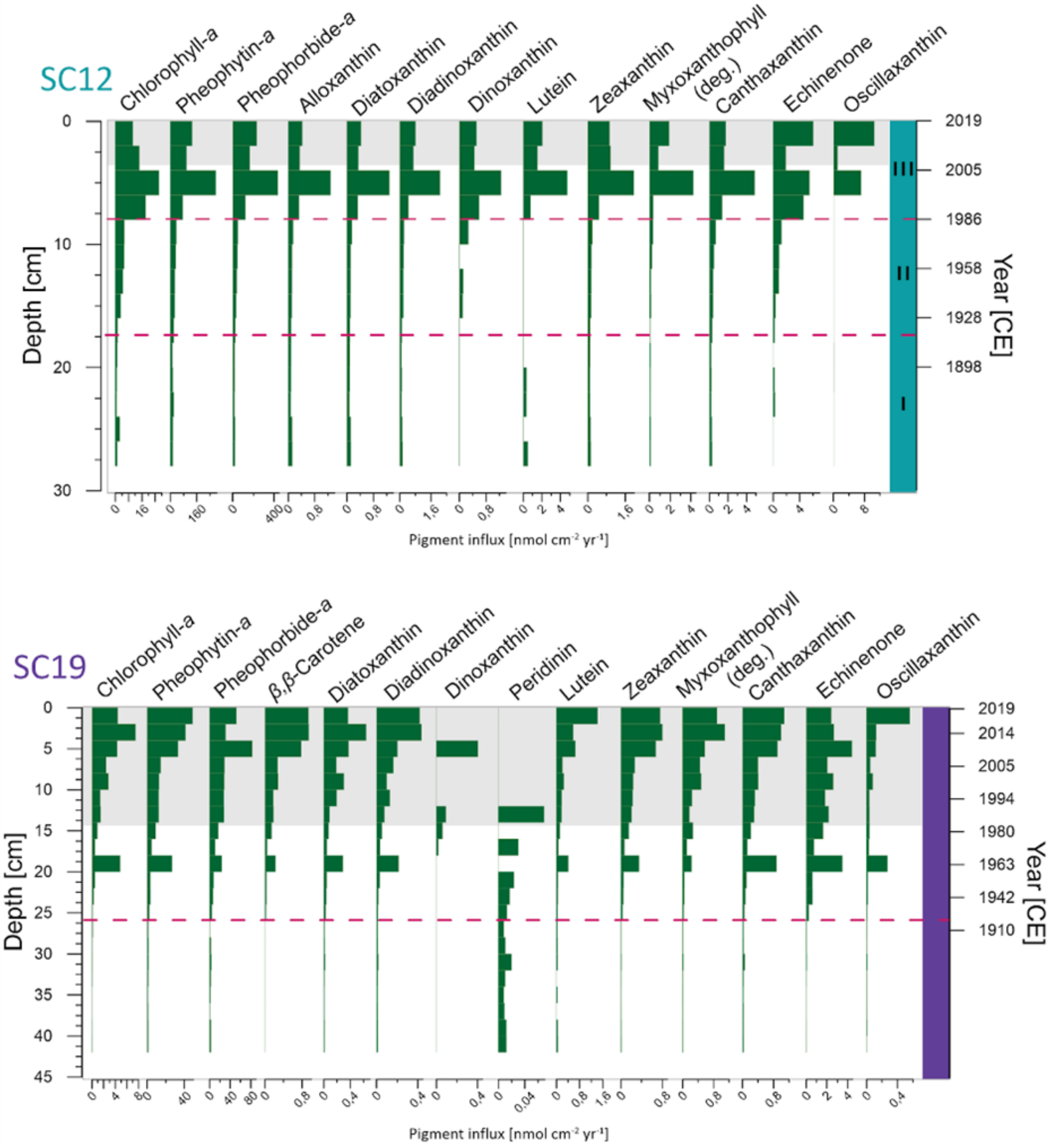

FIGURE S6.4: Pigment influxes for the cores SC12 and SC19.

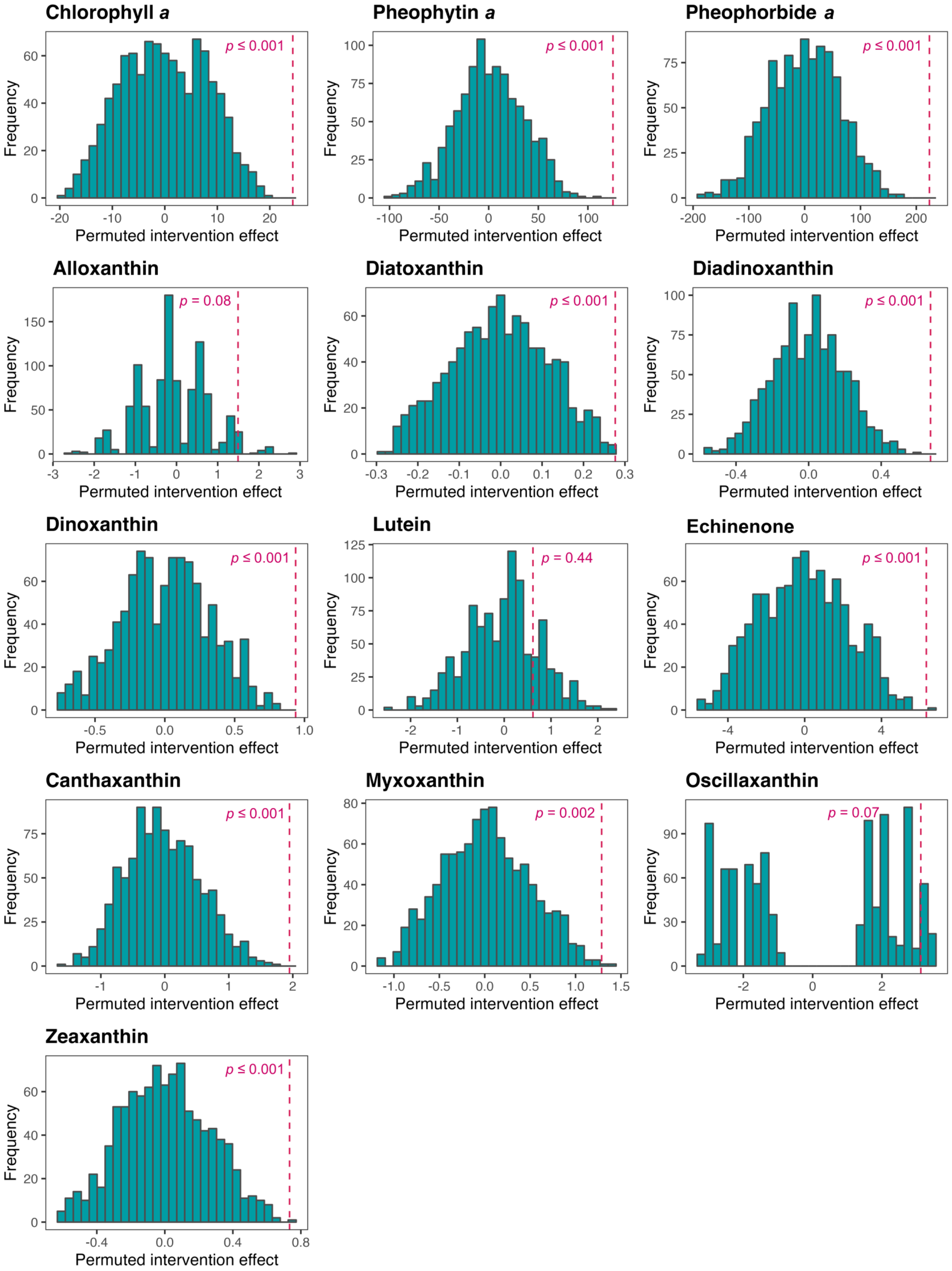

FIGURE S6.5: Intervention analysis of SC12 pigment concentrations using 18 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

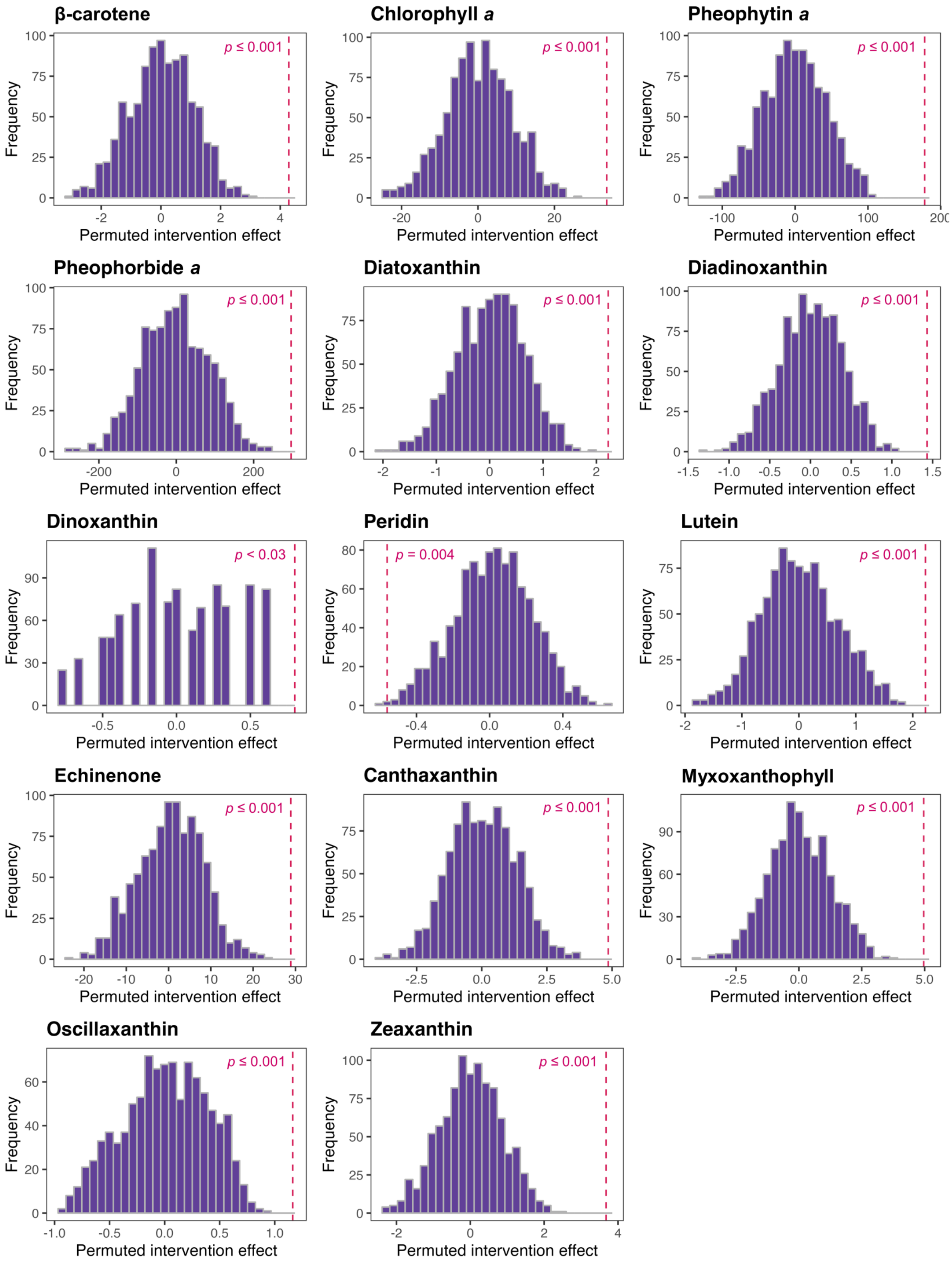

FIGURE S6.6: Intervention analysis of SC19 pigment concentrations using 26 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

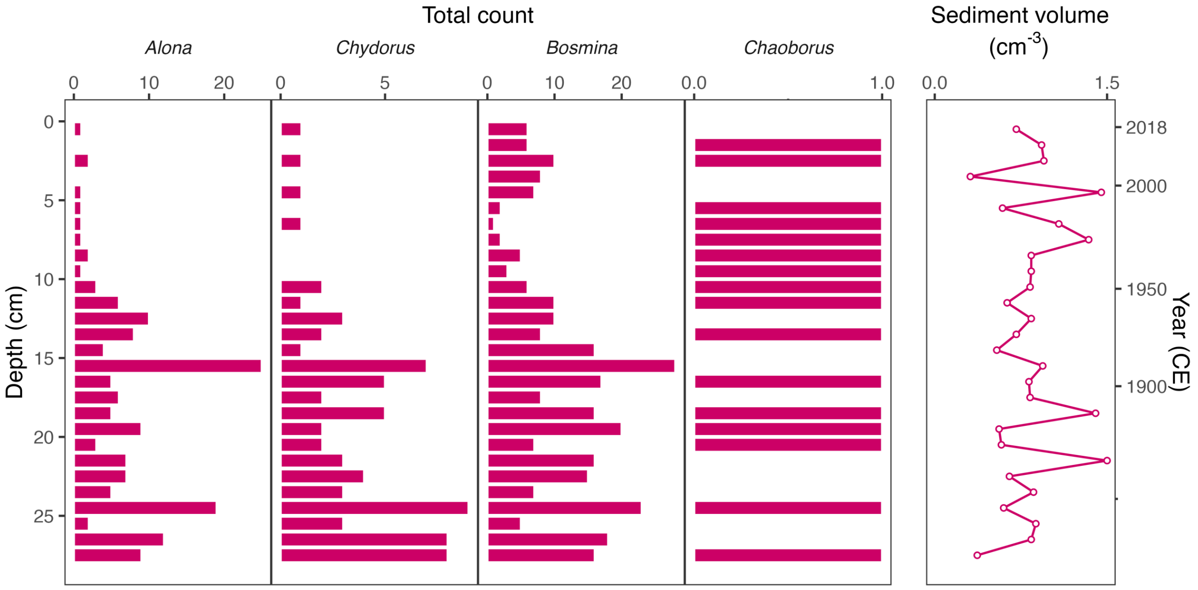

FIGURE S6.7: Total counts of Cladocera and *Chaoborus* individuals, determined by the minimum number of individuals possible given the most abundant body part of each taxon, and the total volume of sediment examined in each subsample.

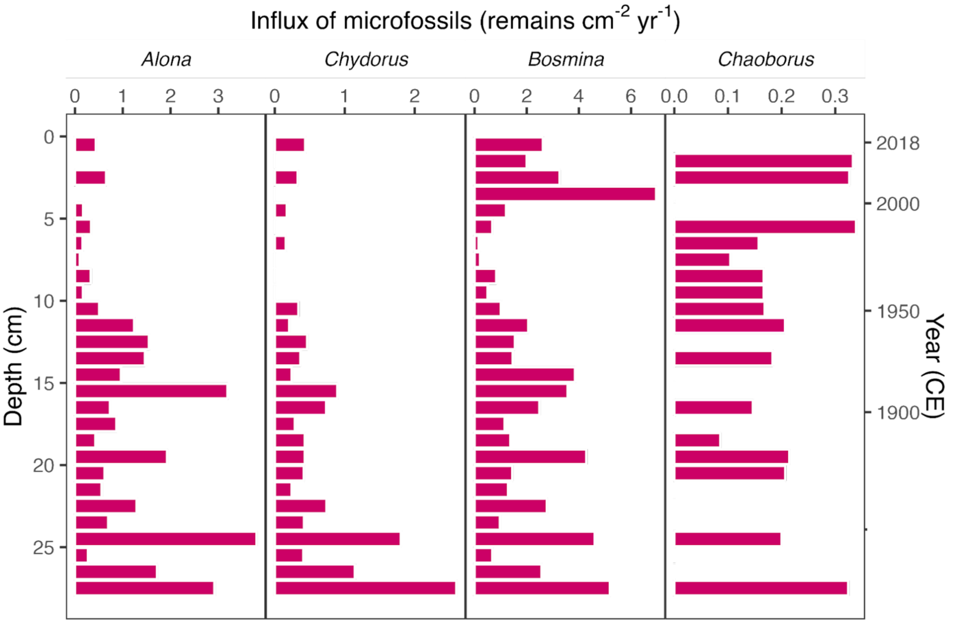

FIGURE S6.8: Influx of Cladocera and *Chaoborus* microfossils counted throughout SC14.

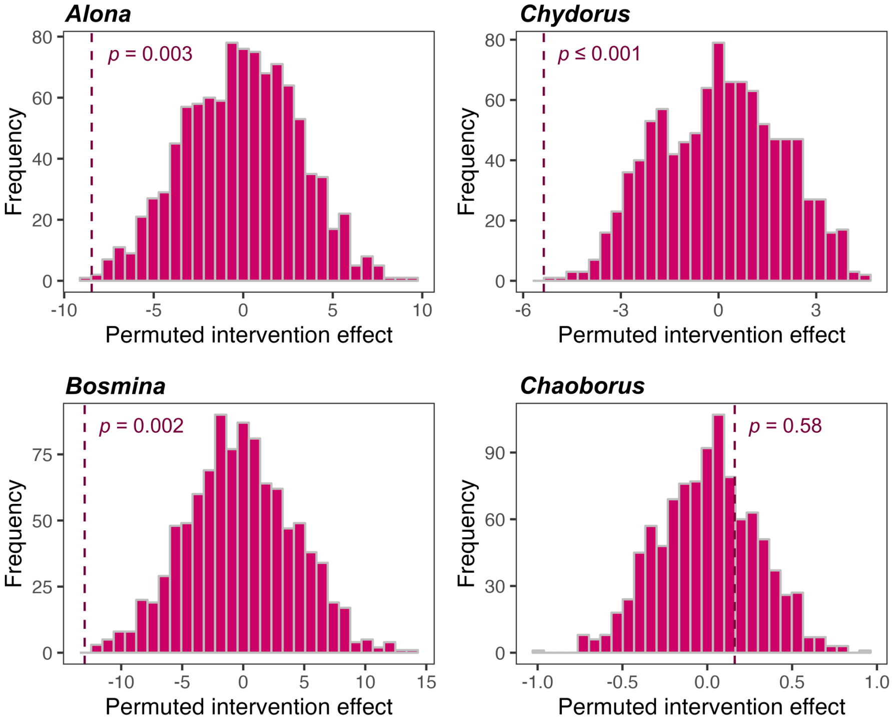

FIGURE S6.9: Intervention analysis of SC14 Cladocera and *Chaoborus* microfossil concentrations using 14 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

TABLE S6.1: Summary of SC12 core collected in October 2018 subsample data incorporated into the *plum* model, using a supported ^{210}Pb concentration of 48.3 (±4.7) Bq kg^{-1} (mean activity from the lowermost part of the core profile; excluding the bottom three samples)

LabID	Depth interval (cm)	Density (g cm^{-3})	^{210}Pb (Bq kg^{-1})	sd(^{210}Pb)
LV_SC12_1	0–1	0.006274	342.1	10.9
LV_SC12_2	1–2	0.012528	358.3	11.1
LV_SC12_3	2–3	0.012311	360.7	11.4
LV_SC12_4	3–4	0.011631	363.4	16
LV_SC12_5	4–5	0.011135	358.1	20.7
LV_SC12_6	5–6	0.011319	324.8	17.4
LV_SC12_7	6–7	0.011559	305.5	14.2
LV_SC12_8	7–8	0.011802	293.4	11.6
LV_SC12_9	8–9	0.011614	287.4	9.1
LV_SC12_10	9–10	0.012136	259.3	8.4
LV_SC12_11	10–11	0.012193	225.1	7.7
LV_SC12_12	11–12	0.011898	210.5	7.5
LV_SC12_13	12–13	0.010945	187.8	7.3
LV_SC12_14	13–14	0.010721	161	6.5
LV_SC12_15	14–15	0.010842	126.1	5.6
LV_SC12_16	15–16	0.010212	111.5	5.2
LV_SC12_17	16–17	0.010161	102.8	4.8
LV_SC12_18	17–18	0.010338	95	4.5
LV_SC12_19	18–19	0.00994	81.2	4.2
LV_SC12_20	19–20	0.009691	76.7	3.9
LV_SC12_21	20–21	0.009101	70.2	3.6
LV_SC12_22	21–22	0.009627	71.5	3.8
LV_SC12_23	22–23	0.00985	72.3	3.9
LV_SC12_24	23–24	0.009292	65.8	3.5
LV_SC12_25	24–25	0.009395	54.3	3.1
LV_SC12_26	25–26	0.00956	52	3.1
LV_SC12_27	26–27	0.009661	50.6	3.1
LV_SC12_28	27–28	0.009665	49.4	3.1
LV_SC12_29	28–29	0.009642	48.7	3.1
LV_SC12_31	30–31	0.019163	46.5	3.2
LV_SC12_33	32–33	0.018397	38.7	2.8
LV_SC12_35	34–35	0.017184	46.1	3.3

TABLE S6.2: Summary of SC19 core collected in October 2018 subsample data incorporated into the Bayesian *plum* model, using a supported ^{210}Pb concentration of 52.6 (±1.3) Bq kg^{-1} (mean activity from the lowermost part of the core profile).

LabID	Depth interval (cm)	Density (g cm^{-3})	^{210}Pb (Bq kg^{-1})	sd(^{210}Pb)
LV_SC19_1	0–1	0.002312	309.6	11.1
LV_SC19_2	1–2	0.004932	268.4	9.4
LV_SC19_3	2–3	0.004925	335	11.2
LV_SC19_4	3–4	0.004454	351.2	10.9
LV_SC19_5	4–5	0.004153	363.5	11.4
LV_SC19_6	5–6	0.004037	397.9	12.8
LV_SC19_7	6–7	0.004065	354.6	11.8
LV_SC19_8	7–8	0.004268	329.5	11.1
LV_SC19_9	8–9	0.004360	267.2	8.9
LV_SC19_10	9–10	0.004476	296.4	9.9
LV_SC19_11	10–11	0.004745	260.9	9.0
LV_SC19_12	11–12	0.004810	269.3	9.3
LV_SC19_13	12–13	0.004654	289.6	10.4
LV_SC19_14	13–14	0.004512	271.3	9.5
LV_SC19_15	14–15	0.004422	276.4	9.7
LV_SC19_16	15–16	0.004430	228	8.4
LV_SC19_17	16–17	0.004552	214	7.9
LV_SC19_18	17–18	0.004730	201.2	7.5
LV_SC19_19	18–19	0.004506	185.7	7.0
LV_SC19_20	19–20	0.004399	191.3	7.3
LV_SC19_21	20–21	0.004544	163.9	6.4
LV_SC19_22	21–22	0.004559	170.2	6.7
LV_SC19_23	22–23	0.004244	158	6.5
LV_SC19_24	23–24	0.004101	154.5	6.4
LV_SC19_25	24–25	0.004056	147.4	6.1
LV_SC19_26	25–26	0.004183	130.5	5.7
LV_SC19_27	26–27	0.004507	107.2	4.9
LV_SC19_28	27–28	0.004856	83.2	4.2
LV_SC19_29	28–29	0.005047	78.9	4.0
LV_SC19_30	29–30	0.005069	69.3	3.7
LV_SC19_31	30–31	0.005268	75.4	4.1
LV_SC19_32	31–32	0.005371	64.4	3.5
LV_SC19_33	32–33	0.005060	68.3	3.9
LV_SC19_34	33–34	0.00498	66.3	3.7
LV_SC19_35	34–35	0.005034	62.5	3.6
LV_SC19_36	35–36	0.005083	53.9	3.2
LV_SC19_37	36–37	0.005179	51.9	3.1
LV_SC19_38	37–38	0.005299	53.4	3.2
LV_SC19_39	38–39	0.005314	50.4	3.3
LV_SC19_40	39-40	0.005330	52.5	13.3
LV_SC19_41	40-41	0.005476	53.4	3.5

TABLE S6.3: Randomized intervention analysis results of photosynthetic pigments

	SC12			SC19		
Pigment	Pre-1920	Post-1920	p-value	Pre-1920	Post-1920	p-value
β,β-carotene	N/A	N/A	N/A	0	3.96	≤0.001
Chlorophyll *a*	6.63	31.01	≤0.001	3.63	34.16	≤0.001
Pheophytin *a*	90.46	215.72	≤0.001	77.45	252.7	≤0.001
Pheophorbide *a*	103.17	326.73	≤0.001	135.46	451.66	≤0.001
Alloxanthin	1	2.49	0.08	N/A	N/A	N/A
Diatoxanthin	0.58	0.86	≤0.001	0.91	3.12	≤0.001
Diadinoxanthin	0.7	1.37	≤0.001	0.76	1.99	≤0.001
Dinoxanthin	0	0.94	≤0.001	0	0.62	0.03
Peridin	N/A	N/A	N/A	0.78	0.44	0.004
Lutein	1.04	1.67	0.44	2.3	4.21	≤0.001
Echinenone	0.59	6.93	≤0.001	3.53	35.11	≤0.001
Canthaxanthin	1.51	3.46	≤0.001	2.06	6.67	≤0.001
Myxoxanthophyll	0.52	1.81	0.002	0.71	5.1	≤0.001
Oscillaxanthin	0.18	3.3	0.07	0.21	1.29	≤0.001
Zeaxanthin	0.65	1.39	≤0.001	0.66	4.14	≤0.001

TABLE S6.4: Randomized intervention analysis results of *Chaoborus* and Cladocera taxa

	SC14		
Zooplankton	Pre-1920	Post-1920	p-value
Alona	11.85	3.39	0.003
Chydorus	6.4	1.03	≤0.001
Bosmina	21.4	8.4	0.002
Chaoborus	0.7	0.86	0.58

Chapter 7

7. Conclusions and outlook

7.1 Conclusions

This thesis presents a comprehensive examination of the paleolimnological history of Lake Victoria. It provides valuable insights into the evolution of the aquatic ecosystem and its dynamic connections to paleoclimate conditions and the lake's development from the Latest Pleistocene to modern times. Using a multiproxy approach, this thesis has integrated high-resolution scanning techniques (HSI and XRF) with multiple analytical methods, including sedimentary pigment biomarkers, which significantly expand the range of paleoenvironmental indicators available for Lake Victoria. Moreover, the analysis of sediment cores at varying water depths has offered new insights and proof of the diverse paleoenvironmental conditions in Lake Victoria, considering its immense size. The following section discusses the outcome of this thesis in relation to the major scientific objectives.

Re-filling of Lake Victoria in the Latest Pleistocene to Early Holocene

One major objective of this thesis was to understand Lake Victoria's paleolimnological evolution during the Latest Pleistocene-Early Holocene transition. Employing a chrono-lithostratigraphic approach, the data reveal strong evidence for extensive wetland ecosystems within the Lake Victoria Basin before the establishment of the present deep-water lake (~14 – 13.5 ka). This novel finding effectively explains the observed variations in basal sediment lithologies within the lake basin and sheds light on the basin's pre-lacustrine environment. Furthermore, the data agree with existing regional paleoclimate records suggesting arid conditions in the Latest Pleistocene (specifically during the Heinrich 1 Stadial) followed by significantly wetter conditions with the onset of the African Humid Period and the Holocene (~14 – 10 ka).

Trends and drivers of past aquatic primary production in Lake Victoria

Another key aspect of this thesis was exploring the long-term lacustrine evolution of Lake Victoria, focusing on changes in primary production, nutrient dynamics, and hydroclimate variability from the Latest Pleistocene to modern times. The results indicate that past primary production in Lake Victoria was primarily driven by hydroclimate changes, water column mixing, and nutrient availability. However, it is important to consider the heterogeneity of these factors across the lake basin and different water depths when interpreting paleoenvironmental changes in the lake.

During the early wetland phase (16.7 – 14.5 ka), Lake Victoria had low aquatic primary production, with predominantly chloro- and chromophytes. The lake's ecosystem and phytoplankton community were likely influenced by emergent aquatic macrophytes. After a rapid rise in lake levels at 14.2 ka and the formation of a deep exorheic lake, productivity increased significantly. Chromophytes and cyanobacteria became dominant in the algal community. Two phases of increased lake mixing and primary production were observed during the Holocene and African Humid Period: one between 11 and 9 ka, and another, less pronounced phase between 7 and 4 ka. Between 9 and 7 ka, the lake experienced stable water conditions with low diatom productivity and nutrient limitation, possibly due to reduced wind stress. In the mid-to-late Holocene, there was a decrease in lake mixing, which coincided with the end of the African Humid Period (~5 – 4 ka). This resulted in a rise in cyanobacteria dominance.

Cultural eutrophication and ecological changes in Mwanza Gulf

The third study investigated the ecological changes and eutrophication in the southern Mwanza Gulf of Lake Victoria over the past century. Our findings indicate that algal production began to increase in the 1920s, and peaked in the 1980s, due to the growing influence of anthropogenic activities on nutrient loading. Additionally, the habitat alteration caused by the lake-level rise in the 1960s primarily affected the cladoceran community. Notably, the data did not provide strong evidence of predation control mechanisms or grazing pressure on planktonic zooplankton and phytoplankton, respectively.

7.2 Final remarks and outlook

In summary, this thesis shows that analyzing lake sediments using multiple methods and interdisciplinary collaboration can yield new insights into geoscientific and biological research. The precise chronology and interdisciplinary approach employed make these records particularly valuable for reconstructing past environmental conditions. Only a few studies in tropical and African regions have used multiproxy datasets to reconstruct past environmental conditions, especially with regard to the application of hyperspectral imaging techniques or pigment biomarkers to infer paleo primary production. In this respect, our study serves as a practical validation of these tools and indicators in a tropical lake system. The thesis presents significant environmental baseline conditions for interpreting the evolutionary trajectories in Lake Victoria. Furthermore, it identifies key areas for further investigation that are essential for deciphering the complex relationship between environmental changes and aquatic evolution:

I. Pigment degradation and preservation: While pigment biomarkers offered valuable insights into past algal communities, their degraded nature in Lake Victoria highlights the need for further research into pigment degradation-preservation dynamics in tropical lakes. It is important to understand these processes, particularly for grazing-indicating pigments like pheophorbide *a*, as they could offer valuable information about food-web dynamics.

II. Spatial heterogeneity: The study uncovered spatial variations in past aquatic conditions. However, the impact on biotic communities, particularly fish populations, remains unclear. To comprehend phytoplankton growth and ecosystem functioning, it is crucial to investigate the drivers of this heterogeneity within the lake, specifically how mixing affects nutrient availability, light penetration, and temperature distribution. Interdisciplinary collaboration is required among various fields, such as meteorology, sedimentology, paleoecology, and ecosystem modeling, due to the complexity of the region's hydroclimatic conditions.

III. Holocene hydrological and climatic instability: The high-resolution XRF data, especially the K profile, holds immense potential for exploring short-term climate perturbations and their impact on lake biota in a paleoclimatological context. This data presents a valuable opportunity for further research and analysis.

By addressing these research areas, we can gain a deeper understanding of the past and present dynamics of Lake Victoria, ultimately informing conservation and management strategies for this biodiverse ecosystem.

I. Appendix I

I.1 Literature review – tables

Symbols for chronology

- ▶ original chronology
- ⧫ incorporation of additional ^{14}C dates in age-depth model
- ◊ revised age-depth model (omission of ^{14}C dates, correction factor)
- ■ single ^{14}C date; no age-depth model
- □ revised ^{14}C date
- • retrieved by correlation using magnetic susceptibility

TABLE AI.1: Overview of cores taken during IDEAL campaign

	V95-1P	**V95-2P**	**V95-3P**	**V96-6P**	**V95-7P**	**V96-7P**
Coordinates	01°13.9′S, 33°11.9′E	00°58.67′S, 33°27.32′E	01°38.58′S, 32°51.22′E	00°19.69′S, 32°19.71′E	00°27.70′S, 33°21.10′E	01°11.3′S, 33°0.65′E
Coring year	1995	1995	1995	1996	1995	1996
Water depth [m]	65.8	67	65	?	63	68
Core length [cm]	909	751	441	420	921	614
Chronology versions	■ DeMaster, 1997 and Johnson et al., 1998 ⧫ Johnson et al., 2000 ⧫Berke et al., 2012 ⧫ Muschick et al., 2018 ◊ Lane et al., 2018	▶ Johnson et al., 1996 ◊ Beuning et al., 1997 ◊ Johnson et al., 1998 and Ngobi et al., 1998 ◊ Stager and Johnson, 2000 ◊ Talbot et al., 2000 ⧫ Beuning et al., 2002 ◊ Stager et al., 2002	■ Johnson et al., 1998 □ Talbot et al., 2000	▶ Muschick et al., 2018	■ Johnson et al., 1998 • Lund et al., 2021	■ Johnson et al., 1998 ⧫ Beuning et al., 2002 □ Stager et al., 2002
Dated material	Bulk OM, pollen-lignin-algae fraction, plant/wood fragment	Pollen-lignin-algae fraction, charcoal	Pollen-lignin-algae fraction	Charcoal, wood fragment, fish fossil	Pollen-lignin-algae fraction	Pollen-lignin-algae fraction, charcoal
Basal age (in figure)	16.6–16.2 ka BP (plant wood fragment) Berke et al., 2012 Lane et al., 2018	14.3 ka BP (charcoal) or 14.2–15.3 ka BP Beuning et al., 2002 Stager et al., 2002				15.86 ka BP (charcoal) or 15.6–16.3 ka BP Beuning et al., 2002 Stager et al., 2002
Others	Two late Holocene cryptotephras (3151–2537 cal. yr BP, 1973–1395 cal. yr BP) Range of basal ages (16.6–21 ka with age reversal)	Date in “transitional mud” 15.9 ka BP (charcoal) 15.6–16.3 ka BP				overpenetration resulted in loss of the upper sedimentary section (<4 ka)
Core description	Two exposure surfaces	Two exposure surfaces Talbot et al., 2000	One exposure surface Talbot et al., 2000	No description, correlation with MS data	No exposure surface	No description

TABLE AI.2: Overview of sediment cores taken prior the IDEAL campaign

	Ibis-3	**Ibis-1 (Damba core)**	**P2 (Pilkington core)**	**64-4**
Coordinates	00°11′0″S, 33°16′5″E	00°05′0″N, 32°48′2″E	00°18′N, 33°20′E	00°18′N, 33°20′E
Coring year	1971	1971	1960	1960
Water depth [m]	66	32	9 (26 m referred to 1997 water levels)	3
Core length [cm]	1030	990	1800	1200
Chronology versions	■ Stager et al., 1986 ◆ Stager et al., 2002	■ Stager, 1984 ■ Stager et al., 1986 ■ Stager and Mayewski, 1997 ◆Stager et al., 2002 ◊◆ Stager et al., 2011	▶ Kendall, 1969 ◊ Stager and Mayewski, 1997 ◊ Stager et al., 2003 ◊ Stager et al., 2002 ◊ Stager and Johnson, 2008	▶ Kendall, 1969
Dated material	Bulk sediment	Bulk sediment, snail shell	Bulk sediment	Bulk sediment
Basal age (in figure)	~17.3 ka BP Two dates at discontinuity: 14.3–15.9 BP (bulk) 17.3–18 ka BP (bulk) Stager et al., 2002	9–13.4 ka BP (bulk) ~13.6 ka BP (= Peak of pennates diatoms) Stager et al., 2011	Regression without the four oldest dates meets discontinuity around 12,300 ^{14}C (=14,000 cal years BP) Stager and Johnson, 2008	A single basal date: 11.5 ka BP Stager and Johnson, 2008
Other notes		Middle shell layer lost due to core handling; diatom information in SOM of Stager et al., 2011	No evidence of a soil stratigraphy, root channels, or unusual numbers of sand grains	
Core description	Stager et al., 1986 Talbot and Livingstone, 1989	Stager et al., 1986 Talbot and Livingstone, 1989 Stager et al., 2011	Kendall, 1969	Kendall, 1969

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II. Appendix II

II.1 Summary of cores and stratigraphic correlation

TABLE AII.1: Summary of all sediment cores taken along the offshore-nearshore coring transect (coring campaign 2018). Analyzed sediment cores used in this thesis are highlighted.

Core ID (Segments)	Coordinates	Depth [m]	Coring Site	Analyses	Composite Core (short name)
Piston cores along transect					
LVC18-4L (1 – 10)	E 33°47,768′ S 01°02,966′	63.0	4	XRF, HSI	LVC18-S4 (LV4)
LVC18-1A (1 – 8)	E 33°55,146′ S 01°06,914′	37.0	1	—	
LVC18-1B (1 – 7)	E 33°54,811′ S 01°06,979′	37.6	1	XRF, HSI	LVC18-S1 (LV1)
LVC18-1C (1 – 6)	E 33°54,804′ S 01°06,982′	37.6	1	XRF, HSI	
LVC18-2D (1 – 8)	E 33°56,780′ S 01°07,850′	22.6	2	—	
LVC18-2E (1 – 9)	E 33°56,779′ S 01°07,850′	22.6	2	XRF, HSI	LVC18-S3 (LV2)
LVC18-2F (1 – 8)	E 33°56,779′ S 01°07,849′	22.6	2	XRF, HSI	
LVC18-3G (1 – 4)	E 33°58,599′ S 01°08,343′	13.4	3	HSI	
LVC18-3H (1 – 3)	E 33°58,579′ S 01°08,345′	13.4	3	XRF, HSI	
LVC18-3J (1 – 3)	E 33°58,593′ S 01°08,344′	13.4	3	XRF, HSI	LVC18-S3 (LV3)
LVC18-3K (1 – 3)	E 33°58,594′ S 01°08,345′	13.4	3	HSI	
Surface cores along transect					
LVC18-S1	E 33°55,146′ S 01°06,914′	37.0	1	XRF, HSI, ^{210}Pb	^{210}Pb Chronology revealed that the top is missing
LVC18-S2	E 33°55,146′ S 01°06,914′	10.0	3	XRF, HSI,^{210}Pb	
LVC18-S3	E 33°58,661′ S 01°08,459′	10.0	3	—	
LVC18-S3	E 33°58,662′ S 01°08,458′	10.0	3	—	

TABLE AII.2: Summary of all surface sediment cores taken at the Mwanza Gulf (coring campaign 2018). Analyzed surface cores are highlighted.

Core ID (Segments)	Coordinates	Depth [m]	Coring Site	Analyses
Surface cores (Mwanza Gulf)				
LVC18-TSE-SC6	S 01°06,914′ E 33°55,146′	10.0	E	—
LVC18-TSE-SC7	S 01°06,914′ E 33°55,146′	10.0	E	—
LVC18-TSE-SC8	S 01°08,459′ E 33°58,661′	10.0	E	—
LVC18-TSF-SC9	S 01°08,458′ E 33°58,662′	10.0	F	HSI, Fish fossils
LVC18-TSF-SC10	S 02°33,612′ E 32°52,852′	12.5	F	—
LVC18-TSF-SC11	S 02°33,612′ E 32°52,852′	12.5	F	—
LVC18-TSG-SC12	S 02°33,473′ E 32°52,470′	14.5	G	^{210}Pb, XRF, HSI, δ^{13}C, δ^{15}N, Pigments, Phosphorus
LVC18-TSG-SC13	S 02°33,473′ E 32°52,470′	14.5	G	XRF, HSI, Plant Protection Products (PPP)
LVC18-TSG-SC14	S 02°33,473′ E 32°52,470′	14.5	G	XRF, HSI, Zooplankton fossils, Fish fossils
LVC18-TSH-SC15	S 02°33,301′ E 32°52,032′	13.5	H	—
LVC18-TSH-SC16	S 02°33,301′ E 32°52,032′	13.5	H	—
LVC18-TSH-SC17	S 02°33,301′ E 32°52,032′	13.5	H	—
LVC18-TSI-SC18	S 02°33,015′ E 32°51,023′	10.5	I	—
LVC18-TSI-SC19	S 02°33,015′ E 32°51,023′	10.5	I	^{210}Pb, XRF, HSI, δ^{13}C, δ^{15}N, Pigments, Phosphorus
LVC18-TSI-SC20	S 02°33,015′ E 32°51,023′	10.5	I	—
LVC18-TSJ-SC21	S 02°32,828′ E 32°50,403′	6.6	I	—
LVC18-TSJ-SC22	S 02°32,828′ E 32°50,403′	6.6	J	—
LVC18-TSJ-SC23	S 02°32,828′ E 32°50,403′	6.6	J	—

II.2 Segment composite correlation

II.2.1 Site LV4

TABLE AII.3: Stratigraphic composite correlation for site LV4.

Core ID (Segments)	Sediment section Top (cm)	Sediment section Bot (cm)	Composite Top (cm)	Composite Bot (cm)	Cumulative length (cm)
LVC18-4L-1	15	100.0	15.0	100.0	84.98
LVC18-4L-2	0.2	100.7	0.2	100.7	185.48
LVC18-4L-3	0.3	101.5	0.6	69.2	254.12
LVC18-4L-4	6.3	100.4	29.3	100.4	325.20
LVC18-4L-5	0.5	101.6	0.5	101.6	426.29
LVC18-4L-6	0.3	100.6	0.3	83.8	509.80
LVC18-4L-7	6.3	100.1	46.8	101.1	564.12
LVC18-4L-8	0.2	100.4	0.2	100.4	664.29
LVC18-4L-9	0.2	100.0	0.2	96.1	760.29
LVC18-4L-10	4.1	80.6	62.6	80.6	778.56
				Total length	778.60

TABLE AII.4: Segment correlation for segments outside the master composite for site LV4. Used for macrofossil analyses.

			corresponds to	
Core segment	Sediment section Top (cm)	Sediment section Bot (cm)	Core segment	Segment length (cm)
LVC18-4L-3	—	100.2	LVC18-4L-4	60.4
LVC18-4L-4	6.3	—	LVC18-4L-3	46.7
LVC18-4L-6	—	100.4	LVC18-4L-7	63.3
LVC18-4L-7	6.3	—	LVC18-4L-6	43.2
LVC18-4L-9	—	100.0	LVC18-4L-10	65.1
LVC18-4L-10	4.1	—	LVC18-4L-9	37.6

II.2.2 Site LV1

TABLE AII.5: Stratigraphic composite correlation for site LV1.

Core ID (Segments)	Sediment section Top (cm)	Sediment section Bot (cm)	Composite Top (cm)	Composite Bot (cm)	Cumulative length (cm)
LVC18-1B-1	13.00	86.0	13.00	86.00	73.00
LVC18-1B-2	2.50	100.3	2.50	103.0	173.50
LVC18-1B-3	1.30	99.4	1.30	91.30	263.50
LVC18-1C-2	0.80	99.8	32.70	70.70	301.50
LVC18-1B-4	6.70	101.5	12.70	101.50	390.30
LVC18-1B-5	0.70	99.8	0.70	99.80	489.40
LVC18-1B-6	0.30	100.3	0.30	53.30	542.40
LVC18-1C-5	0.80	100.4	25.60	100.40	617.20
LVC18-1C-6	0.60	99.2	0.60	93.60	710.20
LVC18-1B-7	0.40	126.5	104.50	117.80	723.50
				Total length	723.50

II.2.3 Site LV2

TABLE AII.6: Stratigraphic composite correlation for site LV2.

Core ID (Segments)	Sediment section Top (cm)	Sediment section Bot (cm)	Composite Top (cm)	Composite Bot (cm)	Cumulative length (cm)
LVC18-2E-1	10.70	98.90	10.70	98.90	88.20
LVC18-2E-2	0.30	100.70	0.30	100.70	188.60
LVC18-2E-3	0.40	100.00	0.40	59.40	247.50
LVC18-2F-4	1.20	100.80	22.90	100.80	325.40
LVC18-2F-5	0.60	100.20	0.60	21.60	346.40
LVC18-2E-5	2.00	100.30	2.00	100.30	444.70
LVC18-2E-6	0.50	99.50	0.50	37.50	481.70
LVC18-2F-6	9.10	100.70	70.70	100.70	511.70
LVC18-2F-7	1.90	100.90	1.90	38.80	548.60
LVC18-2E-7	4.80	68.90	15.80	68.90	601.70
LVC18-2E-8	0.60	100.50	0.60	100.50	701.60
LVC18-2E-9	0.20	100.80	0.20	100.80	802.20
				Total length	802.20

II.2.4 Site LV3

TABLE AII.7: Core composites for site LV3. All analyses presented in this thesis are done on core LVC18-3J. All four parallel cores (LVC18-3G, H, J, K) were opened and scanned with the hyperspectral scanner. Two cores (LVC18-3H, J) were additionally scanned with μXRF.

Core ID (Segments)	Sediment Section Top (cm)	Section Bot (cm)	Composite Top (cm)	Composite Bot (cm)
LVC18-3G-1	10.20	43.10	0.00	32.90
LVC18-3G-2	0.50	100.60	0.00	100.10
LVC18-3G-3	0.50	100.20	0.00	99.70
LVC18-3G-4*	3.30	21.50	0.00	18.20
* 2^{nd} piston core drive				
LVC18-3H-1	3.50	56.50	0.00	53.00
LVC18-3H-2	1.00	99.70	0.00	98.70
LVC18-3H-3	0.80	100.50	0.00	99.70
LVC18-3J-1	8.50	65.00	0.00	56.50
LVC18-3J-2	0.50	100.50	0.00	100.00
LVC18-3J-3	0.50	100.10	0.00	100.60
LVC18-3K-1	10.50	47.30	0.00	36.80
LVC18-3K-2	0.50	100.60	0.00	100.10
LVC18-3K-3	0.50	100.50	0.00	100.00

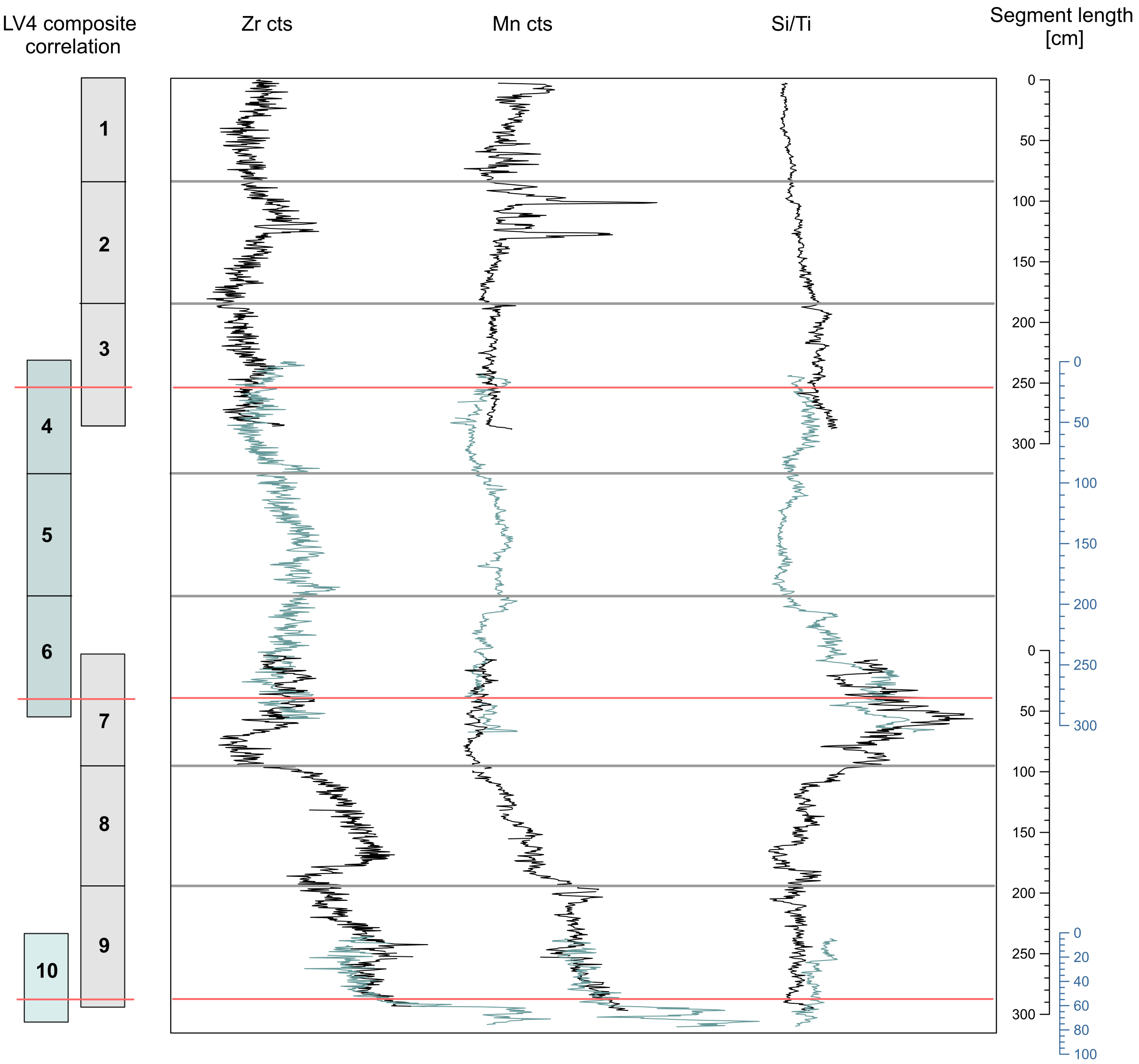

FIGURE AII.1: Example of stratigraphic correlation of core segments using XRF data from LVC18-S4 (LV4).

Declaration of consent

on the basis of Article 18 of the PromR Phil.-nat. 19

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Supervisor: Prof. Dr. Martin Grosjean

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