Lessons from the past:

Exploring invertebrate assemblages of Lake Victoria over decadal to millennial timescales to unravel anthropogenic impacts

Inaugural dissertation
of the Faculty of Science,
University of Bern

presented by

Leighton King

from the United States of America

Supervisor of the doctoral thesis:
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&
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General Introduction

Constituting only 3% of Earth's total surface area, freshwater lakes are amongst the most threatened ecosystems worldwide due to anthropogenic pressures (Downing et al. 2006). Despite their relatively small percentage, they provide numerous ecosystem services, including supporting biodiversity, serving as critical sources of freshwater, and contributing to local livelihoods and economies. For example, the world's largest lakes supply roughly two-thirds of available freshwater and 13% of all harvested fisheries (95% of which originate from within Africa; Sterner et al. 2020). Thus, understanding the ecosystem dynamics underlying anthropogenic change is essential for preserving the ecological functioning and resilience of lake ecosystems that maintain such ecosystem services.

Lakes serve as valuable sentinels of environmental change by providing insights into the impacts of both changing climatic conditions and anthropogenic pressures on freshwater ecosystems through time (Adrian et al. 2009; Williamson et al. 2009). Retrospective analyses of sediment archives can provide critical insight into long-term trends in ecosystem development to inform contemporary ecosystem management practices (Frey 1988; Cohen 2018; Gregory-Eaves and Smol 2024). For example, paleolimnological methods were imperative for recognizing the impact of acid rain on lake ecosystems and spurring appropriate management efforts (Smol 2019). Furthermore, reconstructing past ecological conditions of lakes prior to the cumulative impact of anthropogenic stressors is essential for placing observed changes over the past centuries into the context of natural climate-driven environmental variability over decadal to millennial time scales.

As climate change and anthropogenic activities continue to degrade lake ecosystems worldwide, there is a pressing need for interdisciplinary studies examining the interplay between biodiversity, food web dynamics, and environmental

change over extended timescales (Cohen 2018). The African Great Lakes, exhibiting some of the longest records of environmental variation and harboring high levels of endemic biodiversity, provide ideal systems to investigate these complex interactions (Hampton et al. 2018). Such studies will require the integration of conceptual frameworks across disciplines (*e.g.,* paleolimnology, community ecology, and evolutionary biology) to offer valuable insights into ecosystem structure and function over time.

Located in East Africa and renowned for its exceptional biodiversity, Lake Victoria has undergone unprecedented ecological change over the past century, including the loss of hundreds of endemic fish species (Barel et al. 1985; Witte et al. 1992b). Disentangling the ecosystem dynamics underlying this decline remains a pertinent issue to be addressed given the socioeconomic importance of the lake both regionally and globally. Therefore, throughout this thesis I have attempted to disentangle these food web dynamics, with a focus on invertebrates, over the past century within the context of baseline environmental variability over millennia. In the sections that follow, I introduce several broad ecological themes that are central to the research presented in this thesis. These themes include biodiversity, community assembly and succession, trophic interactions, and anthropogenic disturbance. Additionally, I provide a summary of existing research on the past ecosystem dynamics of Lake Victoria, which serves as the foundation for the questions explored in this thesis.

Biodiversity

Biodiversity is widely recognized as a key factor influencing ecosystem function and resilience (*i.e.,* the capacity of a system to maintain functionality amidst disturbance; Hooper et al. 2005; Tilman et al. 2014; Hodgson et al. 2015). For instance, by maintaining functionally similar interactions amonst species, biodiveristy can stabilize biomass by buffering fluctuations in species abundance and composition through functional redundancy (Allan et al. 2011; Oliver et al. 2015). Diverse biological communities are therefore paramount to ensuring the persistence of ecosystems in the face of anthropogenic disturbance. Freshwater lakes are distinctly susceptible to anthropogenic stressors—consistently exhibiting declines in biodiversity greater than those observed in their terrestrial counterparts (Sala et al. 2000; Vörösmarty et al. 2000; Reid et al. 2019). This loss of biodiversity may be equally as strong a driver of ecosystem change as the direct effects of other anthropogenic stressors over time (*e.g.*, climate warming, non-native species; Hooper et al. 2012). Yet, knowledge of the biodiversity that freshwater lakes host

remains woefully incomplete, particularly for invertebrates at tropical latitudes (Dudgeon et al. 2006; Reid et al. 2019).

Higher levels of biodiversity promote greater temporal ecosystem stability (Cardinale et al. 2012). For instance, compensatory dynamics of functionally similar species can support ecosystem resilience to external perturbations (Fischer et al. 2001). Within natural ecosystems, the current state of biodiversity has evolved over the course of millennia. However, the basis of our understanding of biodiversity dynamics stems from studies that have taken place over less than a decade (Cardinale et al. 2006; Tilman et al. 2014). This limited temporal perspective may present challenges in the future if environmental conditions differ markedly from the present (Oliver et al. 2015). Knowledge of how communities respond to environmental change through time is essential as it allows researchers to identify when the adaptive capacity of communities is declining, which indicates a weakening ability of the community to adapt to its environment (McMeans et al. 2016). Long-term biodiversity datasets are therefore necessary to address questions related to underlying rates and magnitudes of community turnover in order to distinguish anthropogenic-driven change from background change (Magurran et al. 2010).

Community assembly and succession

A major goal of applied and theoretical community ecology is to understand the mechanisms that shape communities (Hutchinson 1961; Leibold et al. 2004; Chase 2010). Community assembly refers to the dynamic processes by which species from a regional pool sequentially colonize and interact within an environment to form local communities (HilleRisLambers et al. 2012). Succession then builds upon this by adding a temporal perspective in which the relative influence of structuring forces can be more or less important at different points in time. Together, community assembly and succession provide a conceptual framework for understanding the processes that influence the occurrence and abundance of organisms across time and space (Chang and HilleRisLambers 2016). The framework can be visualized as species passing through various environmental filters that limit arrival and survival (Lawton 1999; Hillebrand and Blenckner 2002; HilleRisLambers et al. 2012). Regional (*e.g.*, historical factors and events, regional species pool), local (*e.g.*, environmental conditions, competition, predation), and neutral processes can determine the species composition and structure of communities (Shurin et al. 2000; Chase 2003; Leibold et al. 2004). But often, it is the interaction of these processes that together influence the composition of communities (Chase 2003; Cottenie 2005; Montaña et al. 2022).

The relative contributions of different community assembly processes (*i.e.*, biotic versus abiotic) can vary over time (Chang and HilleRisLambers 2016); therefore, incorporating a temporal perspective is essential to better understand the interplay between environmental change and community structure. While mesocosm and pond experiments can be used to study short-term community assembly patterns (*e.g.*, Cohen and Shurin 2003; Louette et al. 2008; Márquez and Kolasa 2013), these studies fail to capture long-term patterns that develop over centuries and may misrepresent the importance of abiotic or stochastic processes (Jackson and Blois 2015; Chang and HilleRisLambers 2016). Furthermore, in a meta-analysis of temporal turnover in aquatic communities, sampling duration was observed to have an influence on the rate of species turnover detected, with turnover slowing down with increasing time (Korhonen et al. 2010). Thus, lake sediment cores offer the opportunity to examine the temporal dynamics of community assembly throughout a lake's ontogeny, from lake infilling to its contemporary ecosystem state, over time scales at which both environmental and evolutionary change actually occur in nature (*e.g.*, Allen et al. 2011; Mergeay et al. 2011).

Food web dynamics

Interactions amongst organisms are integral to the structure and functioning of lake ecosystems. The two classical perspectives of trophic dynamics were presented as simple food chains, one in which energy was passed up trophic levels from primary producers to consumers (Lindeman 1942) and the second in which trophic dynamics are shaped by the effect of top predators on lower trophic levels (Hairston et al. 1960). Over subsequent decades, a more realistic representation emerged that portrayed the complex networks of various types of interactions as food webs consisting of many interconnected food chains with linkages to abiotic resources (Hunter and Price 1992; Polis and Strong 1996; Olff et al. 2009). This complexity contributes to both the sensitivity and persistence of lake food webs to external perturbations, highlighting the importance of considering these dynamics in ecosystem management efforts (Crowder et al. 1988; McCann et al. 1998; Donohue et al. 2016). The feedback between trophic interactions and changing environmental conditions makes food web structure and function highly dynamic over time. Species interactions not only structure biological communities (McCann et al. 1998), but they can also shape their environment and influence the trajectory of ecosystem development and, ultimately, functioning (Harmon et al. 2009; Loreau 2010; Matthews et al. 2014).

While the potential productivity of all trophic levels is determined by nutrient availability and other abiotic factors (Schindler 1978), community structure and

production of each trophic level is also influenced by biological interactions (Carpenter et al. 1985). Consumer-resource and predator-prey interactions govern the flow of energy across trophic levels (Tilman 1982; Atkinson et al. 2017; Mehner et al. 2022). Invertebrates (*e.g.*, Chironomidae and Cladocera) occupy an important position in lake food webs as they play an intermediary role for energy flow between trophic levels and inhabit virtually all lake environments (Korhola and Rautio 2001; Walker 2001). They play multiple roles in aquatic ecosystems, including being active grazers on algae and detritus, and serving as a major food source for higher trophic levels. Due to this intermediary role, they are sensitive to shifts in both bottom-up and top-down controls (Vanni 1987; Brooks and Dodson 1965) and are therefore effective indicators of environmental change (Kerfoot 1981; Hofmann 1996; Shumate et al. 2002; Davidson et al. 2011; Alric et al. 2013). For example, increased primary production in Lake Annecy (France) directly regulated *Daphni*a abundance, while increased whitefish predation selectively reduced *Daphnia* size and indirectly facilitated the establishment of a new *Bosmina* species due to released competition pressures (Perga et al. 2010). Overall, integrating the temporal dimension of trophic interactions is essential to understanding food web dynamics in response to external pressures in a real ecosystem context.

Anthropogenic disturbances to lake ecosystems

Freshwater lakes have experienced unprecedented ecological change over the past few centuries due to the cumulative impacts of numerous anthropogenic disturbances (Huang et al. 2022). Although human settlement near sources of freshwater has led to impacts even earlier (Dubois et al. 2018), the most severe degradation has often taken place starting in the 20th century as land use change and industrial advancements have intensified (Søndergaard and Jeppesen 2007). Anthropogenic stressors that directly threaten freshwater ecosystems include, but are not limited to, anthropogenic eutrophication (Smith and Schindler 2009), introduction of non-native species (Walsh et al. 2016), overexploitation of fisheries (Njiru et al. 2008), and defaunation of megafauna (Young et al. 2016). Furthermore, global-scale climatic change exacerbates such activities and can make isolating the effects of specific anthropogenic drivers difficult, especially in the African Great Lakes (Carpenter et al. 1992; Cohen et al. 1996). Given the complexity of ecosystem responses to multiple concurrent anthropogenic stressors, long-term empirical evidence of changing ecological conditions is critical, especially for lakes that exhibit unique characteristics.

Anthropogenic pressures pose a persistent threat to lake ecosystems, and have significant negative socioeconomic implications. Anthropogenic eutrophication,

characterized by excessive primary production due to increased nutrient loading, remains one of the largest threats to lakes despite decades of research (Schindler 2006; Chislock 2013; Birk et al. 2020). Despite being a natural process occurring over centuries, exponential population growth and its associated land use have accelerated eutrophication by increasing nutrient loading from point-source (*e.g.*, wastewater treatment plants) and nonpoint sources (*e.g.*, agricultural runoff; Carpenter et al. 1998). These nutrients promote dense blooms of phytoplankton, particularly cyanobacteria, which in turn reduces water clarity, depletes bottom water oxygen, and can pose serious health hazards to humans and animals (Downing et al. 2001; Havens 2008). Furthermore, such ecological changes can often have substantial evolutionary consequences by modifying selection processes, reducing ecological specialization of populations, and ultimately leading to a loss of biodiversity (Seehausen et al. 1997; Alexander et al. 2017).

Further complicating the impacts of eutrophication, the widespread introduction of non-native species and systematic overfishing, all of which often occur simultaneously, can have disastrous ecological and socioeconomic consequences (Cohen et al. 1996; Hall and Mills 2000; Allan et al. 2005). A global meta-analysis suggests that species introductions, whether intentional or accidental, have strong negative effects on aquatic communities through both direct biotic interactions and indirect habitat transformations (Gallardo et al. 2016). For example, *Bythotrephes longimanus* (a predatory, non-native cladoceran introduced into numerous North American lakes) has exerted direct influence on prey abundance through predation, while also indirectly altering prey behavior and morphology to better evade capture (Yan et al. 2011). Economically, the global cost of aquatic non-native species (*e.g.*, prevention, management, research) alone has been estimated to exceed $300 billion USD (Cuthbert et al. 2021). Meanwhile, overfishing poses a risk to both commercial and subsistence inland fisheries, which are valued at more than $24 billion USD across Africa (DeGraaf and Garibaldi 2014). Despite this importance, overfishing remains largely underreported and continues to threaten the long-term stability of fish stocks (Allan et al. 2005). Thus, the cumulative and interactive impacts of multiple stressors requires concerted efforts in research, management, and policy interventions to ensure the resilience of lake ecosystems.

Lake Victoria as a study system

Lake Victoria is among the most species-rich freshwater ecosystems in the world, but anthropogenic pressures have led to dramatic ecological change over the past century. Located along the equator in East Africa, Lake Victoria is the largest tropical lake in the world and has a unique ecological, social, and economic

significance. Today, the lake supports the largest inland fishery in the world and provides livelihoods for the millions of people living along the lake's edge (Sterner et al. 2020). The lake's vast resource potential has contributed to exponential population growth within the lake catchment, which is now one of Africa's most densely populated regions (Odada et al. 2009). Extensive land use change from the growing population led to increased nutrient enrichment and promoted excessive phytoplankton growth starting as early as the 1920s (Verschuren et al. 2002; Hecky et al. 2010). Increased primary productivity modified habitat suitability for the endemic haplochromine cichlid community by reducing water clarity and oxygenation, which culminated in the collapse of biomass and species diversity by approximately 40% (Witte et al. 1992a; Seehausen et al. 1997). Further compounding the impacts of anthropogenic eutrophication were the introductions of non-native Nile perch (*Lates niloticus*; a large piscivorous predator) and water hyacinth (*Eichhornia crassipes*; a free-floating macrophyte), as well as changes in lake-level and intensified fishing pressures (Witte et al. 1995; Lehman 2009; van Zwieten et al. 2016).

Prior to the last century, Lake Victoria had a dynamic history of environmental and ecological change. Most prominently, it featured the fastest known species radiation of >500 haplochromine cichlids species (Seehausen 2002; Genner et al. 2004). Yet, until recently, there was limited insight into the ecological conditions within the lake that facilitated such biodiversity. The formation of the lake basin occurred ~400,000 years ago and was presumably followed by multiple cycles of desiccation and refilling (Johnson et al. 2000), the most recent of which was the refilling of the modern lake ~17ka (Johnson et al. 1996; Stager and Johnson 2008; Temoltzin-Loranca et al. 2023a). Upon refilling, wetland conditions were sustained until ~14.5ka when rapid water-level rise established a deepwater lacustrine environment by ~13ka, consistent with regional terrestrial paleoenvironmental reconstructions (Berke et al. 2012; Temoltzin-Loranca et al. 2023b; Wienhues et al. 2023). All major fish taxa were present early in the refilling of the modern lake, suggesting that the adaptive radiation of more than 500 species of haplochromine cichlids was likely due to ecological opportunity and the intrinsic versatility of haplochromines rather than priority effects (Genner et al. 2004; Ngoepe et al. 2023). Subsequently, the lake went through considerable shifts in primary production and algal community structure that were primarily driven by hydroclimatic changes, lake mixing, and nutrient availability (Wienhues et al. 2024; Stager and Johnson 2000).

Reconstructing past ecosystem dynamics of Lake Victoria

The research put forth in this thesis was conducted as part of a broader, interdisciplinary team of researchers funded by a Sinergia grant (CRSII5_183566) from the Swiss National Science Foundation. Collaborators included researchers from the Tanzania Fisheries Research Institute (TAFIRI), the Swiss Federal Institute of Aquatic Science and Technology (Eawag), the University of Bern, the University of Basel, the University of Copenhagen (Denmark), and University of Arizona (United States). The overarching goal of the project was to reconstruct the development of Lake Victoria's ecosystem and biodiversity from its inundation in the late Pleistocene to present. To address this, a series of long and short lake sediment cores were collected in 2018 and 2022 (Figure 1). Long cores representing the past ~17ka were collected from four sites along a depth transect designed to track the high productivity of fish in the littoral zone during lake infilling. Short cores representing the past century were collected along a depth gradient of the Mwanza Gulf to examine the impact of anthropogenic stressors, particularly eutrophication, on the lake food web. The project was partitioned into four major research topics that focused on reconstructing various aspects of the ecosystem, including changes in: 1) terrestrial biomes (Temoltzin-Loranca et al. 2023a,b), 2) lake biogeochemistry and primary production (Wienhues et al. 2023, 2024), 3) invertebrate assemblages (this thesis), and 4) fish assemblages (Ngoepe et al. 2023, 2024). Altogether, the project aimed to provide an integrated understanding of the co-evolution of biodiversity and ecosystem development across an entire food web over eco-evolutionary timescales.

Figure 1. Photos from the coring expeditions to Lake Victoria, Tanzania

Goals and structure of this thesis

The main objective of this thesis is to disentangle the food web dynamics of Lake Victoria over the past century within the context of baseline environmental variability over millennia. Throughout this thesis, I use biological and geochemical indicators from lake sediment cores, with a focus on invertebrate remains, to examine the impact of anthropogenic stressors on the ecosystem dynamics of Lake Victoria. For this purpose, I first investigate how past changes in the invertebrate assemblage coincided with regional climate variability over millennia (Chapter 1, King et al. 2024). I then reconstruct major changes in the food web (*i.e.*, algal and zooplankton community composition) that were driven by anthropogenic stressors (Chapter 2, King and Wienhues et al. *in press*). Third, I examine the spatiotemporal heterogeneity of the chironomid and cladoceran assemblages over the past century (Chapter 3). And last, I explore the influence of invertebrate and fish predation on the abundance and size structure of a planktonic cladoceran over decadal and centennial timescales (Chapter 4). Finally, I conclude with the overarching lessons that can be learned from the research presented throughout this thesis.

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Chapter 1

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

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

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Abstract

1. Preserved assemblages of invertebrate remains in lacustrine sediment reveal temporal variations of community composition and environmental conditions. However, records for large tropical lakes are scarce. Lake Victoria, the largest tropical lake, has a dynamic history of changes in water level, biogeochemistry and fish community composition over the past ~17,000 cal yr BP.
2. In order to quantify changes in the invertebrate assemblage of Lake Victoria from the late Pleistocene throughout the Holocene, we examined chitinous remains of Cladocera and larval dipterans (Chironomidae and Chaoboridae) from a sediment core (37 m water depth) dated from ~13,700 cal yr BP to present.
3. We identified four major phases in the invertebrate assemblage throughout this period of lake history. Firstly, Chironomidae and Chaoboridae appeared at low abundances during the earliest stages of lake inundation in the late Pleistocene, at a time when Cladocera were notably absent. Secondly, chaoborids and chironomids increased in abundance during the mid-Holocene, which coincided with high diatom production toward the end of the Holocene African Humid Period. Thirdly, starting ~4,700 cal yr BP, *Alona*, a predominantly littoral cladoceran genus, consistently appeared in the invertebrate assemblage alongside changes in mixing regimes and persisted throughout the late Holocene to the present. Fourthly, the arrival of both *Chydorus* and *Bosmina longirostris* marked the establishment of an abundant cladoceran assemblage at ~1,350 cal yr BP. The assemblage then gradually shifted toward the increasing dominance of *B. longirostris*, a planktonic cladoceran.
4. Several of the observed changes in the invertebrate assemblage occurred concurrently with changes in climatic conditions in East Africa and diatom productivity that have been previously recorded in Lake Victoria. This multi-millennial record

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of sedimentary invertebrate assemblages in Lake Victoria elucidates some of the temporal development of these communities throughout most of the dynamic modern history of the ecosystem.

KEYWORDS
Chaoborus, chironomids, Cladocera, East Africa, palaeolimnology

1 | INTRODUCTION

One of the major goals of community ecology is to understand covariation of environmental conditions and community composition (Vellend, 2010) over a wide range of timescales (Shurin, 2007; Tomasových & Kidwell, 2010). Species turnover in communities is typically inferred from either among-site variation along broad environmental gradients (Leibold et al., 1997; Shurin et al., 2010), or from within-site variation over long records of ecosystem monitoring (typically decades; Korhonen et al., 2010). Palaeoecological records extend the timescale over which observations of covariation in communities and environmental processes can be made (Rillo et al., 2022). In lakes, long-term dynamics provide unique insights into how processes associated with community (dis)assembly (e.g., timing of species arrival, shifts in dominance) relate to changes in both regional climatic variability and catchment-scale dynamics at centennial and millennial timescales (Jackson & Blois, 2015; Mergeay et al., 2011). As such, these records can help to reveal how environmental change and species interactions jointly influence community dynamics (Gu et al., 2021; Jeppesen et al., 2005; Otake et al., 2021).

Microfossils isolated from lake sediment cores provide the opportunity to examine the temporal patterns of community assembly. In particular, aquatic invertebrate remains are useful biological indicators of past environmental change and to make inferences about trophic interactions within lake ecosystems (Frey, 1960; Hofmann, 1988; Korhola & Rautio, 2001; Walker, 2001). As aquatic invertebrates are sensitive to both bottom-up and top-down trophic controls, observed shifts in community composition are potentially indicative of changes in both the lake environment and food-web structure (Brahney et al., 2010; Eggermont & Heiri, 2012; Frolova et al., 2017; Heiri et al., 2003; Korponai et al., 2011; Labaj et al., 2021; Sweetman & Smol, 2006; Verschuren, Tibby, et al., 2000). Examining multiple invertebrate taxonomic groups in parallel, with different ecological affinities, strengthens inferences about the underlying causes of compositional change of communities (De Meester et al., 2023; Ursenbacher et al., 2020; Verschuren, Tibby, et al., 2000). For example, a previous study that included an analysis of both cladocerans (water fleas; Crustacea: Branchiopoda) and chironomid larvae (non-biting midges; Insecta: Diptera: Chironomidae), suggested that compositional change of cladoceran communities responded to vegetation and fish predation, whereas chironomids communities responded to fluctuating water levels (Płóciennik et al., 2020).

Palaeolimnological studies have disproportionally focused on temperate rather than tropical lakes based on global lake abundance estimates (Escobar et al., 2020; Verpoorter et al., 2014). Many previous studies have documented the history of zooplankton assemblages in temperate lakes, providing important insights into the environmental drivers of changes in these ecosystems over decadal-to-centennial scales (Allen et al., 2011; Cáceres et al., 2005; Otake et al., 2021). However, few palaeoecological records from lakes in East Africa have documented the changes in invertebrate community composition from the initial lake formation and throughout the entire ontogeny of ecosystem development (Table 1). For example, tropical Lake Naivasha varied dramatically in water depth over the past 1,800 years (<5 to ~35-m-deep lake), and zooplankton remains were used to investigate the joint roles of priority effects and species sorting in determining the assembly dynamics of *Daphnia* communities (Mergeay et al., 2011). Invertebrate studies of Lake Victoria have only previously examined changes over the past 200 years (Bridgeman, 2001; Verschuren et al., 2002) despite the modern lake having formed over ~17,000–15,000 cal yr BP (0 cal yr BP = 1950 CE; Johnson et al., 1996, 2000; Temoltzin-Loranca et al., 2023). Additionally, most invertebrate assemblage studies within the region have focused solely on one or two taxonomic groups (Table 1). Therefore, there remains a major gap in our understanding of the long-term successional patterns of invertebrate community assembly in response to environmental variation in large tropical lakes.

Located in East Africa, Lake Victoria (Figure 1) covers an area of ~69,000 km^2 within Kenya, Uganda and Tanzania. As the world's largest freshwater fishery, it supports an estimated 35 million people within the region who rely on the lake as a source of food, employment and water (Njiru et al., 2018). Lake Victoria is of particular interest for the study of community assembly owing to its relatively young geological age (~17,000–15,000 years; Table 1), extraordinary biodiversity and dynamic ecosystem history (Figure 2; Seehausen, 2002). For example, the Lake Victoria ecosystem has not only experienced dynamic periods of climatic variation, water-level fluctuation and ecosystem productivity (Berke et al., 2012; Beuning, Kelts, et al., 1997; Johnson et al., 1996, 1998, 2000; Kendall, 1969; Ngoepe et al., 2023; Stager & Johnson, 2000, 2008; Talbot & Lærdal, 2000; Wienhues et al., 2023), but also has generated a spectacular adaptive radiation of >500 species of haplochromine cichlid fish (Goldschmidt & Witte, 1992; Greenwood, 1974; Meier et al., 2017; Seehausen, 2002). To date, however, no previous study has analysed the fossil invertebrate assemblages of Lake Victoria for a time period spanning more than a few centuries. Here, we examine sedimentary invertebrate remains from a new Lake Victoria sediment core (Figure 1; LVC18_S1, hereafter LV1, located at 01°06.914′ S,

TABLE 1 Palaeolimnological studies within the African Great Lakes region that analysed sedimentary invertebrate remains (✗ indicates that the taxonomic group was included).

Lake	Age of last refilling (calyr BP unless specified)	Time covered (calyr BP unless specified)	Mean sample resolution (years/samples)	Cladocera	Chaoborus	Chironomids	Ostracods	Study
Lake Victoria	~17,000–15,000 (Temoltzin-Loranca et al., 2023)	~13,700[a]	125	✗	✗	✗	–	LV1 (this study)
		200	8			✗		Verschuren et al. (2002)
		80	4	✗	✗			Bridgeman (2001)
Lake Tanganyika	~12–9 Ma (Cohen et al., 1993)	~8,000	235				✗	Kamulali et al. (2022)
		~4,550	270				✗	Palacios-Fest et al. (2005)
		~2,500	60				✗	Alin and Cohen (2003)
		<100	15				✗	Park et al. (2003)
		<10	1			✗		Eggermont and Verschuren (2003a)
		Present	1			✗		Eggermont and Verschuren (2003b)
Lake Malawi	~8.6–4.5 Ma (Delvaux, 1995)	1.2 Ma	620		✗		✗	Ivory et al., 2016
		~145,000	310		✗		✗	Cohen et al. (2007) Park and Cohen (2011) Scholz et al. (2011)
		~75,000 (±250)	6		✗		–	Jackson et al. (2015)
		<100	15				✗	Park et al. (2003)
Lake Albert	~15,000–14,000 (^{14}C) (Beuning, Talbot, & Kelts, 1997)	~13,000	480				✗	Cohen (1987)
Lake Nakuru	~12,800 (Richardson & Dussinger, 1986)	~28,000[a]	280				✗	Cohen et al. (1983)
Lake Edward	~18–15,000 (?) (McGlue et al., 2006)	~11,000	n/a				✗	Russell et al. (2003)
Crescent Island Crater (Lake Naivasha basin)	~1,800 (Van der Meeren et al., 2019)	~1,100	7	✗		✗	✗	Verschuren, Laird, and Cumming (2000) Mergeay et al. (2011) Van der Meeren et al. (2019)
Lake Turkana	~17,000 (Morrissey & Scholz, 2014)	~500	7				✗	Beck et al. (2021)
Lake Oloidien (Lake Naivasha basin)	~200 (Verschuren, 1999)	~120	7	✗		✗	✗	Verschuren, Tibby, et al. (2000)
52 low- to mid-elevation lakes (Uganda, Kenya, Tanzania, Ethiopia)	n/a	<10	1			✗		Eggermont et al. (2006)

[a]Sediment records that cover the duration of lake ontogeny, and dashes indicate that sediments were analysed for the invertebrate group but no remains were found. Shaded row highlights this study.

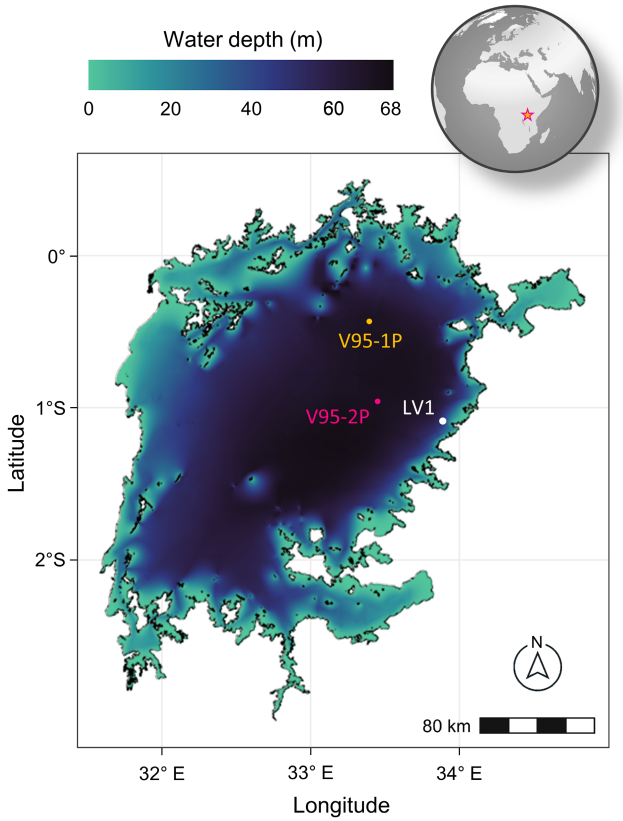

FIGURE 1 Bathymetric map of Lake Victoria, adapted from Hamilton et al. (2022), showing the coring locations of LV1 (white; 01°06.914′ S, 33°55.146′ E at 37 m water depth), V95-2P (pink; 00°58.67′ S, 33°27.32′ E at 67 m water depth; Stager & Johnson, 2000) and V95-1P (orange; 00°27.630′ S, 33°25.090′ E at 68 m water depth; Berke et al., 2012).

33°55.146′ E at a 37 m water-column depth, ~9 km from the nearest shore) to explore changes in invertebrate community composition over ~14,000 years of the lake's history.

The dynamic nature of hydroclimatic and other environmental conditions in East Africa over the past ~17,000 cal yr BP (Figure 2) lends itself to multiple research objectives regarding the invertebrate assemblage of Lake Victoria. Firstly, we examine if the timing of arrival and establishment of invertebrate groups coincides with changing regional climatic conditions (e.g., Holocene African Humid Period; AHP). Secondly, we investigate whether changes in species abundances co-vary with proxies of environmental change within the lake inferred from geochemical analysis of previously collected sediment cores described by Stager and Johnson et al. (2000) and Berke et al. (2012). Thirdly, we explore how compositional change over the whole record might provide insight into invertebrate community assembly processes (e.g., rise of a pelagic environment). Additionally, we discuss our results in relation to other environmental changes in the Lake Victoria region; including the timing of lake filling, the radiation of cichlids, the decline of diatom production in the mid-Holocene and changes in wind-driven mixing inferred from diatoms (Berke et al., 2012; Greenwood, 1974; Johnson et al., 2000; Seehausen, 2002; Stager & Johnson, 2000).

2 | METHODS

2.1 | Study site

Situated in a depression between the eastern and the western branch of the East African Rift, Lake Victoria is moderately shallow (mean depth 40 m, maximum depth 68 m; Johnson et al., 2000) with an extensive surface area of ~68,800 km^2. As a consequence of the shallow nature of the lake, its large size and its positioning along the equator under variable environmental conditions, the ecological dynamics of Lake Victoria are exceptionally sensitive to climatic changes in the region (Figure 2; Beuning, Kelts, et al., 1997; Johnson et al., 2000; Kendall, 1969; Stager et al., 1986; Stager & Johnson, 2000). The lake is at the intersection of savanna, rainforest and Afromontane biomes; thus, minor climatic changes (e.g., precipitation or temperature) can cause major lake-level fluctuations and shifts in the major terrestrial biome surrounding the lake (Temoltzin-Loranca et al., 2023). Previous work has speculated that the formation of the lake basin ~400,000 years ago was followed by several lake level regressions and transgressions that may have occurred corresponding to a combination of high- and low-latitude climate forcing, and catchment hydroclimate and ecosystem variability (Johnson et al., 2000). The most recent major desiccation of the modern lake basin is estimated at ~17,000 cal yr BP (Johnson et al., 1996, 2000; Temoltzin-Loranca et al., 2023), contemporaneous with other lakes in the region (Beuning, Talbot, & Kelts, 1997; Gasse, 2000). Following the late Pleistocene desiccation, the lake began to fill at ~16,600 cal yr BP and modern lake levels were established ~14,000–10,000 cal yr BP (Wienhues et al., 2023). Thus, the coring location of LV1 was continuously inundated over the period which our core encompasses. During this past history of the modern lake, the region experienced alternating wetter and drier periods, most notably during the AHP from ~11,500 to 5500 cal yr BP (Berke et al., 2012; de Menocal et al., 2000), associated with changes from savannah to rainforest and back to savannah, as inferred from pollen data (Kendall, 1969; Temoltzin-Loranca et al., 2023). Additionally, Berke et al. (2012) measured two geochemical proxies, TEX_{86} and δD_{wax}, indicative of lake water temperature and precipitation, respectively (Castañeda & Schouten, 2011), from V95-1P (Figure 1) to examine the surrounding climatic changes. δD_{wax} values are generally inversely correlated with rainfall amount in the tropics (Rozanski et al., 2013), and have been shown to be a useful indicator of hydroclimate variability throughout Africa (Tierney et al., 2008). Previous research has posited that such changes in monsoonal circulation and precipitation–evaporation relationships could be important drivers of community change across the entire food web. For example, previous work has inferred four phases of diatom production based on biogenic silica (BSi) and diatom microfossils preserved in a previously examined sediment core, V95-2P (Figures 1 and 2; Stager & Johnson, 2000). Furthermore, within this relatively short geological history of the modern lake the adaptive radiation of haplochromine cichlid fish produced >500 endemic species spanning 14 different trophic groups (Greenwood, 1974, 1980; Kaufman, 1992; Seehausen et al., 1997; Seehausen, 2002).

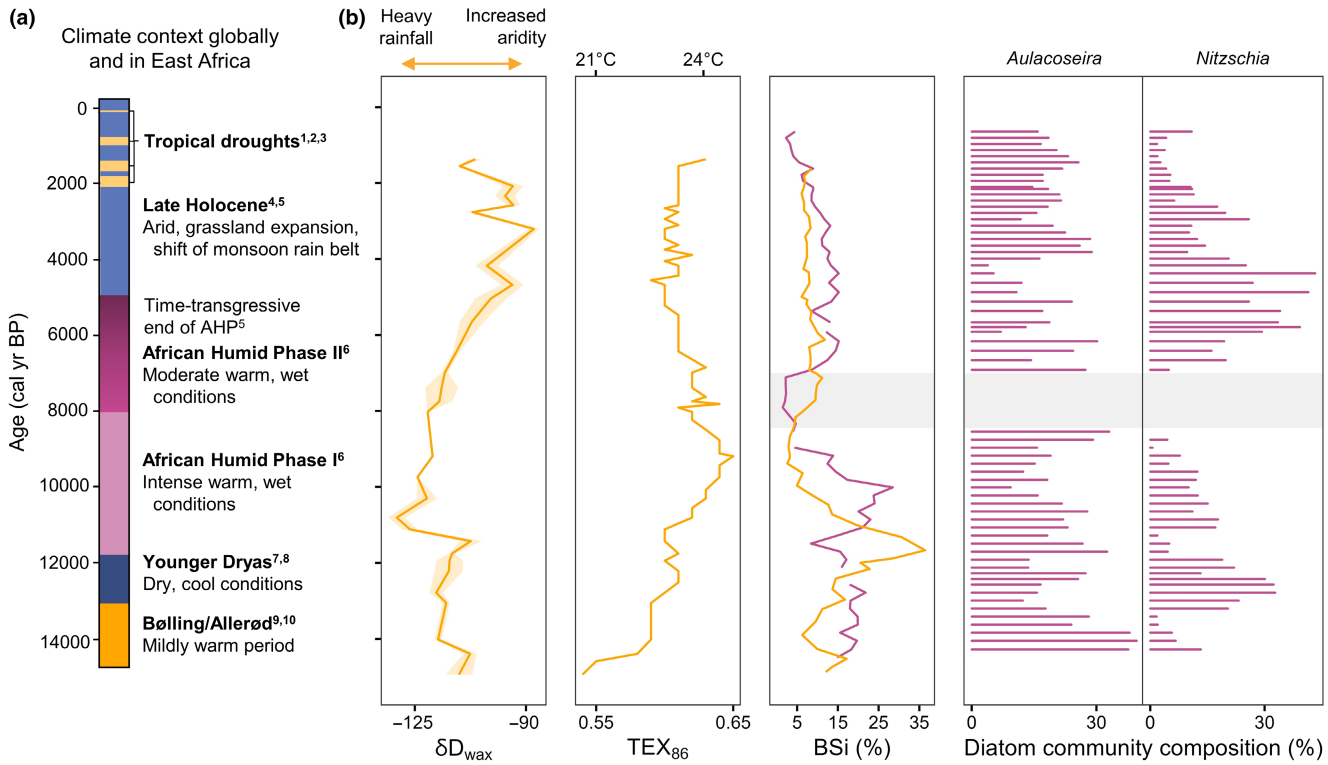

FIGURE 2 Summarised climate context globally and in East Africa over the past ~14,000 cal yr BP (a), as well as geochemical and diatom proxies analysed from two previously collected sediment cores from Lake Victoria, V95-2P (pink lines and bars) and V95-1P (orange lines), plotted along the associated age-depth models (b; adapted from Berke et al., 2012, Johnson et al., 2000, and Stager & Johnson, 2000). Berke et al. (2012) measured TEX_{86} temperature proxy values in V95-1P, to reconstruct down-core records of lake water temperatures, and ice-volume corrected δD_{wax} of the C_{28} leaf wax fatty acid methyl ester (orange shading indicates the mean error of replicated analyses for each sample), to investigate regional rainout history. Stager and Johnson (2000) counted diatom community composition (%; only dominant taxa shown) in deep-water sediments from V95-2P. Biogenic silica (BSi, %) was measured for both cores, with grey shaded area indicating the relative absence of preserved diatom remains in V95-2P. References for human and climate summary include: [1]Russell and Johnson (2005), [2]Marchant (2022), [3]Battistel et al. (2017), [4]Gasse (2000), [5]Shanahan et al. (2015), [6]Liu et al. (2017), [7]Gasse et al. (2008), [8]Carlson (2013), [9]Alley and Clark (1999), [10]Tierney et al. (2008).

2.2 | Sediment core analyses

Sediment cores were collected from Lake Victoria (Figure 1; LV1) in October 2018 using an UWITEC piston corer (Mondsee, Austria) on a floating platform located ~9 km offshore at a water depth of 37 m. Given the relative agreement between BSi profiles of LV1 and other deep-water sediment cores from Lake Victoria over the same age range (V95-2P, $r = 0.54$, $p < 0.001$; V95-1P, $r = 0.56$, $p < 0.001$), our record represents a spatial region toward the eastern sector of the lake that is unlikely to be completely anomalous to deepwater representations of planktonic versus littoral invertebrate assemblages. The LV1 composite stratigraphy of 723 cm sediment depth was created from nine core segments from two parallel coring locations, which were correlated based on X-ray fluorescence element profiles of Zr, Ti and K/Ti because lithological markers were not present in the core. The core consisted of uniform fine organic mud with no erosional unconformities and a sand layer at 720 cm (~13,800 cal yr BP) indicating the inundation of LV1 as lake levels rose (Wienhues et al., 2023). A robust and reproducible chronology for LV1 was established using 30 radiocarbon dates (Figure S1) measured with accelerator mass spectrometry; see Temoltzin-Loranca et al. (2023) for more details on the coring campaign and chronology. Age estimates were rounded to the nearest 50 years and the error represents the 95% confidence interval (CI), which on average represents ±520 years (Figure S1). We extracted the BSi content of LV1 sediments using the procedure by Ohlendorf and Sturm (2008) and then measured it with inductively coupled plasma mass spectrometry. Before leaching, organic material was removed from the sample with hydrogen peroxide (Mortlock & Froelich, 1989). BSi is reported as accumulation rate (mg BSi cm DW^{-2} $year^{-1}$; DW, dry sediment weight) for LV1 to account for variable sedimentation rate (Figure S1).

2.3 | Sediment preparation

Invertebrate remains were isolated from lake sediment subsamples by chemical digestion and wet sieving (≥38- and ≥100-μm size fractions) and prepared for microscopy analyses by mounting on microscope slides for identification (Brooks et al., 2007; Korhola & Rautio, 2001; Szeroczyńska & Sarmaja-Korjonen, 2007; Walker & Paterson, 1985).

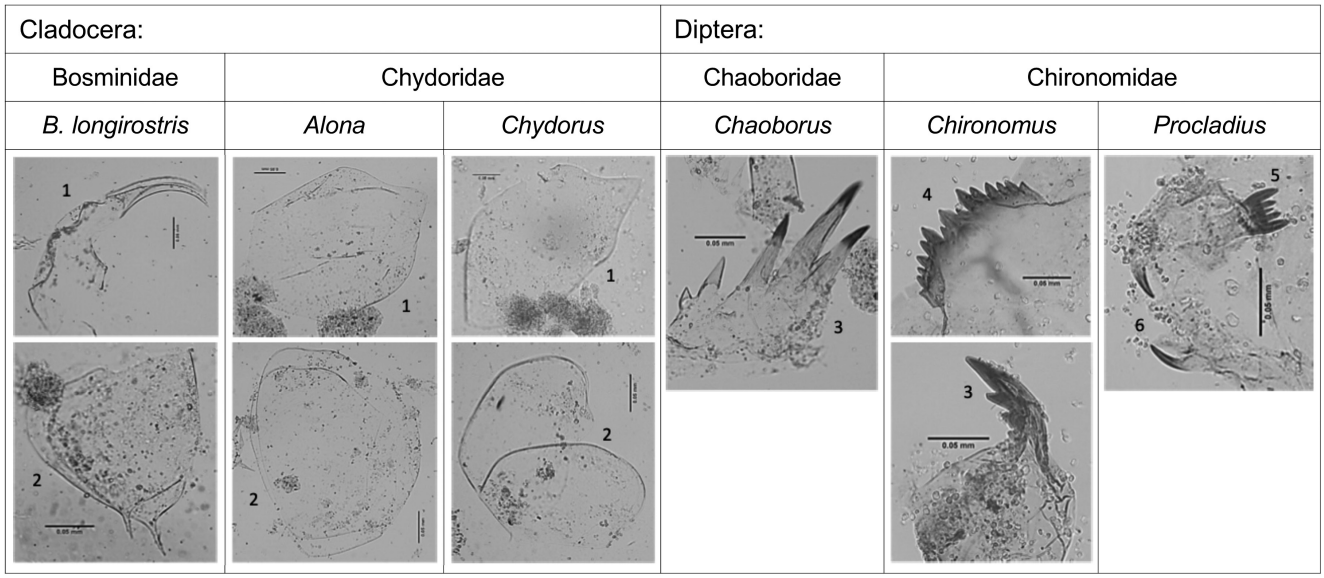

FIGURE 3 Representative images of invertebrate remains identified in Lake Victoria sediments: (1) headshield, (2) carapace, (3) mandible, (4) mentum, (5) ligula and (6) dorsomentum. Scale bars represent 0.05 mm.

All subfossil remains of cladocerans and aquatic dipterans (e.g., carapaces, headshields, mandibles, head capsules) were tabulated separately and used to determine the minimum number of individuals as this method is less likely to overestimate the significance of individual taxa (Zharov et al., 2022). Individual remains were identified to the most detailed taxonomic level possible (Figure 3). Microscope slides were examined in their entirety to avoid bias arising from a non-random distribution of remains under the coverslip. Published identification literature for aquatic invertebrate remains focus on temperate rather than tropical regions (Brooks et al., 2007; Korosi & Smol, 2012a, 2012b); therefore, many of the remains could only be identified to the genus level consistent with identifications of contemporary taxa (e.g., Ngupula et al., 2010; Vincent & Mwebaza-Ndawula, 2012). Taxa that did not occur in more than three samples at ≥1% relative abundance were not included in our analyses (Bredesen et al., 2002).

2.3.1 | Identification and enumeration of Cladocera

Sediment subsamples (~1 cm^3) of 1-cm thickness for Cladocera analysis were collected along the length of the core ($n = 103$; sampling intervals typically ranged from every 2 cm upcore to 15 cm downcore). The sediment was mixed with a 10% potassium hydroxide solution and heated to ~70°C for 10 min with gentle mixing to adequately separate cladoceran remains from other sediment particles and minimise further fragmentation (Frey, 1959; Matveev, 1986; Verbruggen et al., 2010). The mixture was subsequently washed through a 38-μm mesh to remove finer materials. The retained material was rinsed with tap water into labelled vials and a small amount of ethanol was added to prevent fungal growth. In order to calculate the concentration of individuals in each sample, one *Lycopodium clavatum* spore tablet containing a known amount of marker spores (Department of Geology, Lund University, Batch 3862, manufactured October 2015, mean number of spores per tablet = 9,666, σ = 671; Supporting Information S1) was dissolved in each sample vial.

Following sediment preparation, the cladoceran solution (~75 μl) for each sample was mounted on glass slides while ensuring that the sample was adequately mixed. The solution was mounted on glass slides that were examined at ×200–400 magnification via bright-field illumination using a compound microscope. *Lycopodium* marker spores were counted simultaneously to microfossils in order to calculate the concentration of individuals in each sample, and a photo library of microfossil remains was compiled in a data repository for further analyses.

The taxonomic resolution of our analyses was limited by the preservation of conspicuous diagnostic features. All *Bosmina* headshields that displayed a clear lateral headpore were identified as *B. longirostris*, which is further supported by contemporary zooplankton samples that identify it as the only *Bosmina* species in Lake Victoria (Mwebaza-Ndawula et al., 2005; Ngupula et al., 2010; Vincent & Mwebaza-Ndawula, 2012; Waya & Mwambungu, 2004; Yongo & Outa, 2017). Headshields and carapaces of *Alona* and *Chydorus* could not be reliably identified to species.

2.3.2 | Identification and enumeration of Chaoborus and chironomids

Sediment subsamples (~4–7 cm^3) intended for chironomid & *Chaoborus* analysis were collected approximately every 10 cm throughout the composite core ($n = 83$). Subsamples were wet-sieved with no chemical preprocessing into two size fractions: 100–200 μm (intermediate) and ≥200 μm (larger). Chironomid and *Chaoborus* remains were picked individually from both sieved

fractions using a stereomicroscope (×5–60 magnification) and placed on a microscope slide (Brooks et al., 2007). The slides were allowed to air-dry and then permanently affixed using Euparal (Carl Roth), and examined with a compound microscope at ×100–400 magnification. The sum of the remains found in the two sieved fractions was used for analyses.

Similar to Cladocera, Diptera remains were reliably identifiable only to the genus level (based on Brooks et al., 2007; Courtney-Mustaphi et al., 2024). However, previous work on short cores in Lake Victoria identified two species of *Chaoborus*: the large, offshore *C. edulis* and the smaller, littoral *C. anomalus* (Bridgeman, 2001). Earlier sediment core analyses of Lake Victoria identified *Procladius* remains as *P. brevipetiolatus*, which are widely distributed throughout East Africa (Eggermont et al., 2008; Freeman and Cranston, 1980), and the *Chironomus* taxon as *C. imicola* (Verschuren et al., 2002).

2.4 | Data analyses

The influx of individuals to the sediment was calculated by dividing the total number of individuals per cm^3 (concentrations) by the number of years per cm of depth (sedimentation rate; Temoltzin-Loranca et al., 2023). For cladoceran subsamples, the volume of sediment screened for microfossils (Figure S2) was determined by multiplying the volume of the entire subsample by the proportion of marker spores counted relative to the total number of marker spores added (Szeroczyńska & Sarmaja-Korjonen, 2007). The influx of *Chaoborus* was calculated from the sum of *Chaoborus* and sediment volume from both sieve fractions. Influxes were square-root transformed for visualisation purposes. Additionally, we calculated the ratio of benthic to planktonic Cladocera taxa ([*Alona* + *Chydorus*]/*Bosmina*) to examine the succession from a benthic to planktonic community.

Multivariate nonparametric change point analysis (Matteson & James, 2014) was used to detect significant changes in the cladoceran and dipteran assemblages, respectively, as well as environmental variables (Figure 1). The number and location of change points was estimated using the E-Agglo method (*ecp* package, version 3.1.3; James & Matteson, 2023) in R version 4.2.2 (R Development Core Team, 2021). This method performs a hierarchical agglomerative estimation of multiple change points of both the mean and variance ($\alpha = 1$; BSi change point based only on mean) of a time series by optimizing a goodness-of-fit statistic. It uses an initial segmentation of the data (member = number of observations) with the assumption that the observations are independent with a finite moment index. Change points with fewer than three observations on either side were omitted. We completed a linear interpolation of the chironomid taxa time series, to substitute missing values when paired with the *Chaoborus* time series, using the "interpTs" function (*wql* package, version 1.0.0; Jassby et al., 2022) in R version 4.2.2 (R Development Core Team, 2021). Additionally, we performed a permutation test (*wPerm* package, version 1.0.1; Weiss, 2022) for relationships between environmental variables (BSi, TEX_{86} and δD_{wax}; values were linearly interpolated when necessary) and dipteran taxa, using Pearson correlation coefficients. Correlations were not possible for cladoceran taxa because of limited overlap between datasets.

3 | RESULTS

Cladoceran microfossils comprised three major taxonomic groups: *Bosmina longirostris*, *Alona* and *Chydorus* (Figures 4 and S3). Likewise, three main taxa were identified among dipteran microfossils: *Chaoborus*, *Chironomus* and *Procladius* (Figures 4 and S3). Count sizes were relatively low (Figure S2) in comparison to previous analyses in small lakes and in temperate biomes (Kurek et al., 2010). A minimum count threshold was not reached for samples below 140 cm core depth, corresponding to sediments older than ~1,420 cal yr BP, owing to microfossil scarcity; however, sampling effort was consistent, if not greater, downcore in terms of the number of samples and sediment volume examined (Figure S2). Additionally, the number of cladoceran taxa found throughout LV1 is consistent with the number of taxa identified in previous short core analyses from Lake Victoria (Bridgeman, 2001). Likewise, although total counts (ranging from 0 to 87 individuals) of chironomids in each sample were well below the typical recommended number, the total volume of sediment picked was much greater relative to most published analyses (Figure S2; mean = 8 cm^3). Sididae ($n = 9$), *Cricotopus/Orthocladius* ($n = 11$) and *Tanytarsus* ($n = 13$) remains were rarely and intermittently observed, and thus were not included in our statistical analyses (Figure S3). Additionally, other aquatic microfossils were observed throughout the core (Figure S4) and included two groups of algae (siliceous remains of Bacillariophyceae [*Nitzschia* and *Cymatopleura*] and Chlorophyceae [*Pediastrum* spp.; (Millington & Gawlik, 1967)]), as well as organic remains of flatworm oocytes (Platyhelminthes: Rhabdocoela; Haas, 1996).

The overall patterns of LV1 BSi throughout the late Pleistocene and Holocene record of Lake Victoria is strongly correlated with cores V95-1P and V95-2P (correlation with V95-2P, $r = 0.54$; correlation with V95-1P, $r = 0.57$) despite some temporal and spatial offset (Figure 4). Accumulation rates of BSi in LV1 sediments ranged from ~16 to 210 mg BSi cm DW^{-2} $year^{-1}$, displaying maximum values during lake refilling, a subsequent period of low accumulation marked by a significant change point at ~8,750 cal yr BP, and then a slight increase—although not to early Holocene values—near the end of the AHP. Two significant change points were identified in TEX_{86} values throughout the lake's history at ~9,200 and ~11,100 cal yr BP, as well as a change point at ~5,050 cal yr BP in δD_{wax}.

3.1 | Invertebrate community of the late Pleistocene to early Holocene (~13,700–9,100 cal yr BP)

The bottom-most sediments of LV1, representing ~13,700–13,200 cal yr BP, contained remains of *Chironomus* and *Procladius*, with *Chaoborus* emerging shortly thereafter at ~13,200 cal yr BP

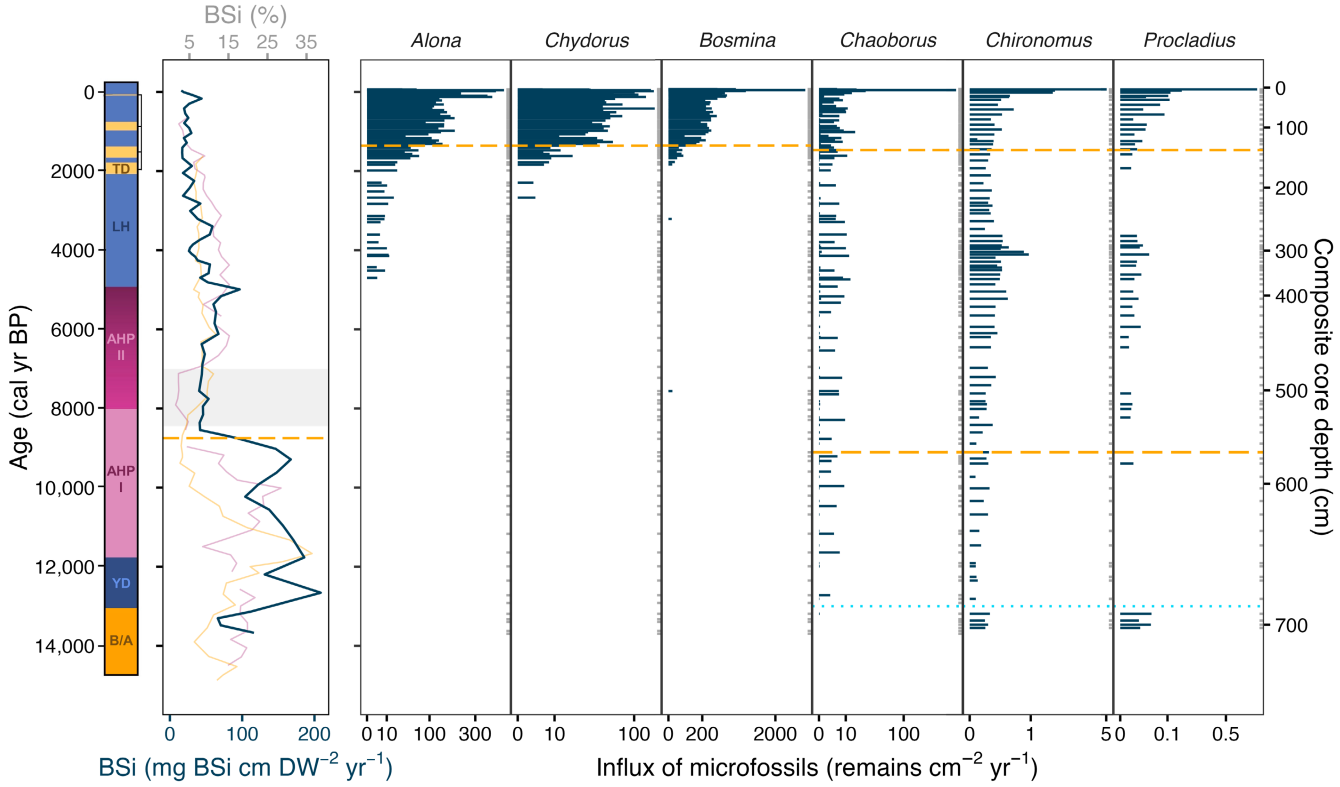

FIGURE 4 Biogenic silica (BSi) concentrations throughout LV1 (dark blue; mg BSi g SW^{-1} year^{-1}), V95-1P (orange; %; Johnson et al., 2000) and V95-2P (pink; %; Stager & Johnson, 2000) plotted along their original age–depth scales, as well as the square-root transformed influx of invertebrate microfossils (≥38 and ≥100 μm size fractions) observed throughout LV1. Grey tick marks on the right axis indicate sampling depths along the core. Orange dashed lines indicate the location of multivariate change points of the cladoceran and dipteran assemblages. The grey shaded zone represents the relative absence of preserved diatom remains in V95-2P (Stager & Johnson, 2000) and the blue dotted line indicates the end of first stage of rapid lake-level rise (Wienhues et al., 2023). Climate zones are referenced in Figure 2 and include: B/A, Bølling/Allerød; YD, Younger Dryas; AHP, African Humid Period (phases I & II); LH; late Holocene; TD, tropical droughts.

(Figure 4). Notably, cladoceran remains were absent during the late Pleistocene and into the Holocene (~13,700–4700 cal yr BP) at LV1. *Chironomus* remains were consistently present at low abundances starting from the inundation of LV1 throughout the entire remaining history of the lake. Meanwhile, *Procladius* abundances fell below detection limits through much of this phase. Despite few *Procladius* observations, TEX_{86} palaeotemperature was negatively correlated with *Procladius* throughout this phase ($r = -0.53$; Table S1). *Tanytarsus* and *Cricotopus/Orthocladius* remains were not present during this early phase of the lake (Figure S3).

3.2 | Rise of Chironomidae and Chaoborus during the African Humid Period (~9,100–1450 cal yr BP)

Chironomidae and *Chaoborus* remains were present at relatively low abundances throughout the sediment record with small, yet significant, increased influxes from ~9,100 to 1,450 cal yr BP as indicated by multivariate change point analysis. *Procladius* appeared consistently in the LV1 record starting at ~6,500 cal yr BP and remained present at low abundances until ~3650 cal yr BP when abundances fell below detection limits. Additionally, *Tanytarsus* and *Cricotopus/Orthocladius* individuals were first observed during this phase of increased Diptera abundances (Figure S3). During this phase, *Chironomus*, but not *Procladius*, was correlated with δD_{wax} ($r = 0.36$) and TEX_{86} ($r = -0.38$, Table S1).

3.3 | Rise of Cladocera in the late Holocene (~4,700–1,350 cal yr BP)

Although individual cladoceran remains were occasionally observed during the first ten millennia of the lake's history (unidentifiable Chydoridae postabdomen: $n = 5$, *B. longirostris* carapace: $n = 1$), Cladocera remains were largely absent throughout the LV1 sediment core prior to the appearance of *Alona* at ~4700 cal yr BP (Figure 4). *Alona* remained at relatively low abundances for the following few millennia until the appearance of *Chydorus* and *Bosmina* consistently in the sediment record at ~1,850 cal yr BP. This appearance was followed by the establishment of an abundant cladoceran assemblage, which is indicated by the multivariate changepoint detected at ~1,350 cal yr BP (Figure 4). Another notable feature of this phase included increased influxes of the diatom genera *Cymatopleura* and *Nitzschia*, as well as oocytes of the flatworm Rhabdocoela (Figure S4).

3.4 | Rise of an abundant cladoceran assemblage with planktonic dominance in the late Holocene (~1,350 cal yr BP–present)

All cladoceran taxa displayed substantial increases in abundance following the establishment of the new abundant cladoceran assemblage at ~1,350 cal yr BP, indicated by multivariate change point analysis (Figure 4). The appearance of *B. longirostris* in the sediment record was followed by a rapid decrease in the proportion of benthic to planktonic cladoceran taxa, and *B. longirostris* quickly became the dominant species within the last ~1,200 years (Figure 5b). Following the transition to *B. longirostris* dominance, the community composition of cladoceran taxa, and thus the proportion of benthic to planktonic taxa, remained relatively stable until the past few 100 years. In the most recent sediments, a dramatic increase in the abundance of *B. longirostris* coincided with decreases in benthic cladoceran taxa (Figure 5b). However, this increase may be an artefact of the increased sedimentation rate in the uppermost samples of LV1 rather than an ecological indicator. Likewise, *Chaoborus*, *Procladius* and *Chironomus* displayed steadily increasing abundances in the top sediment layers, with remains approximately two times greater in surface sediments than other sediment subsamples (Figure 4). BSi accumulation was positively correlated with both *Chironomus* ($r = 0.76$) and *Procladius* ($r = 0.68$) during this phase (Table S1). *Tanytarsus* and *Cricotopus/Orthocladius* individuals continued to be occasionally observed during this phase (Figure S3). The influx of *Nitzschia*, *Pediastrum* spp. and Rhabdocoela oocytes also remained relatively higher than before the late Holocene with major increases in surface sediments (Figure S4).

4 | DISCUSSION

Our results demonstrate multiple major invertebrate assemblage changes related to the first appearance and establishment of taxa for the eastern region of Lake Victoria in Tanzania during the late Pleistocene and Holocene. Firstly, *Chaoborus*, *Chironomus* and *Procladius* were all present at low abundances in the early history of LV1 (i.e., late Pleistocene–early Holocene, ~13,700–9,100 cal yr BP): a period when Cladocera remains were notably absent from the record. Secondly, all dipteran larvae exhibit a phase of increased abundance during the mid-Holocene (~9,100–1,450 cal yr BP) that corresponds with rising diatom production (BSi) after a period of low productivity during the early- to mid-Holocene. Thirdly, cladoceran taxa were largely absent from the sediment record until the appearance of *Alona* at ~4,700 cal yr BP, which coincided with the end of the AHP (Liu et al., 2017; Shanahan et al., 2015). Lastly, the arrival of *Chydorus* and *B. longirostris* in the late Holocene at ~1,850 cal yr BP was followed by the initial establishment of an abundant cladoceran assemblage at ~1,350 cal yr BP. We then observe a progressive shift over the following 500 years toward conditions that continued to favour all cladocerans, particularly planktonic taxa, which has been sustained for the past ~1,200 years. Many species of the plankton community are not preserved in lake sediments (e.g., copepods, rotifers), and only typically well-preserved cladoceran taxa (Bosminidae

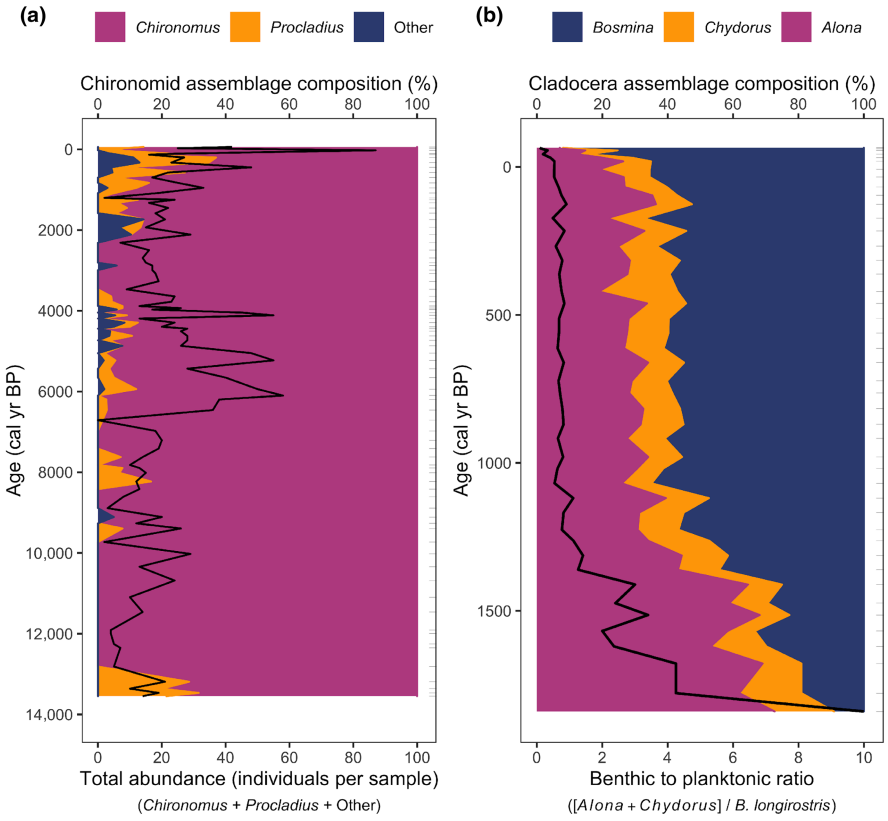

FIGURE 5 Community composition of Chironomidae over the past ~13,700 cal yr BP (a) and Cladocera over the past ~1,850 cal yr BP (b) from LV1. Black lines indicate the total abundance (number per sample) of chironomid individuals (a) and the ratio of benthic to planktonic cladoceran taxa (b).

and Chydoridae; Hann, 1989) were observed in Lake Victoria sediments (consistent with results of short cores; Bridgeman, 2001) compared to the full suite of genera encountered in modern water-column samples (*Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Moina* and *Macrothrix*; Waya & Mwambungu, 2004; Ngupula et al., 2010) that are often not as well-preserved. Therefore, we recognise that the remains of cladoceran and dipteran taxa provide only limited insights into the entire planktonic food web of Lake Victoria. Nevertheless, we present the first study of cladoceran and dipteran assemblages over the modern history of Lake Victoria at a relatively high temporal resolution compared to other studies in the region. The patterns observed indicate major shifts in the invertebrate community that occur concomitant with major regional changes in climate and are consistent with inferences made from previous palaeolimnological proxies from Lake Victoria. Differences between the spatial and temporal uncertainty of the various Lake Victoria sediment cores collected over the years leads to some difficulties integrating our results with those of previous studies (e.g., Berke et al., 2012; Stager & Johnson, 2000). For example, the chronology of V95-2P was based on only three radiocarbon dates, excluding dates between ~1,450 and ~10,300 cal yr BP, compared to the chronology of LV1 based on 30 radiocarbon dates (Temoltzin-Loranca et al., 2023). Therefore, further efforts examining lake conditions throughout the lake's history will be necessary to elucidate the specific drivers of the observed changes in the invertebrate assemblage beyond those examined here. However, this study still provides a valuable contribution by discussing the first long-term record of invertebrate assemblage dynamics in Lake Victoria within the ecological context provided by previous studies, which subsequent studies with greater spatial analyses can build upon further.

4.1 | Invertebrate community of the late Pleistocene to early Holocene (~13,700–9,100 cal yr BP)

During the early dynamic period of -evel change and subsequent stabilization, chironomid remains were consistently present at low abundances starting from the inundation of LV1 at ~13,700 cal yr BP, with *Chaoborus* then appearing ~13,200 cal yr BP. Subsequently, both *Chironomus* and *Chaoborus* are then consistently present into the Younger Dryas and AHP. Although, *Procladius* remains disappear between ~12,800 and ~9,700 cal yr BP, abundances are likely to have fallen just below the detection limits. The oldest sediments at LV1 would have been deposited ~13,700 cal yr BP, almost contemporaneous with a period of very dynamic lake-level variations (Wienhues et al., 2023). Therefore, our record at LV1 may not capture the earliest stage of community succession in Lake Victoria ~17,000–13,700 cal yr BP when the modern lake basin would have consisted of an extensive landscape of wetlands with fluctuating extents of inundation by variation in lake levels (Temoltzin-Loranca et al., 2023; Wienhues et al., 2023). *Chironomus* and *Procladius* are known to be early colonisers, surviving even in temporary pools of water from rainfall (Frouz et al., 2003; Layton & Voshell Jr., 1991; Verschuren, 1997); thus, it is unsurprising that they are established at the base of LV1 immediately following inundation. They tend to predominate in sediments characterised by fine sand or silt with high organic content (Pinder, 1986), which is typical for contemporary Lake Victoria wetlands and sheltered vegetated embayments. Likewise, *Cricotopus/Orthocladius* are commonly found in littoral areas (Coffman & Ferrington, 1996). As lake levels continued to rise as a result of intensification of monsoon systems during the Bølling/Allerød (Wienhues et al., 2023), the appearance of pelagic *Chaoborus* and disappearance of benthic *Procladius* coincided with the transition to open lacustrine conditions at LV1 when water levels would have risen by >30 m within a few centuries. Establishment of a permanent outflow by ~13,200 cal yr BP (Wienhues et al., 2023) coincides with the temporary disappearance of *Procladius* in LV1, indicating that the accompanying environmental shifts (e.g., water depth, nutrient cycling) did not favour high abundances of *Procladius*. In other tropical African Lakes, *Procladius* tends to be less common with increasing salinity (Verschuren, Tibby, et al., 2000) suggesting that lake freshening (i.e., decreased salinity) was not a driver of the decreased abundances. Additionally, *Procladius* was negatively correlated with lake temperature throughout this phase ($r = -0.53$), no major deviations in lake temperature coincided with the disappearance of *Procladius* in the sediment record. Despite climatic changes throughout the rest of this phase, *Chironomus* and *Chaoborus* continued to persist at relatively low abundances concurrent with consistently high diatom production and gradually increasing temperatures.

A notable feature of this early phase is the veritable absence of Cladocera. Cladoceran remains are composed of essentially the same chitinous material as Chironomidae and *Chaoborus*. Therefore, the presence of *Chaoborus* and chironomid remains throughout the lowermost portion of the core suggests that the preservation environment within the sediment column would likely to have been suitable for the preservation of cladoceran microfossils as well. Although we cannot exclude the role of taphonomic processes (e.g., degradation) definitively because cladoceran remains may not be as robust in terms of skeletal thickness as other chitinous remains (i.e., *Chaoborus* and Chironomidae remains), we did not observe substantial changes in preservation quality of the remains across the core. Therefore, we proceeded under the assumption that the absence of Cladocera in lower sediment intervals was not likely to have been the result of differential preservation. This is further supported by the presence of a few cladoceran remains before their initial appearance and community establishment, which suggests that Cladocera were likely to have been present at very low abundance below the detection limit. Owing to their intermediate position in the food web, abundances of cladoceran taxa would have been limited by climatic factors influencing habitat conditions (e.g., water chemistry) and food availability, competition with other zooplankton, or predation pressures (de Bernardi et al., 1987; Dodson et al., 2010). For example, large zooplankton herbivores have been observed to suppress abundances

of small cladocerans (Vanni, 1986). However, given the ubiquitous nature of Cladocera across almost all freshwater, including in the tropics (Dumont, 1994), their relative absence throughout this time is notable. Their rarity upon first occurrence in the core also leads to some uncertainty over our inference about the precise arrival time in the lake and the dynamics of their rise in abundance.

4.2 | Rise of Chironomidae and Chaoborus during the African Humid Period (~9100–1450 cal yr BP)

During the AHPI, increased abundances of *Chaoborus*, *Chironomus*, and *Procladius* occurred around ~9,100 cal yr BP. This timing coincided well with both the decrease in diatom production inferred from BSi, which exhibited a significant change point at ~8,750 cal yr BP with decreases observed even earlier and the TEX_{86} lake temperature change point at ~9,200 cal yr BP. Although *Chironomus* and *Procladius* co-varied throughout this phase ($r = 0.6$, $p = 0.001$), *Chironomus* were consistently more abundant than *Procladius*. Both taxa are known to be abundant in warm water lakes (Heiri et al., 2011) and lake temperatures were consistently within the optimal range for both *Chironomus* and *Procladius* (16–26°C; Eggermont et al., 2010). Taxon-poor assemblages that are dominated by *Chironomus* and *Procladius*, are commonly indicative of oxygen limitation (Brooks et al., 2007; Quinlan & Smol, 2001). Whereas *Chironomus* is one of the most tolerant genera of low oxygen conditions as a result of their high haemoglobin concentrations (Nagell & Landahl, 1978; Panis et al., 1996), *Procladius* are typically less tolerant of anoxic conditions (Verschuren et al., 2002). Thus, the ratio of *Procladius* to *Chironomus* has previously been used in palaeolimnological research in Lake Victoria to make inferences about hypolimnetic oxygen (short core V96-5MC representing the past 20 years, 68 m water depth; Verschuren et al., 2002). Increasing relative contributions of *Procladius* to the chironomid assemblage during the AHPII through much of the late Holocene, as well as *Tanytarsus* and *Cricotopus/Orthocladius*, may be indicative of increased water-column mixing promoting oxygenation of bottom waters. This is supported by the diatom record of V95-2P in which Stager and Johnson et al. (2000) attributed the transitions in the diatom assemblage, particularly increased BSi and replacement of *Aulocoseira granulata* with the more buoyant *A. nyassensis*, to a shift in seasonally restricted water-column mixing that allowed increased diatom resuspension at the end of the AHPII (~5,000 cal yr BP). *Procladius* then drop below the detection limit around ~3,500 cal yr BP, which again coincides with a change in diatom deposition indicating progressive reduction of monsoonal wind activity (Stager & Johnson, 2000). Assuming that changes in diatom deposition were driven by water-column mixing (Stager & Johnson, 2000), the concurrent timing of changes in both diatoms and chironomids, as well as the moderate BSi correlation between influxes of *Chironomus* and *Procladius* suggests that the increase in chironomid abundance is influenced by water-column mixing.

By contrast, the transition between phases of the AHP is reported to have exhibited reduced duration and intensity of monsoonal wind activity that led to stronger lake stratification and considerable reduction in offshore diatom production, indicated by the low BSi concentrations observed in all three cores and the absence of diatoms in V95-2P (Stager & Johnson, 2000). The reappearance of *Procladius* during this period of reduced diatom production suggests that other factors in addition to water-column mixing influence their abundances in Lake Victoria. Next to oxygen concentrations, food quality and availability also may have favoured increased *Procladius* abundances given the (marginally significant) positive correlation with BSi. The consistent presence of *Procladius* occurred concurrently with the increased diatom production toward the end of the AHPII. *Procladius* larvae are omnivores, and are known to engulf Cladocera, copepods, oligochaetes, and other chironomids, as well as algae (Antczak-Orlewska et al., 2021), and are considered to be more selective feeders than *Chironomus* (Hershey, 1986; Macdonald, 1956). Comparatively, *Chironomus* larvae are filter-feeders of sedimenting algal material (Walshe, 1947) and/or non-selective deposit feeders (Kelly et al., 2004; Ptatscheck et al., 2017).

Similar to chironomids, *Chaoborus* abundances are regulated by both abiotic and biotic factors, including habitat structure (Luoto & Nevalainen, 2009), hypolimnetic oxygen (Quinlan & Smol, 2010; Ursenbacher et al., 2020), fish predation pressure (Sweetman & Smol, 2006; Uutala, 1990) and the zooplankton community (Sarmaja-Korjonen, 2002). *Chaoborus* also displayed a mid-Holocene increase in abundance at the end of the AHPII. The observed increase of *Chaoborus* coincided with the period of increased diatom production around 5,000 cal yr BP, inferred from the BSi profile of LV1, which may have indirectly promoted the increase in *Chaoborus* through increased food availability for their zooplankton prey. However, this is difficult to assess because *Chaoborus* often prefer feeding on copepods rather than cladocerans (Swift & Fedorenko, 1975), and only the latter preserve in lake sediments. In addition, *Chaoborus* are known to tolerate low oxygen conditions (Jager & Walz, 2002), which enables diel vertical migration to optimise predator avoidance and foraging opportunities (Dawidowicz et al., 1990; Dodson, 1990; Irvine, 1997). Abundances of *Chaoborus* remains have been reported to be primarily driven by changes in hypolimnetic oxygen (Quinlan & Smol, 2010). Thus, their persistence in the deep-water lake conditions of Lake Victoria throughout its history suggests the presence of bottom water refugia that limited visual predation, particularly by insectivorous and zooplanktivorous pelagic haplochromines (Witte et al., 1995). However, the concurrent increase in *Procladius* and changes in the diatom assemblage suggests increased oxygenation during this phase. The insignificant correlations between *Chaoborus* and the environmental proxies investigated here suggests that other factors, such as predation, influence changes in *Chaoborus* abundance. Disentangling the (potentially interacting) effects of changes in hypolimnetic oxygen and predation pressure over millennial timescales will require further inference about the timing of trophic

guild emergence and changes in relative abundance of the fish haplochromine community over time, which is potentially attainable from future morphological and ancient DNA analyses of fish bone and tooth fossils (Muschick et al., 2023).

4.3 | Rise of Cladocera in the late Holocene (~4,700–1,350 cal yr BP)

As the AHP came to a gradual end, and drier, cooler conditions prevailed over Lake Victoria (Berke et al., 2012; Shanahan et al., 2015), *Alona* was the first cladoceran taxon to emerge at ~4,700 cal yr BP. The appearance coincided with the late Holocene BSi maximum at ~5,000 cal yr BP and the significant change point in δD_{wax} at ~5,050 cal yr BP driven by increased aridity suggesting that climatic changes in the region indirectly facilitated habitat conditions that favoured *Alona*. Following its appearance, *Alona* persisted at relatively low abundances for the following three millennia. Although typically known to be littoral, *Alona* species segregate spatially across the littoral zone based on water depth, macrophytes, total organic carbon, conductivity and pH (Adamczuk, 2014). Thus, it is difficult to make additional inferences into their environmental tolerances owing to taxonomic uncertainty related to differentiating species in understudied tropical regions.

The appearance of *Alona* at the end of the AHPII may have been influenced by changes in both abiotic (e.g., hypolimnetic oxygen) and biotic (e.g., lake food-web structure) factors. For instance, increased oxygenation of bottom waters, resulting from the return of seasonally-restricted wind mixing as suggested by the diatom assemblage following the mid-Holocene diatom decline, would have fostered a more suitable environment for benthic *Alona* because they have been observed to disappear if bottom waters become hypoxic (Sakuma et al., 2004). The concurrent increase of *Procladius*, *Tanytarsus* and *Cricotopus/Orthocladius*, which are typically less tolerant of anoxic conditions (Verschuren et al., 2002), further suggests increased oxygenation that favoured *Alona*. Alternatively, the late Holocene increase in diatom production, at ~5,000 cal yr BP, may have shifted the competitive outcomes in favour of small-bodied *Alona*. Stager and Johnson et al. (2000) reported increased abundances of *Nitzschia fonticola*, a diatom taxa that is often epiphytic on cyanobacteria in African lakes (Kilham et al., 1986). In turn, cyanobacterial blooms would have benefitted *Alona* as they are often associated with increased dominance of small-bodied zooplankton (Jiang et al., 2017). A further possibility, although speculative, is that predation on Cladocera by both vertebrate and invertebrate predators altered the competitive interactions between *Alona* and other zooplankton taxa. Abundances of invertebrate predators (e.g., *Chaoborus* and Rhabdocoela, some of which are predatory) remained relatively stable throughout the early history of modern Lake Victoria, exhibiting a small increase in abundance concurrent with the appearance of *Alona*. Moreover, the influence of predation pressures of zooplanktivorous fish on *Chaoborus*, cladocerans and copepods throughout history remains a major question to be addressed for the Lake Victoria ecosystem.

4.4 | Rise of an abundant cladoceran assemblage with planktonic dominance in the late Holocene (~1,350 cal yr BP–present)

The final major phase of change was the transition to an abundant cladoceran assemblage at ~1,350 cal yr BP following the appearance of *B. longirostris*, *Chydorus* and Sididae. All cladoceran taxa were consistently more abundant throughout this phase compared to their absence throughout the early Holocene, indicating a major change in lake conditions that favoured all cladocerans. The timing of this rise is consistent with increased late Holocene aridity as indicated by increasing phytolith and diatom abundances since ~1,400 cal yr BP (Stager & Johnson, 2000); however, BSi remained relatively stable at LV1 during this time. Overall, the regional climate was becoming increasingly arid following the end of the AHPII (Temoltzin-Loranca et al., 2023), culminating in a severe drought between ~2,050 and 1,850 cal yr BP (Russell & Johnson, 2005). Subsequent arid periods occurred from ~1,700 to 1,400, ~1,000–800, and ~150–100 cal yr BP (Battistel et al., 2017; Marchant, 2022). Although these climatic changes led to lake-level fluctuations throughout the past millennium (Tierney et al., 2013), the magnitude of changes in water depth for Lake Victoria is unclear, although certainly minor (<5 m) compared to its earliest stages of refilling (i.e., ~60 m; Wienhues et al., 2023). Rainfall and lake temperature proxies do not extend into this part of the lake's history. Furthermore, the relative error associated with our age-depth model makes inferring the precise timing difficult, particularly given the rapidly changing climate and intensification of human activities over the past millennia (Marchant, 2022).

In addition to the increased abundances of all cladocerans, a relatively quick transition to planktonic dominance suggests that the shift within the lake environment favoured dominance of planktonic cladocerans. Within the cladoceran community, *B. longirostris* was the only planktonic species observed, whereas both *Alona* and *Chydorus* typically represent littoral taxa (Frey, 1988). Previous studies have revealed that the replacement of benthic Cladocera by pelagic ones has been observed in response to increasing phytoplankton abundance (Otake et al., 2021). Furthermore, *B. longirostris* has been reported to dominate cladoceran assemblages following their invasion (Nevalainen et al., 2014; Nevalainen & Luoto, 2012). Ngoepe et al. (2023) observed an increase in pelagic haplochromine cichlid abundance, and a return of cyprinids, preceding the rise of the abundant cladoceran assemblage observed here. Changes in the fish community within the past century have led to shifts in abundances of small-bodied Cladocera (Van Zwieten et al., 2016). Thus, this transition may rather be linked to a restructuring of the lake food web through a combination of increased food availability (despite declines in diatom abundance) and change

in predation pressure. However, given the unknown changes in primary production and the extent of zooplanktivory associated with the emergence of the Lake Victoria cichlid fish radiation, it is unclear what food-web effects there may have been on the invertebrate community at this time. Size structure analyses of key morphological features of *B. longirostris* might provide additional insight into potential changes in zooplanktivorous fish predation during this phase (Korosi et al., 2013).

The expansion of all invertebrate taxa in the most recent surface sediments may be related to recent ecological changes in Lake Victoria, yet the age uncertainties of the topmost sediments of LV1 limit our ability to identify specific drivers. Recent ecological changes to the Lake Victoria ecosystem have been caused by anthropogenic pressures that occurred in short succession over the past century, including increases in phytoplankton production starting in the 1930s that parallel human-population growth and agricultural activity in the catchment (Hecky, 1993; Mugidde, 1993; Verschuren et al., 1998), the explosion of the population of the introduced Nile perch in the 1980s (*Lates niloticus*) (Ogutu-Ohwayo, 1990; Pringle, 2005), the major population declines of many native haplochromine cichlids (Barel et al., 1985; Witte et al., 1992) and the recent recovery of a subset of these (Witte et al., 2012). For such questions and analyses, short cores collected from key areas of Lake Victoria and examined at a higher temporal resolution are needed to assess how recent ecosystem changes coincide with compositional changes in the invertebrate assemblage.

5 | CONCLUSIONS

Few multi-millennial records of invertebrate population and assemblage dynamics exist in the African Great Lakes region, of which many focus on only one taxonomic group (e.g., chironomids) rather than the broader invertebrate community. Our late Pleistocene and Holocene record of the invertebrate assemblage preserved in a sediment core of Lake Victoria provides novel insights into the temporal dynamics of invertebrate community assembly, as well as the long-term nature of ecosystem change in the world's largest tropical lake. We observed long phases of relative stability and minor changes in chironomids followed by a very dynamic late Holocene phase with the appearance of several cladoceran groups and the expansion of Cladocera, *Chaoborus* and chironomids. Several of the observed changes in the invertebrate assemblage occurred concurrently with changes in climatic conditions of East Africa and diatom productivity that had been previously recorded in Lake Victoria. However, a key question that remains is how the observed changes in the invertebrate assemblage are related, or not, to the adaptive radiation of endemic haplochromine cichlid fish in Lake Victoria. Palaeolimnological archives can help reveal how the temporal development of past ecological environments may be related to evolutionary change within the lake community (Cuenca-Cambronero et al., 2022). In order to achieve progress toward that goal, a multi-proxy approach of multiple sediment cores is needed to help make inferences about changes in organism–environment interactions that have culminated in the unique community composition of Lake Victoria today.

AUTHOR CONTRIBUTIONS

Conceptualisation: LK, BM, OS. Developing methods: LK, BM, CCM, OH, OS. Conducting the research: LK, GW, MCC, CCM. Data analysis: LK. Preparation of figures and tables: LK. Data interpretation and writing: All authors.

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CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

All data are available in Zenodo: https://doi.org/10.5281/zenodo.10090595.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Chapter 2

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

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Author Contributions:

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.

Highlights:

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

ABSTRACT

Discerning ecosystem change and food web dynamics underlying anthropogenic eutrophication and the introduction of non-native species 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 endemic fish biodiversity over the past several decades, but changes in the plankton communities over this same time remain unclear. To fill this gap, we examined sediment cores from a eutrophic embayment, Mwanza Gulf, to determine the timing and magnitude of changes in the phytoplankton and zooplankton assemblages over the past century. 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 ~1960 CE, in response to the cumulative effects of eutrophication and lake-level rise, 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 over the past century in the biomass structure and taxonomic composition of Mwanza Gulf phytoplankton and zooplankton communities, providing a historical food web perspective that can help understand the recent changes and inform future resource management decisions in the Lake Victoria ecosystem.

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 and others 2009). Lake Victoria (Figure 1) plays a vital role in providing ecosystem services to the local population, most notably by supporting the world's largest inland fishery (Sterner and others 2020). The lake has experienced rapid ecological change in the past century driven by various climatic and anthropogenic pressures (Figure 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 and others 2022) and are particularly rare in tropical regions (Plisnier and others 2022). 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 and Jeppesen 2013).

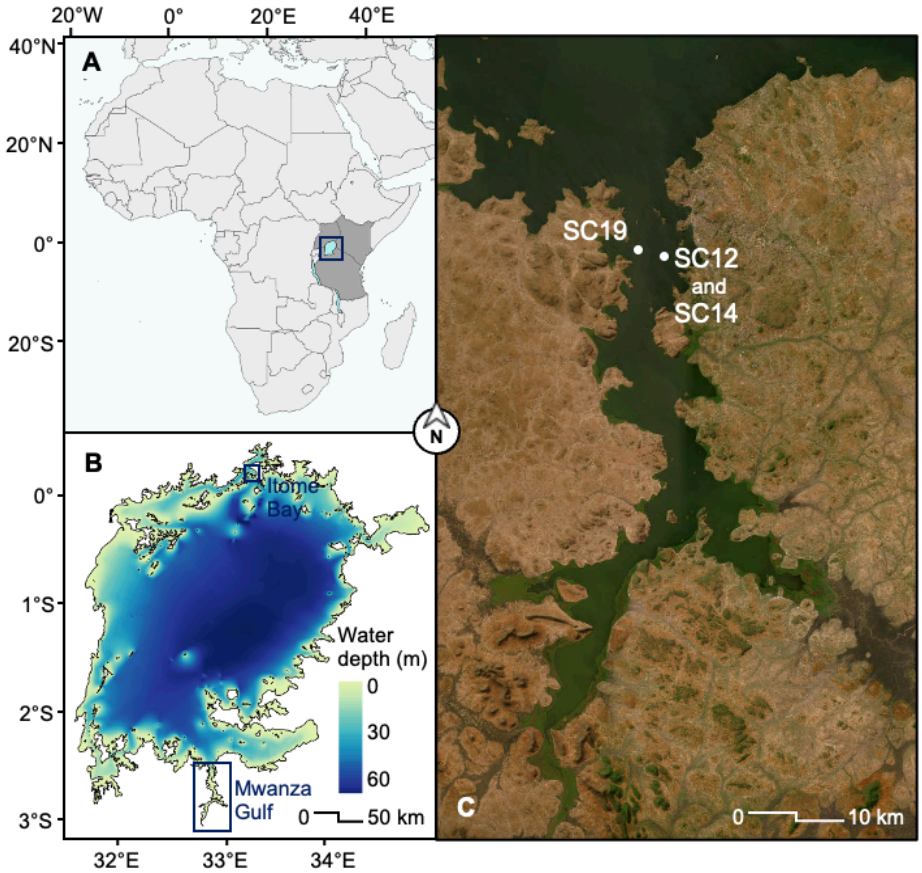

Figure 1.
(A) The African continent with Lake Victoria. (B) Bathymetry of Lake Victoria and location of the Mwanza Gulf estuary. (C) Satellite imagery (2018–2023) of the Mwanza Gulf (Esri, Maxar, Earthstar Geographics, and the GIS User Community) with coring locations marked with white circles.

Anthropogenic eutrophication (Smith and Schindler 2009) of Lake Victoria began as early as the 1920s in response to land use change within the catchment (Verschuren and others 2002; Hecky and others 2010; Njagi and others 2022). 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 (Figure 2A). Accelerated population growth (Figure 2B) led to increased agriculture, urbanization, and deforestation, which culminated in substantial nutrient enrichment to the lake (Figure 2C–D; Hecky 1993). Subsequently, phytoplankton production increased and shifted to greater cyanobacterial dominance (Hecky 1993; Verschuren and others 2002). Increased productivity led to decreased water transparency and decreased bottom water oxygenation, which in turn impacted habitat suitability for many fish species (Kaufman 1992; Hecky and others 1994; Seehausen and others 1997).

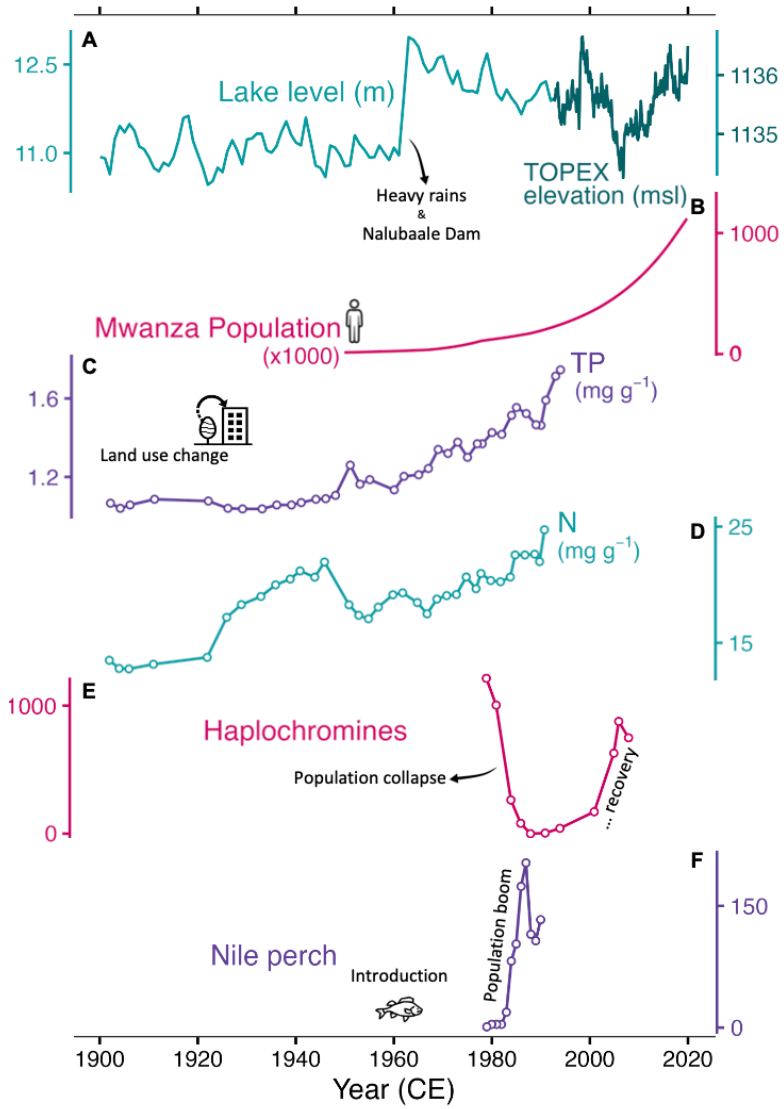

Figure 2.
Time series data collected for Lake Victoria, including lake level monitoring (A; 1900–2023), the population of Mwanza City (B; 1950–2023), weight concentrations of nutrients (C–D; 1900–2000), and mean number of key fish taxa caught in fish trawls in Mwanza Gulf (E–F; 1979–2008). Lake levels were adapted from Levêque (2017; light teal line, m above Nalubaale Dam gauge) 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 (UN DESA 2018). Sediment extracted nutrient concentrations (TP, total phosphorus; N, total fixed nitrogen) were adapted from Hecky and others (2010) and measured from a nearshore sediment core collected from Itome Bay (Uganda). Fish survey data was obtained from Natugonza and others (2021).

There have been several significant changes in Lake Victoria's fish community that have been documented over the past century, the most notable of which was the decline in species diversity and biomass of haplochromine cichlid fishes (Figure 2E) and the introduction and population expansion of Nile perch (*Lates nilotocus*, Figure 2F). Fisheries records from the 1960s (compiled in Figure 2E), suggest that endemic haplochromine cichlids constituted >80% of total fish biomass in Mwanza Gulf (Kudhongania and Cordone 1974), and this biomass constituted more than 120 different species in the Mwanza Gulf alone (Witte and others 1992). However, there was a major decrease in haplochromine biomass and diversity in the 1980-90s, which 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 (Witte and others 1992; van Zwieten and others 2016), and iii) the introduction and later population explosion of Nile perch (a large piscivorous predator) along with the early loss of piscivorous haplochromines that feed on juvenile Nile perch (Witte and others 2007). 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 (Wanink 1999; Goldschmidt and Witte 1992). Some recovery of the haplochromine cichlid biomass has been observed in the past decades (Figure 2E), but much of the species diversity remains lost (Witte and others 2000; Kishe-Machumu and others 2015).

Despite intensive research on Lake Victoria's fish community in the past few decades (Kolding and others 2014; van Zwieten and others 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 and Hodgson 2001) and subfossil remains of Cladocera and *Chaoborus* aquatic insect larvae (Korhola and 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 and others 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 (Figure 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, zooplankton 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 the abundance and composition of primary producers, as well as fish community structure (Figure 2E,F).

MATERIALS AND METHODS

Study site description

Located in equatorial eastern Africa, Lake Victoria (Figure 1) is the world's largest tropical lake (surface area = 68,800 km^2, 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 and others 2004). Previous paleolimnological research has investigated eutrophication in northern Lake Victoria (Verschuren and others 2002; Hecky and others 2010; Njagi and others 2022) but its impact in southern inshore areas of Lake Victoria remains understudied. Specifically, the Mwanza Gulf (Figure 1; 60 km long, 2.5–11 km wide) is the largest Tanzanian port on Lake Victoria and has previously been recognized for receiving the highest daily municipal water pollution within Tanzania (Juma and others 2014). The composition and abundance of phytoplankton in Mwanza Gulf varies from that observed in the open water and northern gulfs (Frank and others 2023). The surrounding land is primarily agricultural (>60%) and urban (~16%), with less than ~5% remaining as unconverted wetlands and woodland (Cornelissen and others 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 and others 1995), respectively. However, the Nile perch population remained low until the early 1980s when the population increased exponentially (Witte and others 1992).

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; Figure 1c). Two of the cores were collected as a paired set (SC12 and SC14, length = 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.

Geochronological dating

Sediment samples from the cores SC12 and SC19 were analyzed for

Cs and ^{226}Ra using gamma-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 (Table S1, Table S2; Aquino-López and others 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 (Figure S1; Appleby and 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 (Figure S2).

Biogeochemical indicators

Non-destructive 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 and others, 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 50mA, 30kV, 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 and others 2001) with modifications following Tu and others (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 and 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 (Figure S3) following Verburg (2007). TC corresponds to total organic carbon as prior tests indicated inorganic carbon was absent in sediment samples.

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 and others (1994; 2000) by high performance liquid chromatography (HPLC). Analysis was restricted to taxonomically diagnostic pigments (Table 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 and Catalan 2007).

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 (based on Szeroczyńska and Sarmaja-Korjonen 2007; King

Table 1. Biological indicators used and their first-order interpretation. Pigment affiliations are based on Leavitt and Hodgson (2001), Buchaca and Catalan (2007), and Lami and others (2009). Asterisk indicates only detected in degraded form.

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 (microfossils)	Cladocera: *Alona*	Littoral, scraper feeders (Fryer 1968)
	Chydorus	Littoral, scraper feeders (Fryer 1968)
	Bosmina	Planktonic, selective feeders (Korhola and Rautio 2001)
	Diptera: *Chaoborus*	Planktonic larvae with diel vertical migration, predatory (Dawidowicz and others 1990)

and others 2024) and counted separately. The minimum number of individuals was determined by the most abundant body part of each taxon (Zharov and others 2022). Concentrations were calculated by dividing the minimum number of individuals by the volume of sediment screened (determined by multiplying the total subsample volume by the proportion of marker spores counted relative to the total number of marker spores added). The influx of individuals to the sediment was then calculated by dividing the concentrations by the number of years per cm of depth.

Statistical analyses

Stratigraphically constrained cluster analysis (CONISS; Grimm 1987) was performed on the SC12 pigment and SC14 cladoceran datasets to identify the timing of shifts between distinct assemblages. Prior to clustering, pigment and cladoceran concentrations were log-transformed (pigments only) 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. A modified randomized intervention analysis (RIA; Carpenter and others 1989), which excluded the calculation of interecosystem differences, was performed on the individual pigments and zooplankton taxa to assess the significance of observed changes between pre- and post-intervention data. 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), which represented the onset of eutrophication determined from pigment clustering. For the Cladocera taxa, we proceeded using the onset of eutrophication rather than the changepoint identified by CONISS as we cannot exclude the possibility of cumulative effects between eutrophication and other events. The observed change was calculated as the difference in mean before and after the intervention. The test statistic was then derived by performing one thousand random permutations of each time series and calculating 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.

RESULTS

Geochronology

Total ^{210}Pb was observed to decline downcore in both cores, reaching supported ^{210}Pb levels at 25 cm (SC12) and 35 cm (SC19), respectively (Figure 2). Sediment disturbance and/or bioturbation was inferred from increasing downcore ^{210}Pb specific activities in the uppermost 4 cm of SC12 and 6 cm of SC19, which deviate from the ideal exponential decline expected for unsupported ^{210}Pb. Additionally, the section from 10 to 15 cm in SC19 showed a lack of ^{210}Pb decay, which indicates deeper sediment disturbances due to shallower water depth or the higher potential of trawling at this site (Witte and others 2012). Alternatively, increasing sedimentation rates may have compensated for the radioactive decay of ^{210}Pb. The majority of our subsequent analyses focused on SC12 due to the lesser degree of sediment disturbance. Age-depth models extended back to ~1900 (± 9 yrs), with age estimates

before this year having large uncertainties (Figure 2). Given the relative agreement between modeling approaches (Figure S1), we proceeded using the Bayesian *plum* model as it provides more realistic conservative estimates for deeper sediments (Aquino-López and others 2018; Hunter and others 2023). 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 and He 2000). Thus, downcore ^{137}Cs concentrations (Figure 3) were attributed to post-depositional diffusion through pore waters (Klaminder and others 2012) or sediment mixing.

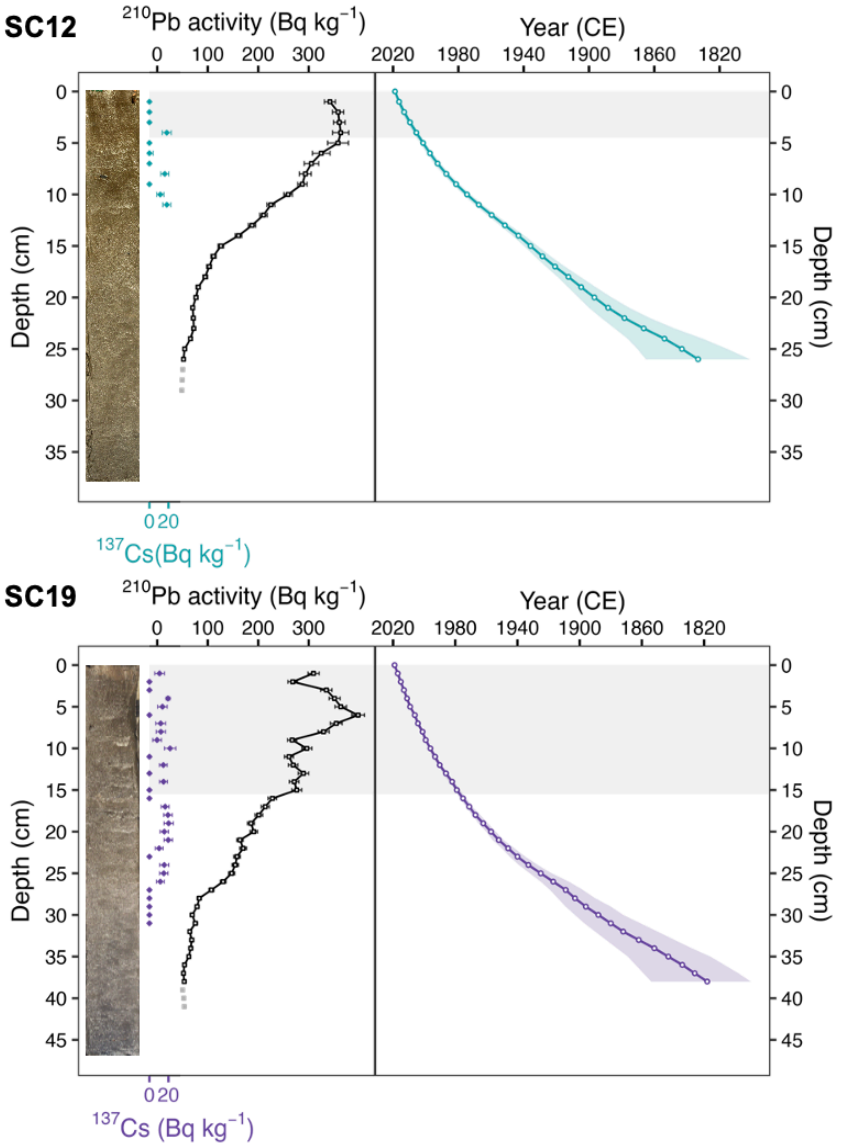

Figure 3.
Total ^{210}Pb (black open squares) and ^{137}Cs (diamonds) specific activity with error bars, measured throughout SC12 (teal) and SC19 (purple). The lowermost parts of the profiles indicate the supported ^{210}Pb (gray filled squares). Age-depth models were calculated for SC12 and SC19 based on the Bayesian *plum* model (Aquino-López and others 2020; 95% confidence interval indicated by shaded ribbon). Gray shading indicates core layers with turbated sediment.

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 (Figure 4). Values of lithogenic material (Ti, Zr, K, Fe, Si) remained relatively stable over the past century, while organic material (Br) increased after 1920 (Figure 5). Atomic ratios of TC:TN (range = 9.3–11.0) exhibited decreasing trends in both cores over the past century (Figure 5). Values of $\delta^{15}N$ displayed minor changes across both cores (range = 0.4–1.3‰). Suess-corrected $\delta^{13}C$ 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 (Figure 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.

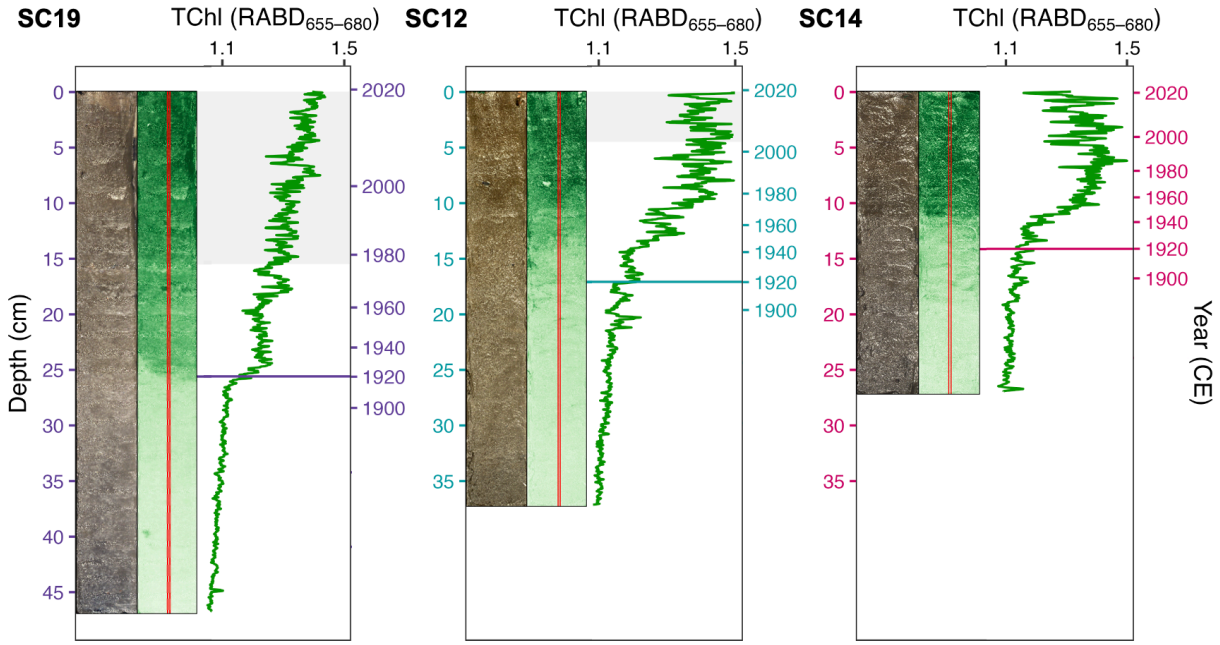

Figure 4. Color photographs of split core faces, colorized image for chloropigment stratigraphy and total chloropigment (TChl) moving average (k = 13 samples) profiles of SC19 (purple), SC12 (teal), and SC14 (pink). Solid horizontal lines indicate the year 1920 CE (± 7 yrs, 95% CI) based on the chronology of each core, and gray shading indicates core parts with turbated sediment.

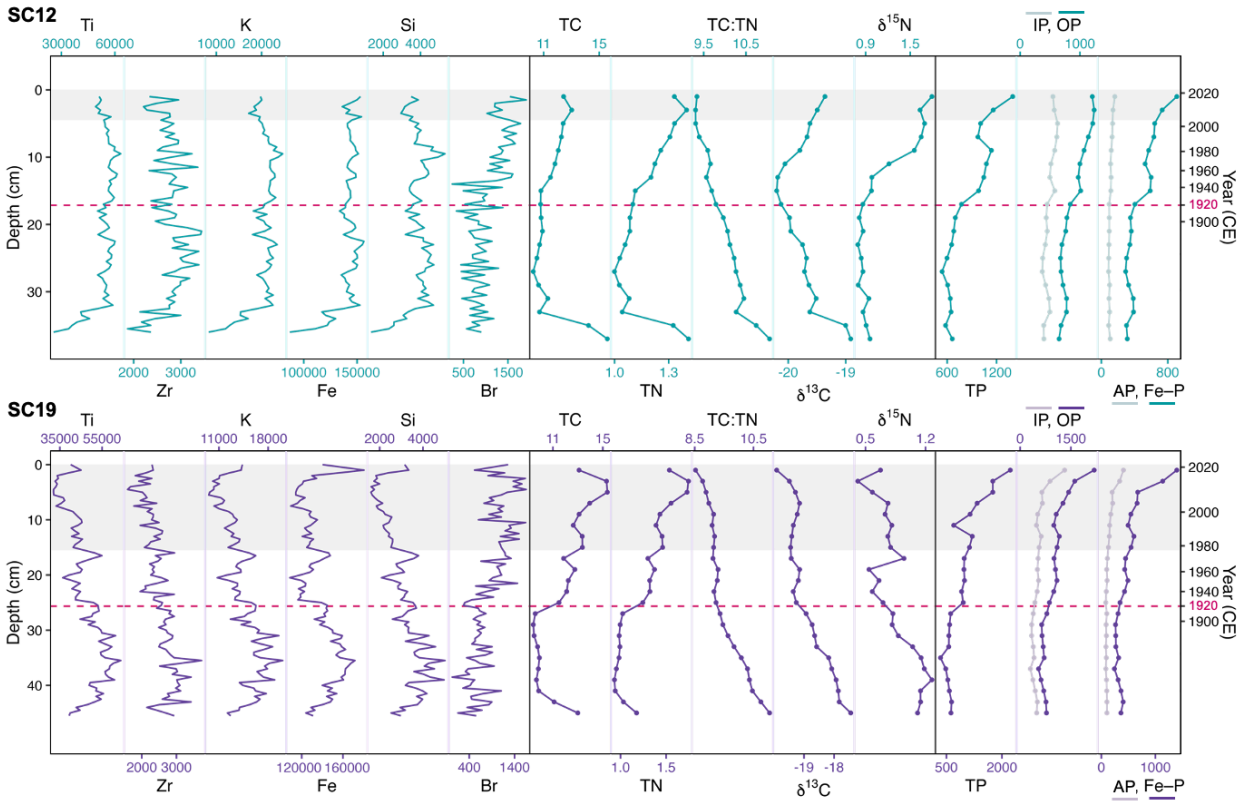

Figure 5. Biogeochemical proxies analyzed in SC12 (teal) and SC19 (purple), including: XRF (Ti, Zr, K, Si, Br; total counts), carbon and nitrogen isotope geochemistry (TC, %; TN, %; C:N; Suess-corrected $\delta^{13}C$, ‰; $\delta^{15}N$, ‰), and phosphorus concentrations (TP, IP, OP, AP, Fe–P; µg P $g^{-1}{}_{d.s.}$). Dashed horizontal lines indicate the year 1920 (± 7 yrs, 95% CI), and gray shading indicates core parts with turbated sediment.

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 (Figure 6; Figure S4). Most pigments were detected in both SC12 and SC19, with the exception of β,β-carotene and peridinin in SC12, and alloxanthin in SC19. CONISS revealed three zones consisting of distinct pigment assemblages: pre-eutrophication (prior to 1920), onset of eutrophication with increases of most pigments (1920–1990), and sustained eutrophication with cyanobacterial dominance (1990–present). RIA indicated mean concentrations increased to values ~2–10x times higher than the low stable concentrations observed prior to 1920 (Figure S5, S6, Table S3).

The zooplankton of SC14 consisted of three genera of cladoceran taxa, including benthic chydorids (*Alona* and *Chydorus*) and planktonic *Bosmina*, as well as

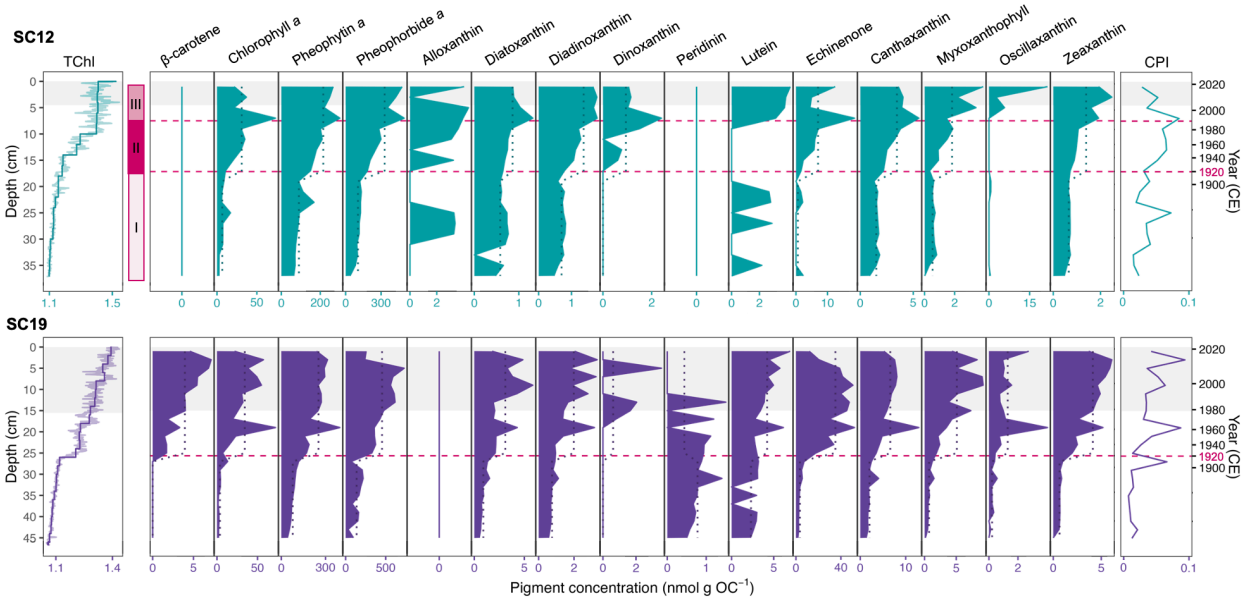

Figure 6. Binned (2 cm intervals) hyperspectral total chloropigments (TChl), relative concentrations of photosynthetic pigments (nmol g OC^{-1}), and chlorophyll preservation index (CPI) measured throughout SC12 and SC19. Zone (I-III) differentiation was based on cluster analysis. Dashed horizontal lines 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 1.

Chaoborus mandibles (Figure 7). All cladoceran taxa exhibited steadily high concentrations until the early-1900s followed by a major decrease around ~1957 (± 5 yrs, Figure S7) despite consistent sampling effort (Figure S8) and changes in sedimentation rates (Figure S9). RIA suggested a significant change in each cladoceran genus after 1920, exhibiting decreased mean concentrations by ~60–85% (Figure 7, S10; Table S4). Notably, *Bosmina* remains were consistently present with a subsequent increase, whereas *Alona* and *Chydorus* remain at low abundances. *Chaoborus* mandibles were rarely encountered, with at most two individuals being found per subsample (Figure S7); thus, no significant change was detected by RIA.

DISCUSSION

Our results suggest that anthropogenic eutrophication of Lake Victoria and the increase in lake level (Figure 2) have had major impacts in the plankton communities of Mwanza Gulf. Nutrient enrichment (P and N) began ~1920 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

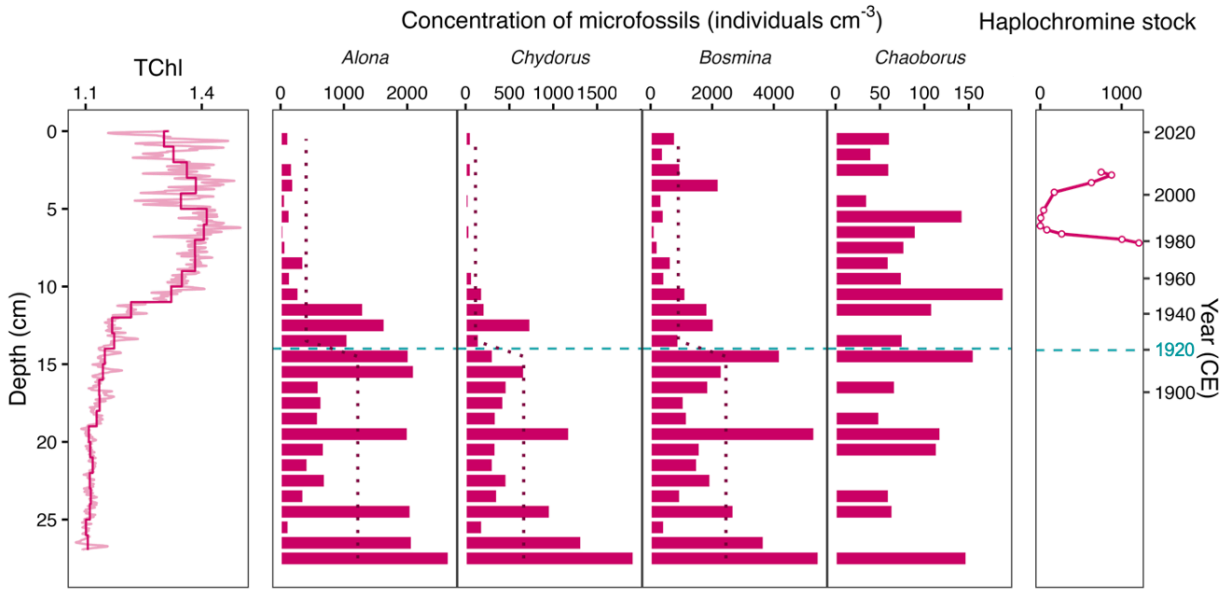

Figure 7. Binned (1-cm intervals) hyperspectral total chloropigments (TChl) and concentration of zooplankton microfossils counted throughout SC14, as well as mean haplochromine stock from trawling surveys (Natugonza and others 2021). Dashed horizontal line indicates 1920 CE (± 7 yrs, 95% CI). Dotted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

eutrophication (1920–1990), and sustained eutrophication (1990–present), that featured increasingly higher pigment concentrations. The cladoceran assemblage, particularly the benthic groups, collapsed in the late-1950s/early-1960s and then partially recovered following the recovery of the haplochromine cichlid population in the 1990s. The timing of the decline is most likely attributable to rising water levels and reduced resource quality that resulted from eutrophication.

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 (Figure 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 and others 2010). TP and bioavailable P (OP and Fe–P)

concentrations exhibited an increasing trend since ~1920, contrasting with low stable values of AP (Figure 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 and others 2010). The stability of AP (non-bioavailable in sediments; Tu and others 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.

Primary production in the Mwanza Gulf reached unprecedented levels in the history of the modern lake in the ~1980-90s and subsequently stabilized (Frank and others 2023). Analysis of bulk organic matter using TC:TN ratios revealed steady declines (Figure 5) consistent with increasing algal dominance. High ratios (>20) are typically indicative of vascular land plants, while lower ratios (5–8) represent plankton dominance (Meyers 1994; Finlay and Kendall 2007). Thus, declining ratios are typical of lakes experiencing shifts to turbid, phytoplankton-dominated conditions (*e.g.*, King and others 2024). 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 and others 2007). TC:TN ratios of Mwanza Gulf were well within the range (typically 8.3–14.6) indicative of moderate N-limitation (Hecky and others 1993), which is consistent with previous reports of Lake Victoria (Talbot and Lærdal 2000). At SC12, the reversal of the Suess-corrected $\delta^{13}C$ trend (Figure 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 $\delta^{13}C$ (Wu and others 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 and Teranes 2001). Lastly, the obtained $\delta^{13}C$ values (Figure 5) are typical of autotrophic lakes (>-27‰) and consistent with expectations for Lake Victoria (Verburg 2007). The lack of increasing $\delta^{13}C$ in SC19 (Figure 5) may result from deeper sediment mixing (as suggested by the ^{210}Pb profile) compared to SC12 due to the higher potential of trawling at the SC19 coring site (Witte and other 2012), which may have stimulated selective preservation of specific fractions of organic matter (Lehmann and others 2002).

Food web responses to eutrophication

Anthropogenic eutrophication led to major shifts in the algal (Figure 6) and cladoceran (Figure 7) assemblages of Mwanza Gulf. Despite low pigment preservation in tropical lakes (Buchaca and others 2019), pigments have been used to successfully reconstruct major shifts in primary production in Lake Victoria (Wienhues and others 2024). In Mwanza Gulf, pigment degradation remained relatively stable across the cores (CPI <0.1; Figure 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 (Figure 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 (± 2 yrs) 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 (Figure 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 (Franke and others 2023). Accordingly, diatoms and cyanobacteria have been the main phytoplankton groups in the Mwanza Gulf, whereas chlorophytes have remained very low or absent. Increased abundances of phytoplankton occurred despite relatively stable $\delta^{15}N$, suggesting that other factors (*e.g.*, temperature) may be influencing algal abundance in addition to increased nutrients.

Changes in the abundance and composition of primary producers did not coincide with the major shift in the cladoceran assemblage in ~1957 (± 5 yrs; Figure 7, S7). Despite the significant decline in cladocerans, the phytoplankton assemblage did not exhibit a corresponding increase in abundance, suggesting that reduced cladoceran grazing pressure did not contribute to the increase in phytoplankton. It is important to note that not all zooplankton taxa (*e.g.*, copepods) are preserved in lake

sediments; thus, reductions in cladoceran abundances do not necessarily imply a reduction in overall zooplankton biomass. However, the decline in cladoceran abundance may be partially attributed to changes in the nutritional quality of the phytoplankton community (Cebrian and others 2009). In eutrophic lakes, zooplankton biomass can be uncorrelated with phytoplankton biomass (Yuan and Pollard 2018) in large part due to the proliferation of inedible phytoplankton, particularly cyanobacteria (Heathcote and others 2016). Cyanobacteria are poorly utilized by herbivorous zooplankton as a food source because they offer low nutritional value, pose toxicity risks, and have physical features that make them challenging to ingest (Vanni 1987; de Bernardi and Giussani 1990; Müller-Navarra and others 2000). Notably, *Bosmina longirostris* can be resistant to some toxins, allowing it to coexist with toxic cyanobacteria blooms (Adamczuk 2016), which may help explain its rising abundances at the turn of the century (Figure 7).

Abundances of all cladoceran taxa in Mwanza Gulf decreased substantially in ~1957 (± 5 yrs), possibly due to the cumulative impacts of lake-level rise and anthropogenic eutrophication. The parallel decline of both benthic chydorids and *Bosmina* (Figure 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 and others 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 and others 2000). Comparatively, rising lake levels may have made planktonic *Bosmina* more vulnerable to predation by reducing refuge afforded by submerged open-water macrophytes (Iglesias and others 2007). Together with the higher water levels, enhanced algal production in the Mwanza Gulf (Figure 6) could have led to decreased water transparency (Verschuren and others 2002) and light availability for littoral macrophytes (Natugonza and others 2021). Turbid waters likely inhibited macrophyte establishment due to reduced light penetration and reduced suitable chydorid habitat (Whiteside and 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 (Figure 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 and Hairston 1988; Branstrator and others 2003). Discontinuous monitoring indicates that decreased cladoceran abundances in Mwanza Gulf were accompanied by increased cyclopoid copepod abundances, which are cladoceran predators (Wanink and others 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 and others 2009) or better predator avoidance (Semyalo and others 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 contained relatively few *Chaoborus* remains, likely due to not reaching the minimum threshold of remains for reliably estimating past abundance (Figure S8; Quinlan and Smol 2010). This limitation arose from our sampling strategy, which primarily targeted Cladocera rather than *Chaoborus.* 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 and others 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 and others 2002). Whereas some studies have speculated that the shift in zooplankton assemblage is attributable to increased dagaa abundances (van Zwieten and others 2016), our time series demonstrate that the collapse of cladocerans clearly predates changes in the fish community in Mwanza Gulf (Figure 7). However, as nearshore turbidity improved in the 1990s (Sitoki and others 2010), ongoing fishing pressures contributed to declines in Nile perch population and the recovery of haplochromines in the Mwanza Gulf (Witte and others 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 and others 2007). The concurrent increases

in *Bosmina* (Figure 7) suggest that the recovery of haplochromines may have released some of the controls (*e.g.*, *Chaoborus* or copepod predation) limiting *Bosmina* abundance.

CONCLUSIONS

This study demonstrates that anthropogenic eutrophication profoundly altered planktonic community structure of Mwanza Gulf. Nutrient increases beginning in ~1920 promoted higher algal abundances, particularly of cyanobacteria, which in combination with rising lake-levels in the ~1960s 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.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY

All data are available in Zenodo: https://doi.org/10.5281/zenodo.10870087.

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Supplementary Material

King L[*1,2], Wienhues G[*3], Misra P[1,2], Tylmann W[4], Lami A[5], Bernasconi SM[6], Jaggi M[6], Courtney-Mustaphi CJ[7,8], Muschick M[1,2], Ngoepe N[1,2], Mwaiko S[1,2], Cohen A[9], Kishe MA[10], Heiri O[7], Seehausen O[1,2], Vogel H[11], Grosjean M[3], Matthews B[1]. In press. Anthropogenic eutrophication drives major food web changes in Mwanza Gulf, Lake Victoria. *Ecosystems*.

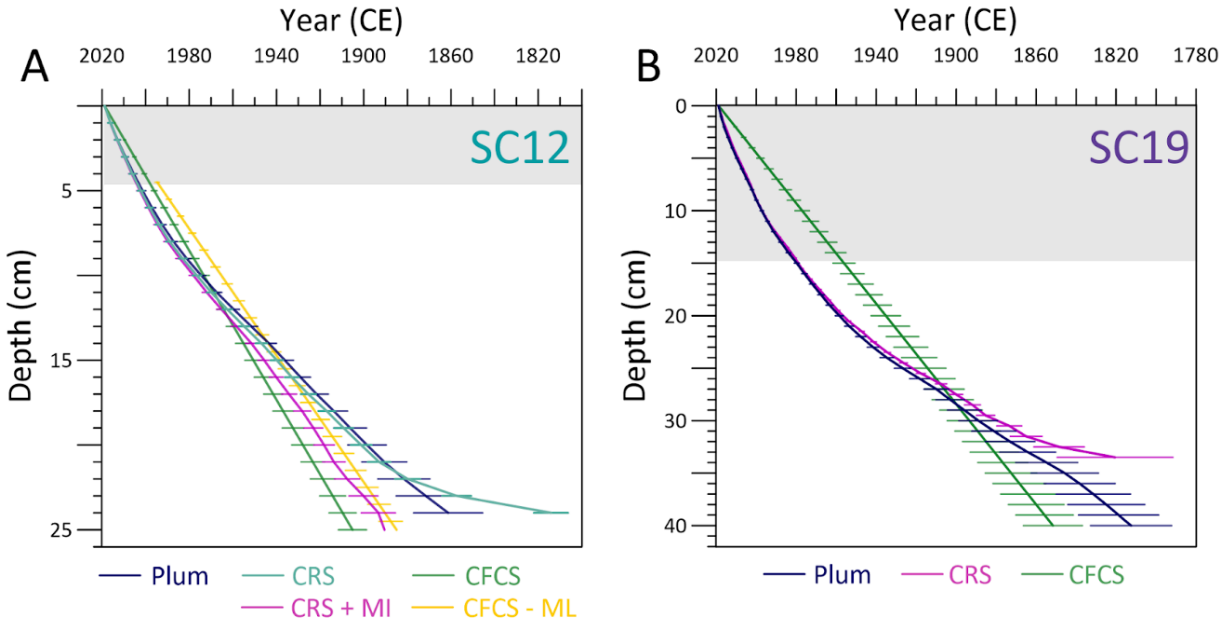

Figure S1. Alternative age-depth models considered for SC12 (A) and SC19 (B), including the Constant Rate of Supply (CRS), missing inventory corrected Constant Rate of Supply (CRS + MI), Constant Flux:Constant Sedimentation (CFCS), Constant Flux:Constant Sedimentation excluding the turbated layer (CFCS - ML), and Bayesian *plum* models. Gray areas indicate core layers with turbated sediment.

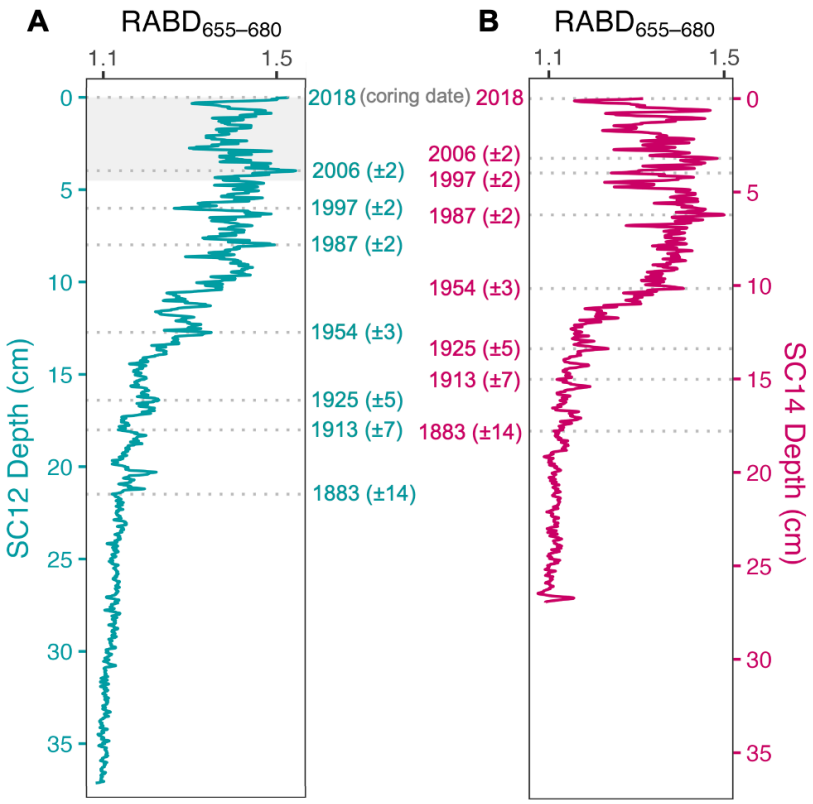

Figure S2. Correlation points between hyperspectral-inferred $RABD_{655\text{-}680}$ profiles used to apply the SC12 (A) chronology to its paired core, SC14 (B), with ages linearly interpolated between correlation points.

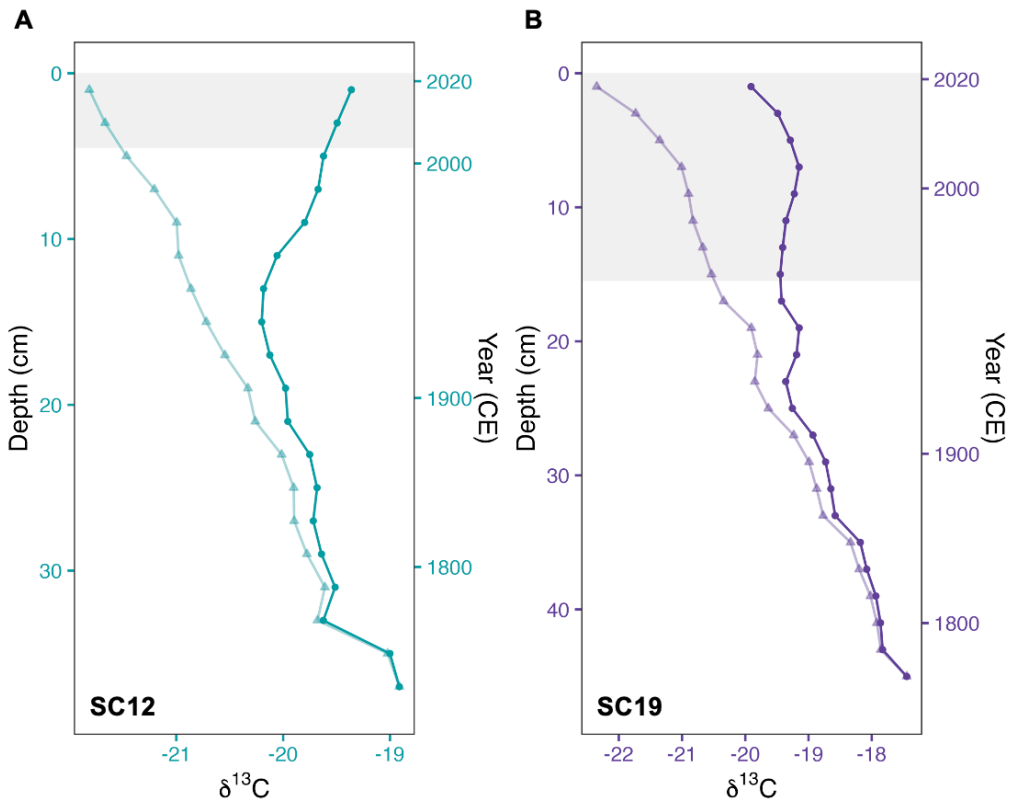

Figure S3. Suess-corrected $\delta^{13}C$ values (dark circles), following Verburg (2007), compared with original $\delta^{13}C$ signatures (light triangles) of SC12 (A) and SC19 (B).

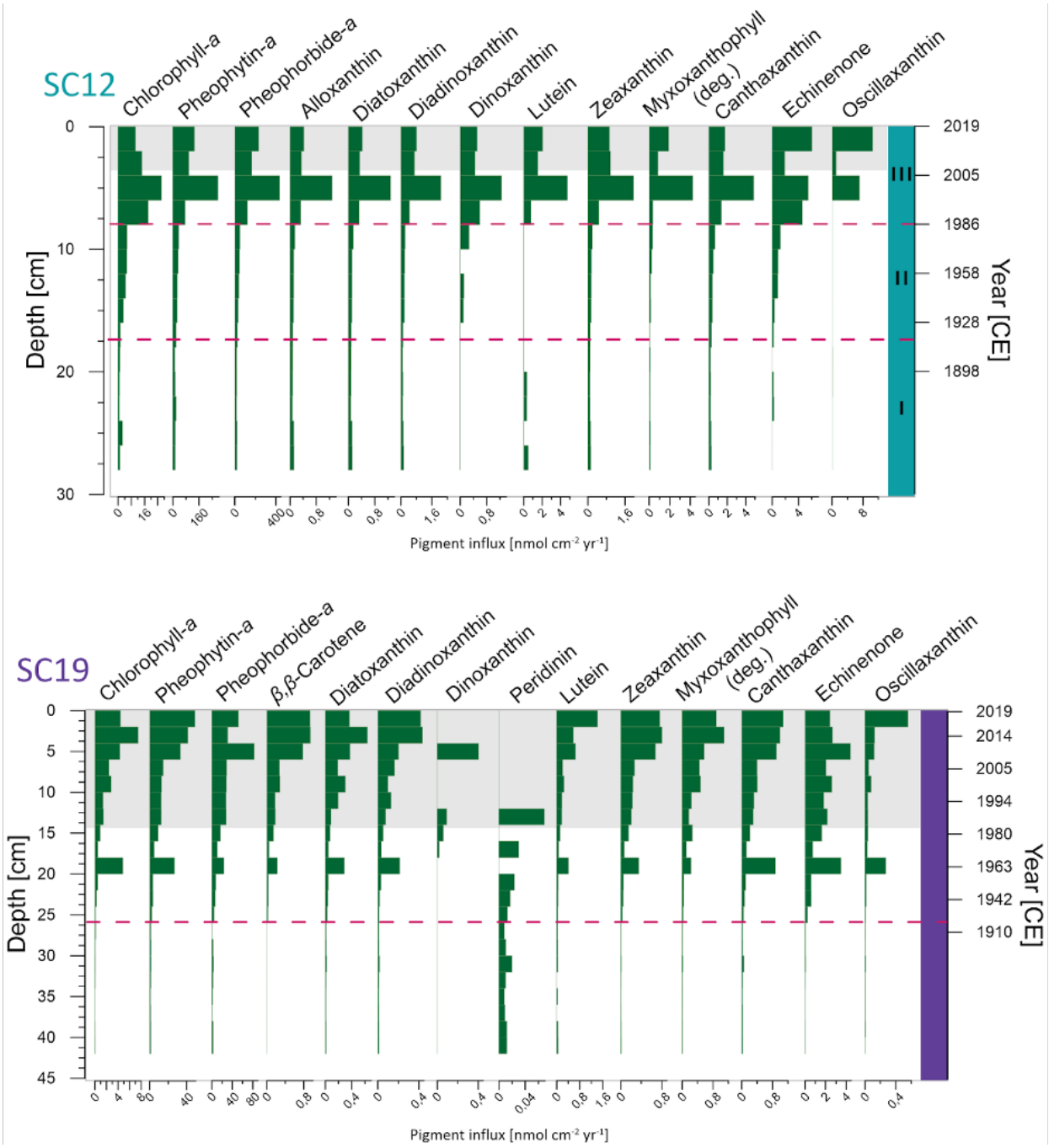

Figure S4. Pigment influxes for the cores SC12 and SC19.

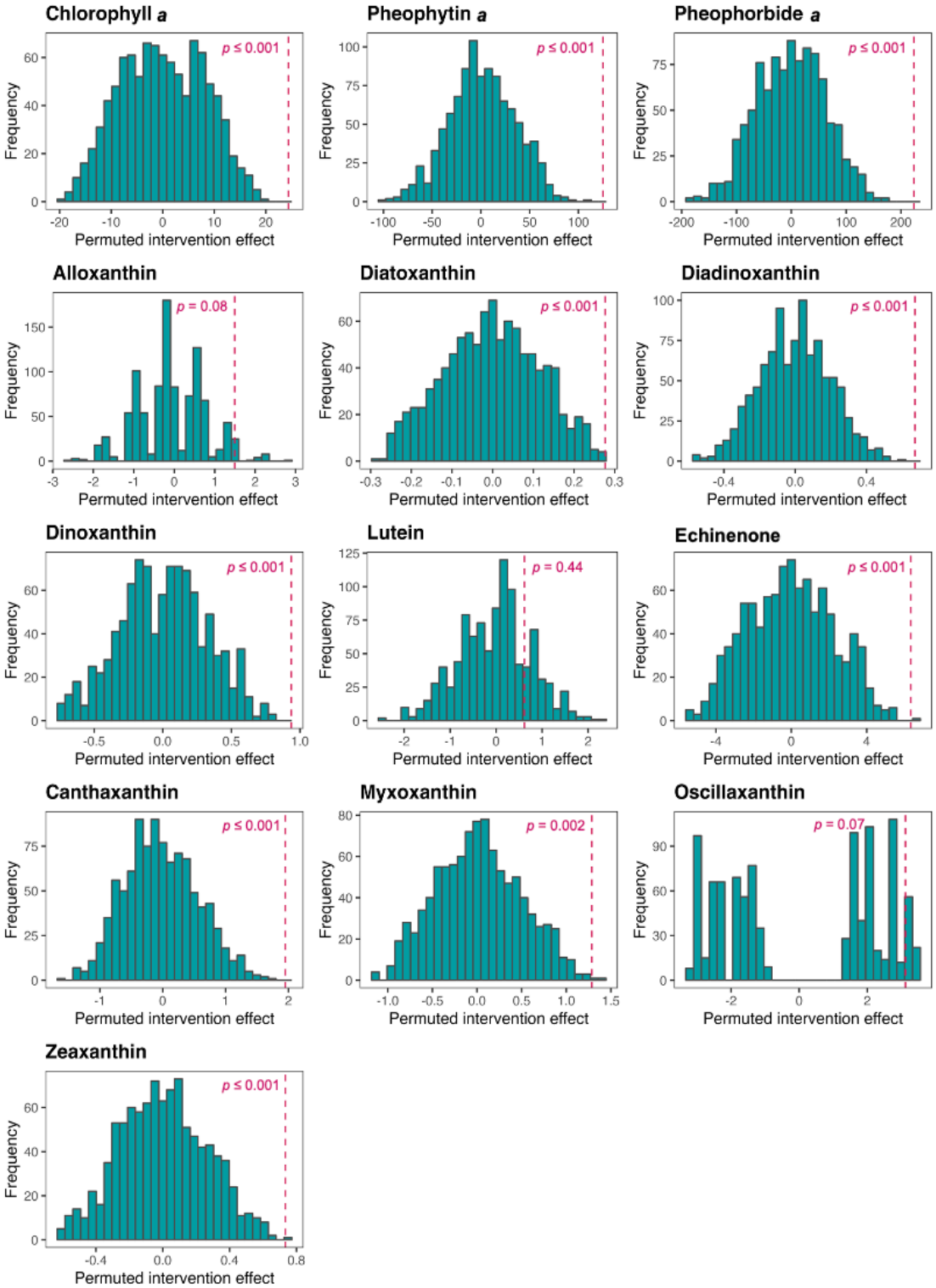

Figure S5. Intervention analysis of SC12 pigment concentrations using 18 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

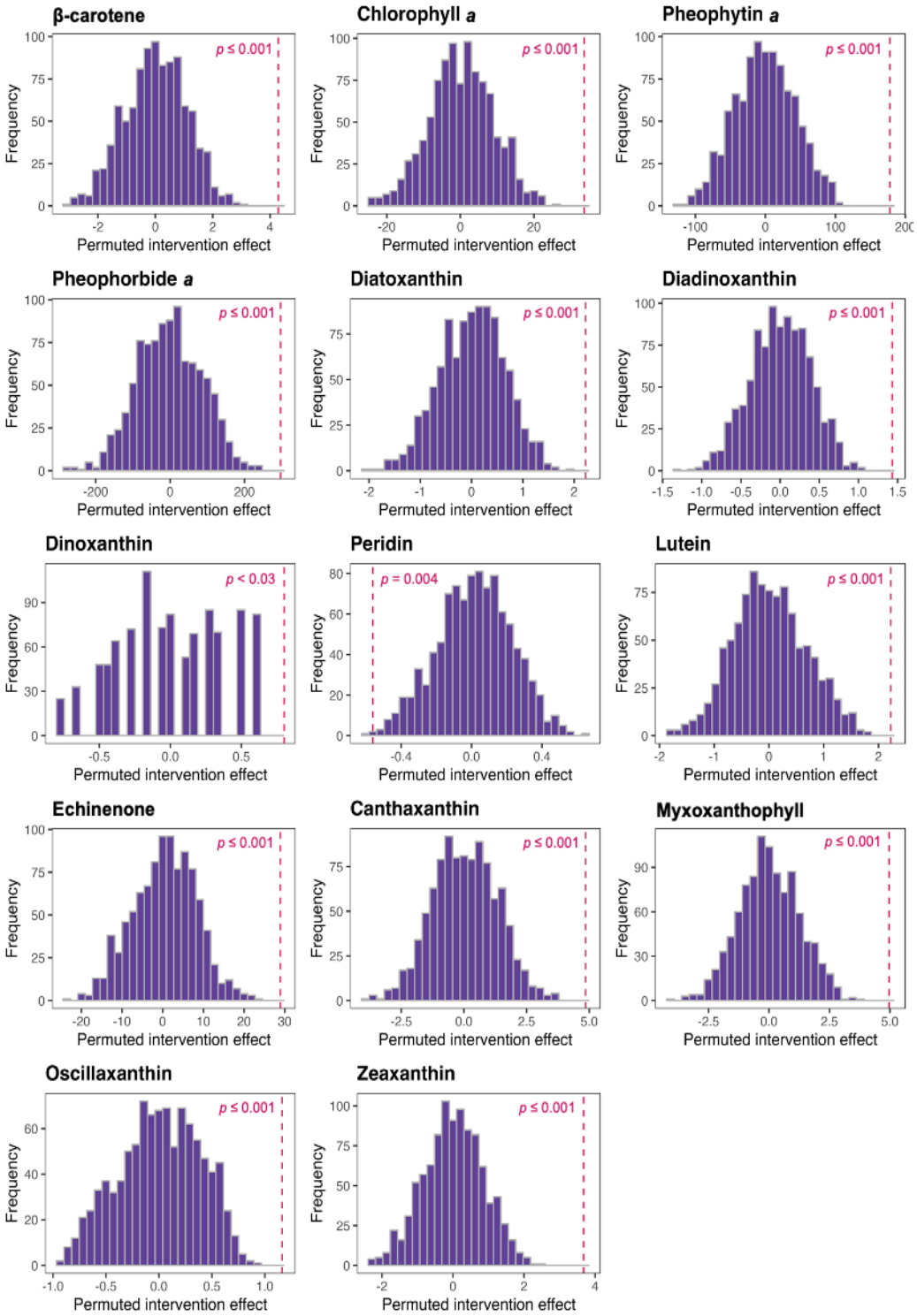

Figure S6. Intervention analysis of SC19 pigment concentrations using 26 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

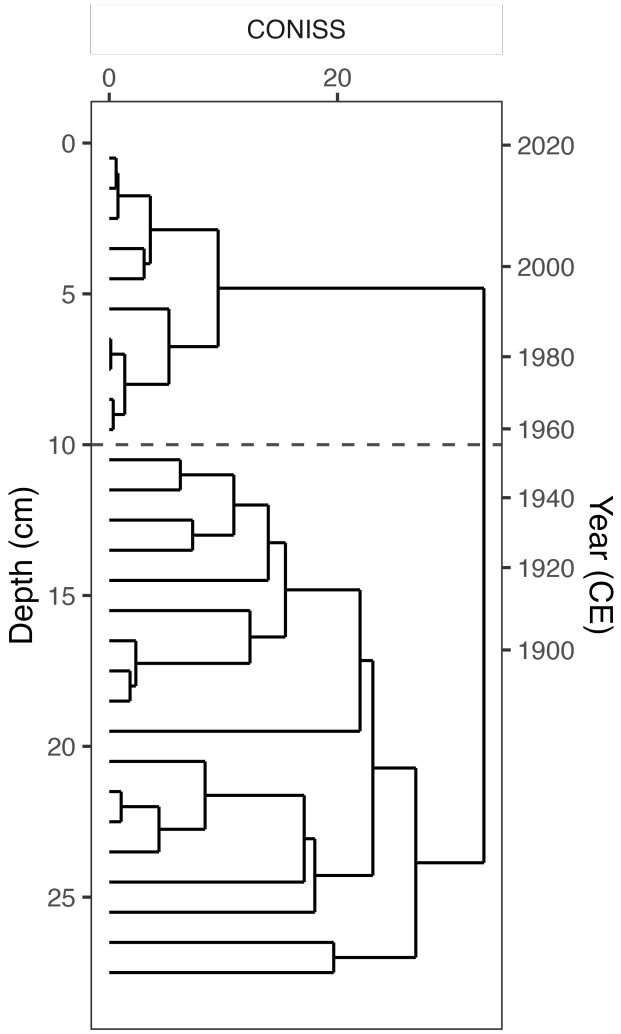

Figure S7. CONISS dendrogram for SC14 with dashed line indicating distinct cladoceran assemblages.

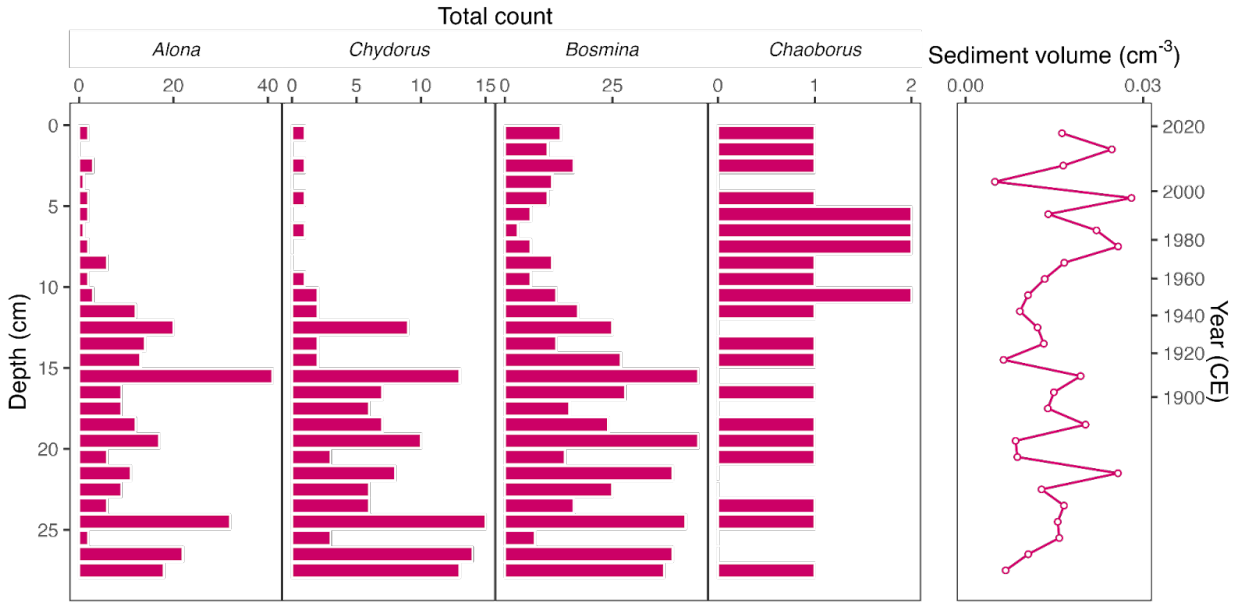

Figure S8. Total counts of Cladocera and *Chaoborus* individuals in SC14, determined by the minimum number of individuals possible given the most abundant body part of each taxon, and the total volume of sediment examined in each subsample.

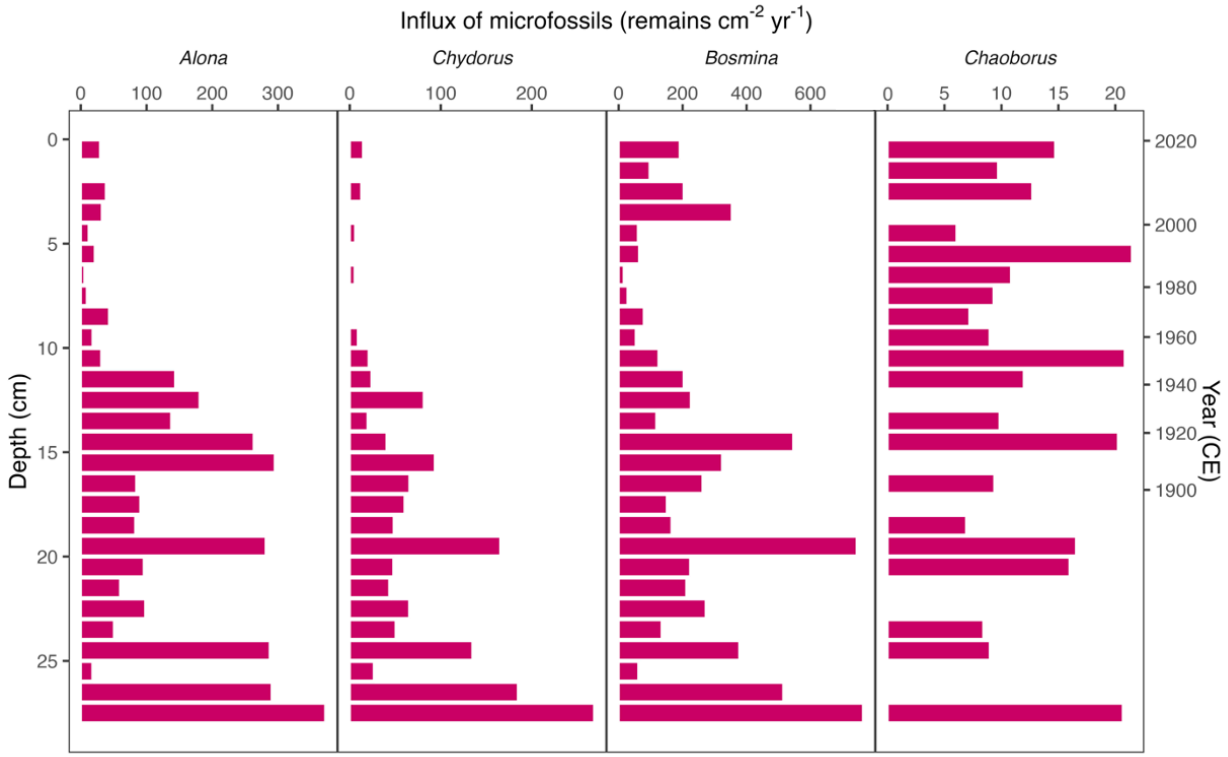

Figure S9. Influx of Cladocera and *Chaoborus* microfossils counted throughout SC14.

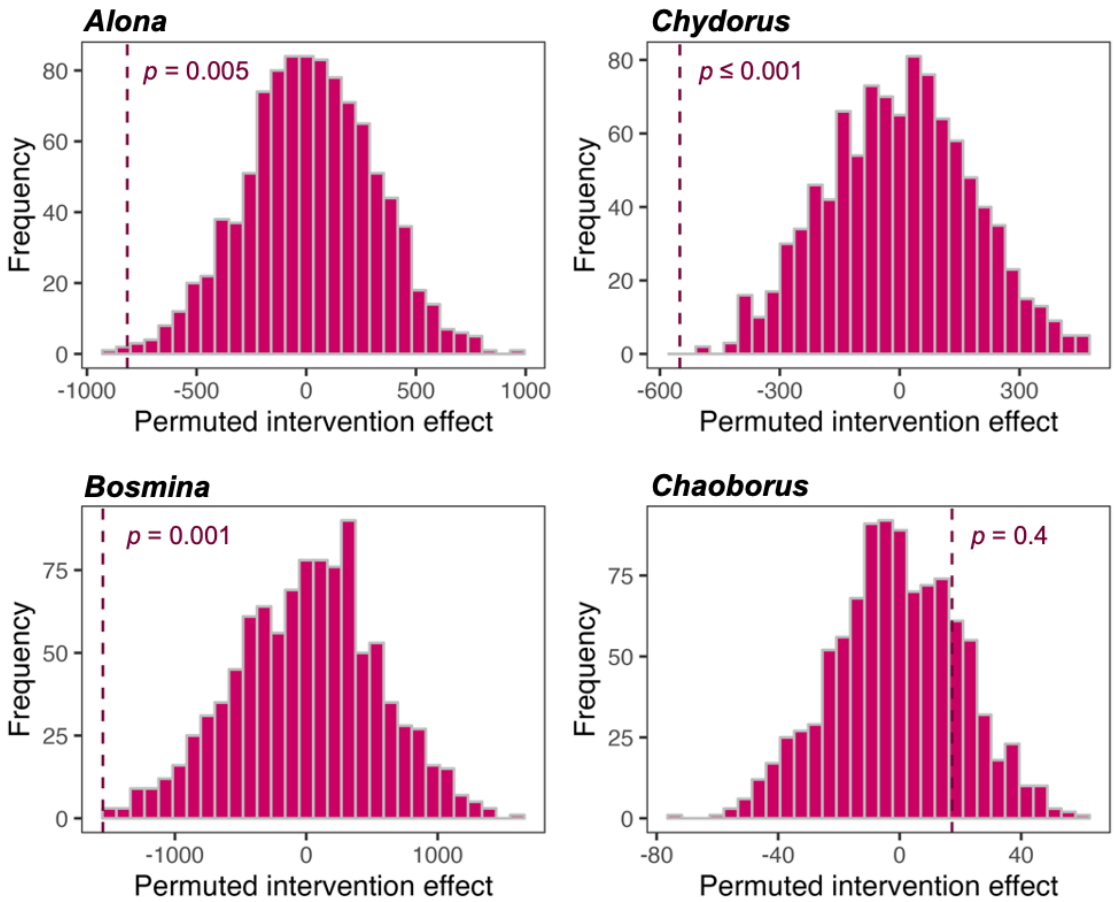

Figure S10. Intervention analysis of SC14 Cladocera and *Chaoborus* microfossil concentrations using 14 cm core depth as the intervention point to represent 1920 CE. Dashed lines indicate the observed intervention effect.

Table S1. 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).

Lab ID	Depth interval (cm)	Density (g cm^{-3})	Total ^{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	16.0
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 S2. 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	3.3
LV_SC19_41	40–41	0.005476	53.4	3.5

Table S3. 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
Peridinin	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 S4. Randomized intervention analysis results of Chaoborus and Cladocera taxa.

	SC14		
Zooplankton	Pre-1920	Post-1920	p-value
Alona	1219	403	0.005
Chydorus	663	113	≤0.001
Bosmina	2448	899	0.001
Chaoborus	55	73	0.4

Chapter 3

Spatiotemporal heterogeneity of sedimentary invertebrate assemblage responses to anthropogenic disturbance in Mwanza Gulf, Lake Victoria

ABSTRACT

Understanding species-specific responses in relation to spatiotemporal environmental heterogeneity of anthropogenic eutrophication is an ongoing challenge for aquatic ecologists. For example, it is well known that chironomid and cladoceran taxa are often distributed by water depth, but such specificity in niche use, both within and among broad taxonomic groups, is rarely accounted for in efforts to characterize eutrophication impacts on lakes. Here, we examine the patterns of shifts in invertebrate assemblages along a large-scale (>30 km) nearshore to offshore transect of the Mwanza Gulf in Lake Victoria, a region that has been heavily impacted by various types of anthropogenic disturbance, most notably eutrophication. Sediment cores were collected along a water depth gradient and subsequently scanned with hyperspectral imaging to obtain a high-resolution record of past algal production over the past century. Identification of invertebrate subfossils were used to reconstruct cladoceran and chironomid assemblages over the past ~150 years. Our findings highlight the spatiotemporal heterogeneity associated with the onset of eutrophication in large lakes. Increased algal abundance was observed across all sites, but while chironomid abundances increased, cladoceran abundances decreased. Furthermore, variation in community structure according to water depth suggests that pre-disturbance conditions ultimately influence assemblage responses. Overall, this study emphasizes the need to account for the spatial and temporal variability of anthropogenic impacts and community responses across the complex mosaic of lake habitats.

INTRODUCTION

Understanding the spatiotemporal heterogeneity of community structure is crucial for preserving ecosystem function when confronted with anthropogenic disturbances that have heavily degraded lake ecosystems worldwide (Kratz et al. 2005). As the nexus of human interactions with lakes, the nearshore littoral zone is often more negatively affected by anthropogenic stressors than offshore regions (Vadeboncoeur et al. 2011). Large lakes, in particular, exhibit substantial spatial and temporal variation in water quality parameters and community composition between offshore and nearshore regions, and therefore can respond differently to environmental changes (Yurista et al. 2016). In light of this, assessments of community structure should account for spatiotemporal variation when inferring the interplay between anthropogenic activities and lake ecosystems.

Over the last several decades, lake sediment records have become increasingly important in providing long-term assessments of community structure in response to human stressors (Quinlan et al. 2008; Goodenough and Webb 2022). Changes in the species composition of Cladocera (Crustacea) and Chironomidae (Diptera) can be indicative of habitat alterations and changes in lake trophic structure driven by anthropogenic stressors (Jeppesen et al. 2001; Brodersen and Quinlan 2006). Because of their central position in lake food webs and short generation times, they respond rapidly to disturbances and changes in community structure track changing environmental conditions (Korhola and Rautio 2001). The assumption that a single core is representative of the entire lake community (Smol 2008) may introduce biases by differentially integrating taxa from across heterogeneous basins (Nevalainen 2011). Numerous invertebrate taxa are spatially distributed across a lake based on habitat type, such as littoral versus pelagic zones. Consequently, lake sediments integrate subfossil remains of locally living cladocerans and chironomids, particularly with respect to water depth (Eggermont et al. 2007; Kattel et al. 2007; Kurek and Cwynar 2009; Nevalainen 2011). Thus, a multi-core approach is necessary to capture the spatiotemporal variability of large, complex lake systems.

Lake Victoria is the largest tropical lake (surface area = 68,800 km^2) in the world, and is renowned both for its species-richness and its extent of nutrient pollution (Izmailova and Rumyantsev 2016). The lake supports the largest human population along its shoreline and fisheries harvest of any large lake worldwide (Sterner et al. 2020). Previous neo- and paleo-ecological research has demonstrated major shifts in community structure across the entirety of the food web that have occurred in response to excessive nutrient enrichment, changes in water level, intensified fishing

pressures, and the introduction of non-native species (Witte et al. 1992; Seehausen et al. 1997; Verschuren et al. 2002; Wanink et al. 2002; Hecky et al. 2010; van Zwieten et al. 2016; Deirmendjian et al. 2021; Natugonza et al. 2021; Frank et al. 2023). Shallow, nearshore gulfs have been more heavily impacted by eutrophication, exhibiting chlorophyll *a* concentrations ~60% higher than offshore regions (Mugidde 1993). While the onset of anthropogenic eutrophication and in turn, the declines in cladoceran abundance differed by up to two decades between northern and southern nearshore areas of the lake (King and Wienhues et al. *in press*), there has yet to be an investigation of the spatiotemporal variability of invertebrate community composition between nearshore and offshore lake habitats.

Here, we aimed to examine the intralake spatiotemporal heterogeneity in the onset of anthropogenic eutrophication and changes in invertebrate assemblages along a nearshore to offshore transect of Mwanza Gulf, Lake Victoria (Figure 1). High-resolution hyperspectral imaging (HSI) and x-ray fluorescence were used to examine changes in total chloropigments as an indicator of past algal production (Butz et al. 2015) and elemental composition as an indicator of changing catchment and in-lake dynamics respectively. Identification of preserved subfossil remains were used to reconstruct past cladoceran and chironomid assemblages (Korhola and Rautio 2001; Walker 2001). The main objectives were to **(1)** reconstruct changes in Cladocera and chironomid assemblages across a water depth transect in response to past anthropogenic pressures, and **(2)** assess the temporal and spatial (dis)similarity of shifts in species abundance.

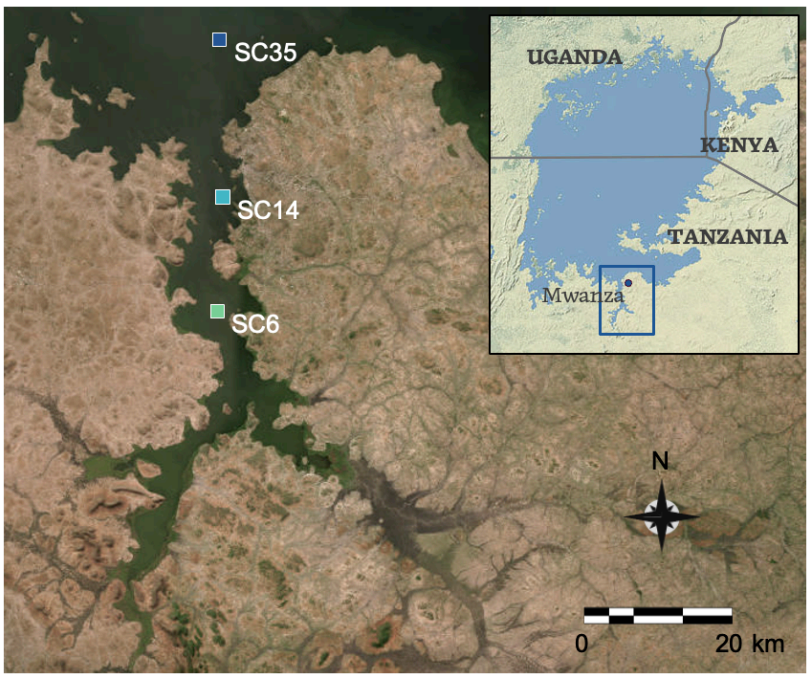

Figure 1.
Map of coring locations (squares) in the Mwanza Gulf, Lake Victoria (map inset).

METHODS

Study area

Located in the south-east of the lake, Mwanza Gulf has undergone major ecological change over the past century due to anthropogenic pressures. Excessive nutrient enrichment began in the 1920s, which rapidly led to increases in primary production (King and Wienhues et al. *in press*). Subsequently, non-native Nile perch (*Lates niloticus*) and water hyacinth (*Eichhornia crassipes*) were introduced in the 1950s (Pringle 2005) and 1980s (Witte et al. 1995), respectively. Construction of the Nalubaale Dam (Jinja, Uganda) further complicated ecological dynamics by sustaining increased water levels from higher than average rainfall from 1961–1964 (Awange et al. 2008). Cumulatively, these pressures led to a significant decline in cladoceran abundance, particularly of littoral taxa, that preceded the loss of endemic haplochromine cichlids in the 1980–90s (King and Wienhues et al. *in press*). Today, spatial heterogeneity of water quality parameters (*e.g.*, light availability), algal biomass, and fish distribution has been observed within Mwanza Gulf (Getabu et al. 2003; Cornelissen et al. 2014, 2015, 2018; Frank et al. 2023).

Sediment core collection and processing

Sediment cores were collected along a 35 km water depth transect of the Mwanza Gulf (Figure 1) in 2018 and 2022 using a UWITEC gravity corer. The coring locations included a littoral shallow water core (SC6, ~6.5 m water depth; 2°41'37.6"S, 32°52'02.9"E), an intermediary core (SC14, ~14.5 m water depth; 2°33'28.4"S 32°52'28.2"E), and a pelagic deepwater core (SC35, ~35 m water depth; 2°22'20.0"S, 32°52'13.9"E). Note that the core labels refer to the respective water depth at which they were collected.

After collection, all cores were transported to the University of Bern (Switzerland) where they were split lengthwise and scanned using non-destructive geochemical methods. High-resolution hyperspectral imaging (HSI) was used to examine changes in total chloropigments (TChl: chlorophyll *a*, *b*, and derivatives) as an indicator of past algal production (Butz et al. 2015). All cores were scanned using a Specim Single Core Scanner system (Spectral Imaging Ltd., Oulu, Finland) equipped with a Specim PFD-xx-V10E camera at the University of Bern (Switzerland). Reflectance data was acquired from 400–1000 nm across the visible to near-infrared spectrum, and total chloropigment abundances were quantified using the relative absorption band depth index ($RABD_{660-670}$). Elemental composition of the sediment was determined using x-ray fluorescence (XRF). Scanning was carried out using an ITRAX (Cox Ltd., Sweden) at

the University of Bern with a chromium anode at 50mA, 10kV, and 30 seconds integration time over 0.5 cm intervals.

Thereafter, both core halves were contiguously subsampled in 1 cm intervals for further analyses. Freeze-dried and homogenized sediment subsamples from SC35 and SC6 were analyzed for estimates of ^{210}Pb, ^{137}Cs and ^{226}Ra activity using gamma-spectrometry (High-Purity Germanium Well Detector, HPGe, Canberra, USA) at the Swiss Federal Institute of Aquatic Science and Technology (Eawag, Dübendorf, Switzerland). SC14 was stratigraphically correlated using TChl profiles to a paired core that was analyzed for ^{210}Pb (via^{210}Po) using alpha-spectrometry (King and Wienhues et al. *in press*).

Invertebrate analyses consisted of the identification of morphological remains of Cladocera and Chironomidae. The volume of sediment of each subsample (~0.2–1.5 cm^3 for Cladocera, ~2–12 cm^3 for Chironomidae) was measured via water displacement. Cladocera and Chironomidae subsamples were then wet sieved through a 38 µm mesh or 100 µm mesh, respectively, and rinsed into labeled vials with a known amount of water (~9–21 cm^3). The cladoceran solution was pipetted (~0.1 cm^3) onto glass slides and permanently affixed using glycerin jelly. Chironomid remains were separated from sediments by manual picking with forceps under a stereomicroscope (~25x), allowed to dry, and mounted on glass slides using Euparal (Carl Roth). All mounted slides of chironomids and cladocerans were then examined across their entirety via bright-field illumination with a compound microscope (100–400x). Individual remains were tabulated separately and identified to the highest taxonomic resolution possible following published literature (Eggermont and Verschuren 2004a,b; Verschuren and Eggermont 2006; Brooks et al. 2007; Szeroczyńska and Sarmaja-Korjonen 2007; Korosi and Smol 2012a,b), with the most frequent remain (*i.e.*, carapaces, headshields) used to estimate to the minimum number of individuals (Korhola and Rautio 2001).

Data analyses

Chronologies of SC35 and SC6 were modeled using Bayesian statistics (*Plum*), as well as the Constant Flux Constant Sedimentation (CFCS) and the Constant Rate of Supply (CRS) models to ensure relative conformity between approaches. The Bayesian *Plum* model was developed using the 'rplum' package (Aquino-López et al. 2018) and the CFCS and CRS models were developed using the 'serac' package (Bruel and Sabatier 2020) in R (version 4.3.3, R Core Team 2024). The excess fraction of ^{210}Pb

from atmospheric fallout was calculated as the total ^{210}Pb activity minus the ^{226}Ra activity (Bruel and Sabatier 2020).

For chironomid and cladoceran assemblages, the influx of individuals to the sediment was calculated by dividing the minimum number of individuals per cm^3 of sediment (concentration) by the number of years per cm of depth. Stratigraphically constrained cluster analysis (CONISS, Grimm 1987) was performed using the *tidypaleo* package (version 0.1.3, Dunnington et al. 2022) to identify the timing of shifts between distinct assemblages for each coring location. Unknown taxa were omitted, and influxes were scaled to a mean of 0 and variance of 1 prior to clustering. Non-metric multidimensional scaling (NMDS) was conducted using vegan (version 2.6-4, Oksanen et al. 2022) to examine spatial and temporal development of chironomid and cladoceran assemblages, excluding unknown taxa. The analysis was applied collectively across all cores using Bray-Curtis similarity matrices of influx data in order to assess differences in assemblages and their responses between cores.

RESULTS

Depth-time profile

Declines of excess ^{210}Pb activity were observed downcore in SC35 and SC6 (Figure 2).

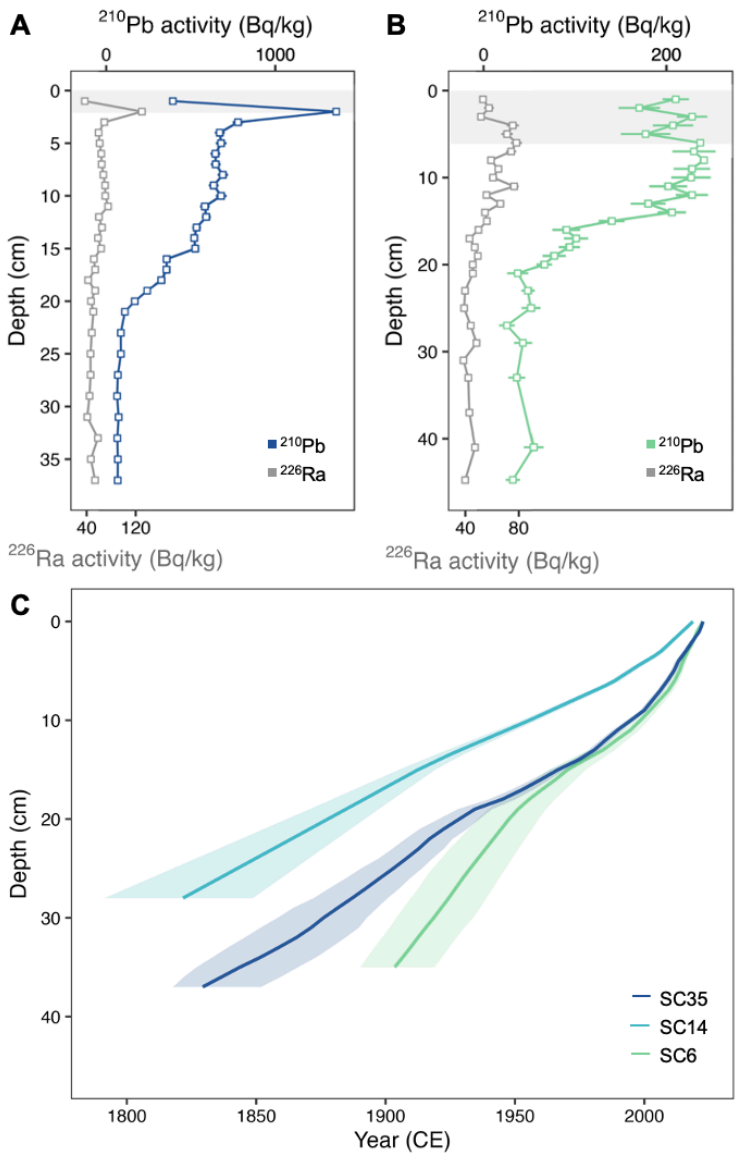

Figure 2.
Total ^{210}Pb and ^{226}Ra activity measured in SC35 (A) and SC6 (B) used to establish the age-depth model of each core (C) using Bayesian statistics. The age-depth model for SC14 was obtained from (King and Wienhues et al. *in press*).

Sediment mixing/disturbance in the uppermost sediments of SC35 (2 cm) and SC6 (6 cm) was inferred from inconsistencies in the expected pattern of declining ^{210}Pb activity. Given the relative agreement between age-depth models (Figure S1), we proceeded to use the *Plum* age-depth model for consistency with SC14.

The *Plum* age models indicated that SC35 represented ~1820–2022 CE and SC6 represented ~1870–2022 CE. The age-depth model for SC14, obtained from (King and Wienhues et al. *in press*), represented ~1845–2018 CE. Age estimates prior to 1900 CE had relatively large confidence intervals (ranging more than ±15 yrs) and were therefore excluded from any ecological interpretation. Downcore activity of anthropogenic ^{137}Cs (Figure S2) were not used to constrain the age models because of the possibility of downward diffusion and complexities of interpreting these records in tropical African lakes (Walling and He 2000; Klaminder et al. 2012).

Algal production

The onset of anthropogenic eutrophication, as indicated by TChl profiles, differed slightly between cores (Figure 3). The increase was first observed in SC14 around 1920 (±6 yrs; King and Wienhues et al. *in press*). Subsequently, the onset in SC35 was detected at ~1920 (±10 yrs). The

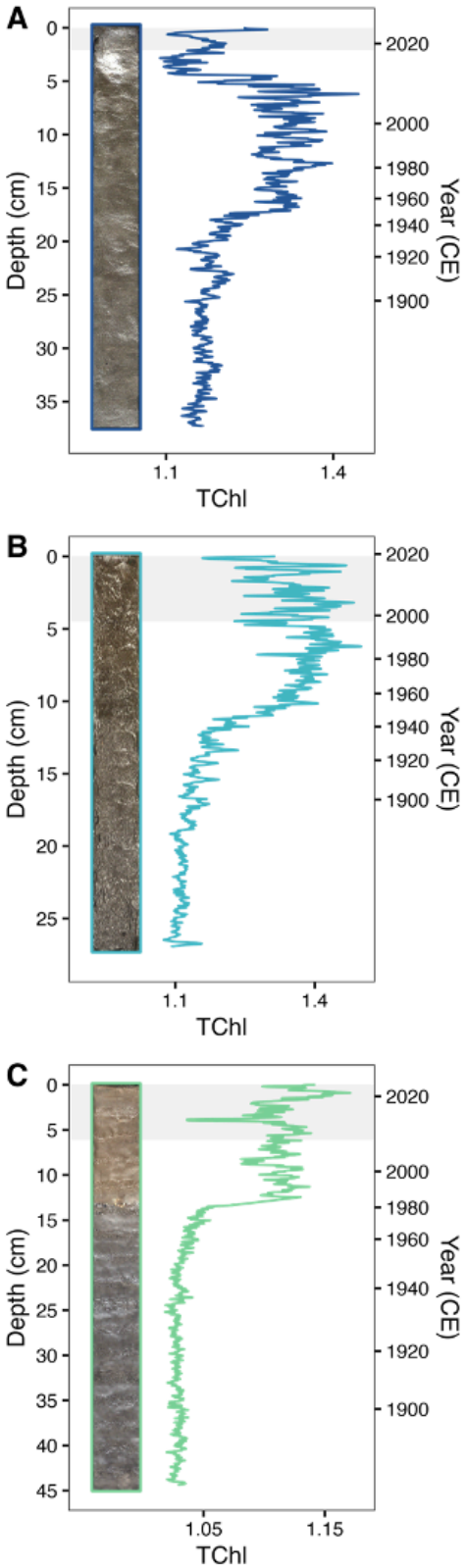

Figure 3.
Moving-averages (k = 13 samples) of total chloropigment (TChl, $RABD_{660\text{-}670}$) profiles of SC35 (A), SC14 (B, modified from King and Wienhues et al. *in press*), and SC6 (C). Photographs of core faces are inset, and gray shading indicates sections of inferred sediment mixing.

major decrease in the uppermost intervals of SC35 were attributed to poor quality reflectance from water-saturation (see core image; Figure 3) rather than a true ecological signal. Lastly, minor increases in SC6 started as early as ~1940 (±13 yrs), with major increases not occurring until ~1980 (±6 yrs). The elemental profiles measured using XRF (Figure S3) indicated relative stability, with some minor deviations, in SC6 of detrital input (Ti, Zr, K, Fe; Davies et al. 2015), decreasing Si, and increasing productivity (Br). In SC35, detrital inputs exhibited a sharp decrease around ~1960 that never recovered to pre-disturbance levels, as well as increased productivity and hypolimnetic hypoxia.

Invertebrate subfossils

Total abundance and species composition varied amongst cores, and timing of changes in the chironomid assemblage varied between cores (Figure 4). Total

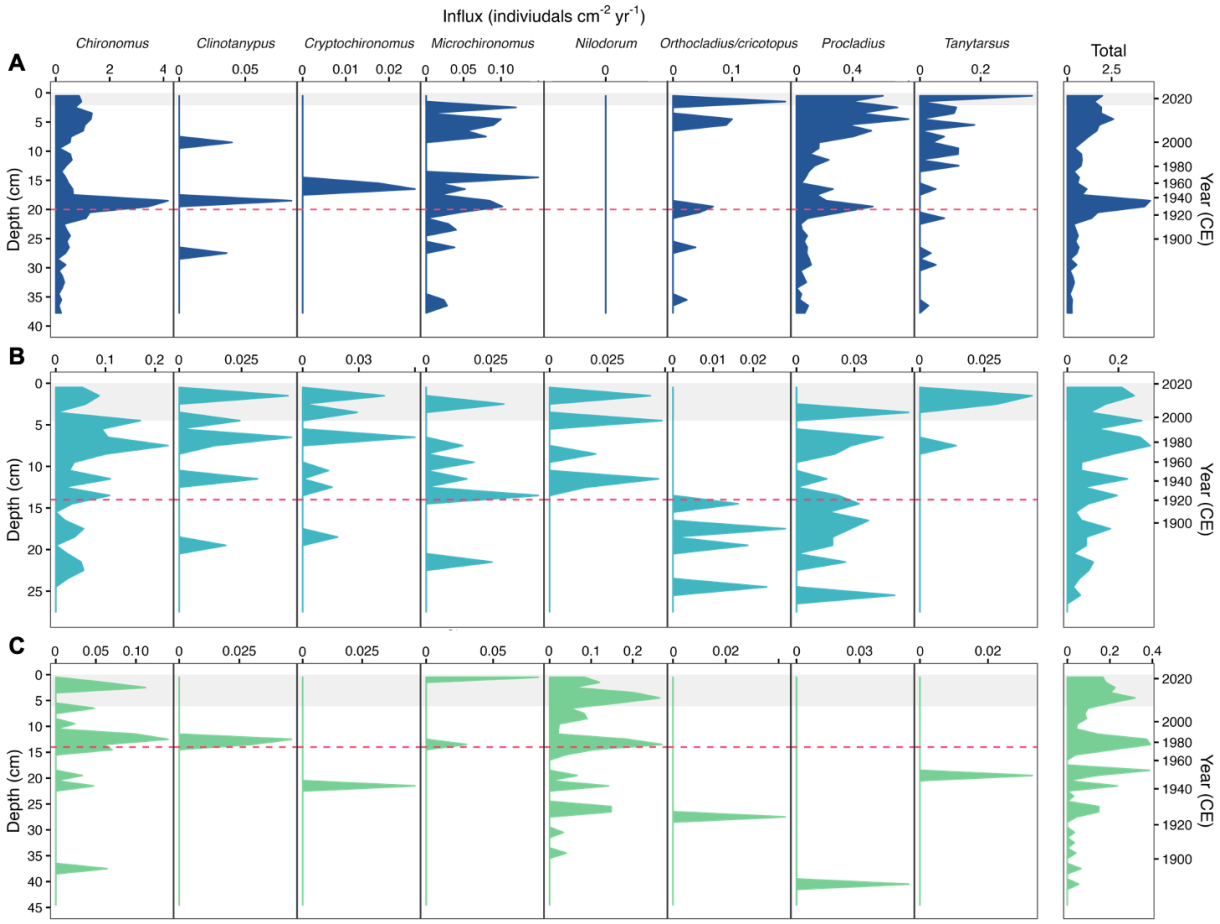

Figure 4. Influx of chironomids to the sediment in SC35 (A), SC14 (B), and SC6 (C). Dashed lines indicate significant shifts in assemblage identified with CONISS, and gray shading indicates sections of inferred sediment mixing.

abundances were highest in SC35 and lowest in SC6 but exhibited increased abundances upcore in all cores. The most abundant taxa in SC35 and SC14 consisted of *Chironomus* and *Procladius* (Figure 6a). Comparatively, the most abundant taxa in SC6 consisted of *Nilodorum* (which was notably absent in SC35) and *Chironomus* (Figure 6a), with all other taxa being exceedingly rare (Figure S4). Other taxa found at variable, but lower, abundances in all cores included *Clinotanypus*, *Cryptochironomus*, *Microchironomus*, *Orthocladius/Cricotopus*, and *Tanytarsus*. CONISS revealed a shift in distinct chironomid assemblages occurred in ~1928 (±8 yrs; 20 cm core depth), ~1921 (±6 yrs; 14 cm core depth), and ~1977 (±6 yrs; 14 cm core depth) for SC35, SC14, and SC6, respectively (Figure S6).

Cladoceran taxa generally declined in abundance over the eutrophication history of the Mwanza Gulf (Figure 5, S5). Assemblages consisted of three genera and included two benthic chydorids (*Alona* and *Chydorus*), as well as planktonic *Bosmina longirostris.* Chydorid remains were not identifiable beyond the genus level. One *Daphnia* ephippia was found in SC14 at a core depth of 23–24 cm but was not included in subsequent analyses. *Bosmina* was the most abundant taxon at SC35 and SC14 compared to *Alona* dominating the assemblage at SC6 (Figure 6b).

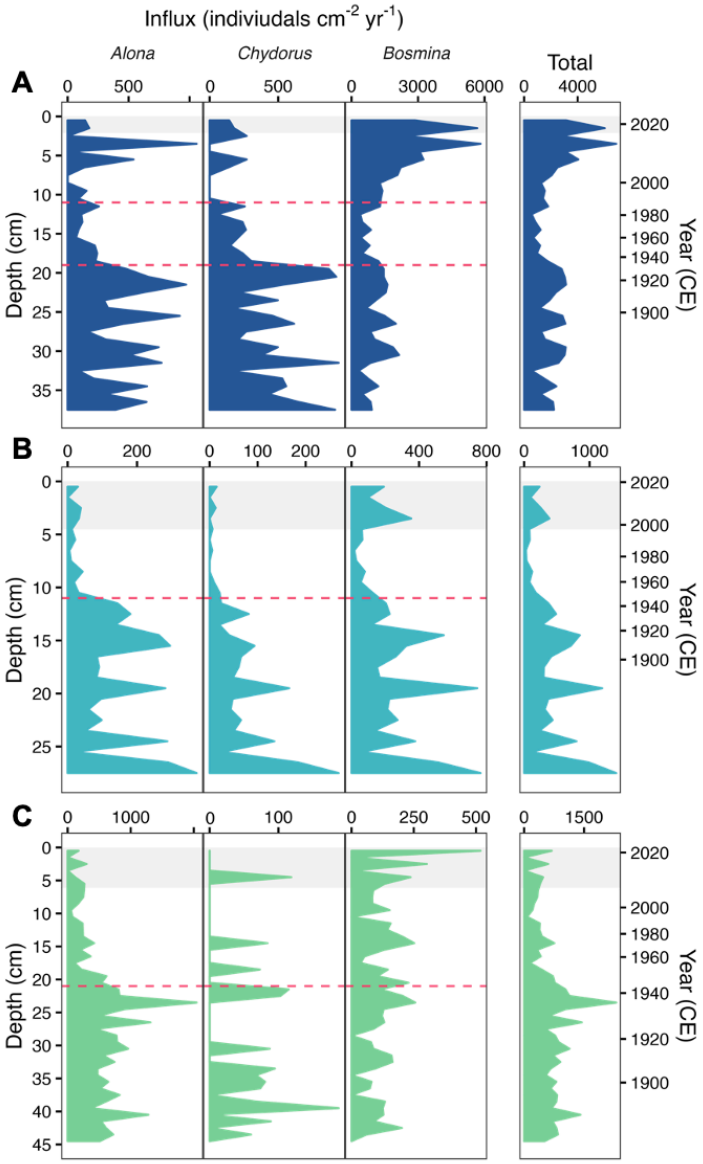

Figure 5.
Influx of Cladocera to the sediment in SC35 (A), SC14 (B), and SC6 (C). Dashed lines indicate significant shifts in assemblage identified with CONISS, and gray shading indicates sections of inferred sediment mixing.

The shifts in assemblage identified by CONISS occurred in ~1934 (±7 yrs; 19 cm core depth), ~1947 (±4 yrs; 11 cm core depth), and ~1945 (±13 yrs; 21 cm core depth) for SC35, SC14, and SC6, respectively (Figure S6). A subsequent shift was identified only in SC35 in ~1990 (±3 yrs; 11 cm core depth) when abundances rebounded.

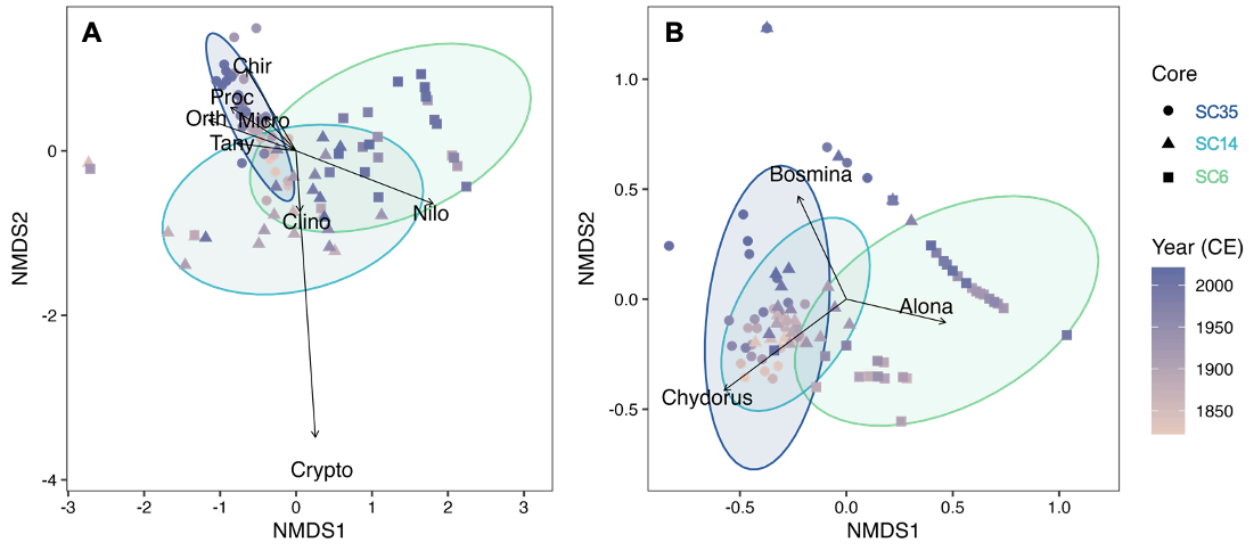

Figure 6. Non-metric multidimensional scaling plot of chironomid (A) and cladoceran (B) assemblages across all cores based on Bray-Curtis distance matrices. Ellipses indicate the 95% confidence interval of the assemblages from SC35, SC14, and SC6.

DISCUSSION

Our results provide critical insight into the spatiotemporal heterogeneity of community responses with the onset of eutrophication along a large-scale inshore-offshore transect of the Mwanza Gulf. Chironomid and cladoceran assemblages in the Mwanza Gulf underwent marked shifts in structure that varied both spatially and temporally in response to anthropogenic eutrophication. The spatiotemporal variation highlights the complexity of eutrophication processes and underscores the importance of local environmental conditions in modulating the response of aquatic ecosystems to eutrophication pressures.

Algal productivity

Increases in total algal production associated with anthropogenic eutrophication displayed substantial temporal variation along the nearshore to offshore gradient of the Mwanza Gulf (Figure 3). King and Wienhues et al. (*in press*) demonstrated that at

intermediate water depth (*i.e.*, SC14), algal productivity surged following the onset of anthropogenic nutrient enrichment around 1920 (±6 yrs). The deeper waters of SC35 exhibited increasing productivity roughly a decade later (~1920 ± 10 yrs). In comparison, the shallow water TChl profile of SC6 indicated minor productivity increases starting around 1940 (±13 yrs), with major increases not occurring until ~1980 (±6 yrs). This spatial heterogeneity is consistent with site-specific response patterns observed in other large lakes undergoing eutrophication (Huang et al. 2018; Rowland et al. 2020; Xu et al. 2020). Typically, nearshore productivity is thought to sequester nutrients and limit nutrient delivery to offshore regions (Stadig et al. 2020). Thus, the closer proximity of Mwanza City to the intermediate and deepwater coring locations likely explains, at least in part, the delayed response observed in the shallow water core. Alternatively, the delayed response may be attributed to nearshore habitats being more resistant to nutrient loading, possibly due to increased turbidity interfering with productivity, considering that this pattern of timing was similarly observed in nearshore versus offshore productivity in northern Lake Victoria (Hecky et al. 2010). However, further research is necessary to elucidate the specific mechanism underlying these temporal disparities. Unfortunately, differential pigment preservation between coring locations precludes comparisons regarding the magnitude of observed changes between cores.

Nevertheless, water depth has been demonstrated to play a key role in eutrophication processes (Qin et al. 2020). Contemporary spatial assessments of primary production in Lake Victoria indicate higher chlorophyll *a* concentrations in nearshore habitats compared to offshore (Mugidde 1993; Sitoki et al. 2010; Frank et al. 2023), consistent with other large lakes (Hall et al. 2003). Regardless, the spatiotemporal variation of anthropogenic eutrophication in Mwanza Gulf highlights the complexity of eutrophication processes and underscores the need to consider a heterogeneous environment when assessing water quality and implementing eutrophication mitigation measures (Cornelissen et al. 2014).

Chironomid assemblages

Although community structure and total abundance of chironomids varied between cores, significant shifts in assemblage occurred simultaneously to increased algal production (Figure 4). Increased lake productivity is typically accompanied by increased abundances of *Chironomus*, *Microchironomus*, and *Procladius* (Brodersen and Quinlan 2006), which is evident throughout the Mwanza Gulf. Food availability can be a major determinant of total chironomid abundances (Itkonen et al. 1999; Anderson

et al. 2008). Therefore, the rise in algal production, particularly diatoms (King and Wienhues et al. *in press*), which is a frequent component of filter-feeder diets (*e.g., Chironomus*, *Nilodorum*, *Tanytarsus*; Kajak and Warda 1968), likely contributed to increased abundances of chironomids. Across all cores, increased algal productivity was accompanied by increased abundances of all taxa. *Orthocladius/Cricotopus* was the only taxa observed to decrease following eutrophication, but this may not reflect an actual shift in abundance given that a maximum of one individual was found per subsample. Alternatively, changes in chironomid assemblages have been attributed to changes in hypolimnetic oxygen concentrations driven by the rise of organic matter flux to the sediment (Pinder 1986; Belle et al. 2017; Nieoczym et al. 2020). Although widespread anoxia has been reported in deeper waters of Lake Victoria (Hecky et al. 1994; Verschuren et al. 2002), we only see evidence of persistent deoxygenation at SC35 in the XRF data (*i.e.*, Fe:Ti; Figure S3). Furthermore, decreased oxygen availability has been observed to co-occur with decreased abundances of *Procladius* in Lake Victoria (Verschuren et al. 2002; King et al. 2024), which contrasts with the pattern observed in SC35. Additionally, increased abundances of chironomids at SC14 and SC35 preceded both the early 1960s lake-level rise (Lehman 2009) and the 1980s decline of haplochromine cichlids (Witte et al. 1992), indicating that changes in fish predation pressure (*e.g.*, Nieoczym et al. 2020) and changes in water level (*e.g.*, Verschuren 1994) were not the main driver, though they may have subsequently contributed to increased chironomid abundances. Overall, the concurrent increase in algal production and chironomid abundance across the Mwanza Gulf strongly implicates anthropogenic eutrophication as the main driver of shifts in chironomid abundance and structure.

Chironomid community structure and diversity demonstrated substantial spatial variation between core locations, similar to other large lakes (Hayford et al. 2015), indicating that the nature of the response is dependent on pre-disturbance community structure (Figure 6a). Generally, all chironomid taxa observed throughout Mwanza Gulf are associated with productive lakes and vary by habitat type (Brooks et al. 2007). Notably, *Nilodorum* remained the dominant species both before and after eutrophication in the shallow water core, contrasting sharply with its absence in deeper waters. This pattern is consistent with previous studies indicating a preference for shallow waters with abundant macrophytes (Verschuren 1997). Comparatively, *Procladius* and *Microchironomus* are typically considered profundal taxa (Brooks et al. 2007), which is evident by their higher abundances in the deeper waters of the Mwanza Gulf. While this dependence on pre-disturbance community structure has

been noted previously in response to eutrophication amongst lakes (Langdon et al. 2006), our results demonstrate that this extends to intra-lake responses in lakes that exhibit a wide range of habitats that can indirectly mediate community responses. Water depth, in particular, seems to be the primary factor controlling intra-lake distributions of chironomid subfossils (Luoto 2012).

Cladoceran assemblages

Similar to chironomids, Cladocera are sensitive to changes in lake trophic status (Hann et al. 1994; Jeppesen et al. 2001; Chen et al. 2010). We observed widespread declines in cladoceran abundance, which coincided with the onset of eutrophication at each of the coring sites throughout the Mwanza Gulf (Figure 5). Such a large decline across all of these taxa contrasts with the overall trend of increasing abundance observed over the past two millennia in Lake Victoria (King et al. 2024). Although the timing of the shift in the SC14 assemblage did not coincide directly with the onset of eutrophication (King and Wienhues et al. *in press*) as it did in SC35 and SC6, declining abundances are evident prior to the shift. Interestingly, the shift in cladoceran assemblage in SC6 coincided with minor increases in productivity observed in the ~1940s (Figure 5), whereas the shift in chironomid assemblage did not occur until the major increase in productivity around ~1980 (Figure 4).

By integrating insights from the additional two cores examined here, which more precisely coincide with the timing of eutrophication, we can more definitively implicate eutrophication as the primary factor influencing cladoceran abundances, rather than rising lake levels (*e.g.*, Szeroczyńska 2002), throughout Mwanza Gulf. Despite increased food availability for cladocerans, which in theory should benefit small-bodied cladocerans (Vanni 1987; Sweetman and Finney 2003; Jeppesen et al. 2011), nutritional quality of primary production likely declined due to the proliferation of cyanobacteria (de Bernardi and Giussani 1990; King and Wienhues et al. *in press*). Additionally, increased turbidity resulting from excess phytoplankton production would suppress macrophyte growth, thereby reducing ideal habitat for littoral cladocerans (Scheffer 1999; Nevalainen and Luoto 2013), especially at the shallow-water site. Regardless of the mechanism, eutrophication-associated changes in ecological conditions of Mwanza Gulf did not favor small-bodied cladoceran taxa. We should note, however, that the taxa identified in the Mwanza Gulf cores exclusively comprise small-bodied cladocerans; therefore, interpretations should not be generalized to represent large-bodied cladocerans (*e.g.*, *Daphnia*) or other zooplankton taxa (*e.g.*, copepods) that typically do not preserve as well in lake sediments. For instance,

Nevalainen and Luoto (2013) observed that *B. longirostris* and *Chydorus* abundances decreased, whereas *Daphnia* abundances increased, following eutrophication. Furthermore, contemporary studies of Lake Victoria have also suggested that copepod dominance has increased over the past century (Ngupula et al. 2010).

While species richness was uniform amongst cores, species composition varied according to water depth (Figure 6b). Prior to the onset of eutrophication, planktonic *Bosmina* dominated the two deeper coring sites (SC35 and SC14), whereas littoral-associated *Alona* dominated the shallow water site, reflecting their respective habitat preferences. Interestingly, although littoral *Chydorus* exhibited similar abundances to *Alona* at the intermediate and deepwater sites, it was significantly less abundant at the shallow water site, potentially due to competition and/or habitat suitability. Such habitat separation of benthic taxa has been observed previously along water depth gradients (Nevalainen 2012; Adamczuk 2014). Typically, *Alona* are larger than *Chydorus*, suggesting that *Alona* may have a competitive advantage over *Chydorus* for resources if predation by vertebrate planktivores is weak (Brooks and Dodson 1965). However, given that body size is also influenced by other factors that can vary significantly at different water depths, such as predation pressure or temperature (Korponai et al. 2020), our data is not able to fully disentangle these species-specific (*e.g.*, Nevalainen 2012) competitive interactions underlying differences in habitat dominance. *Alona* and *Chydorus* have been observed to invade open waters in tropical lakes and in nutrient-rich lakes, particularly when predation is low, suggesting that these taxa are opportunistic in their spatial location (Fernando et al. 1990; Lennon et al. 2003). Abundances of *B. longirostris* may also be influenced by predation pressures (*e.g.*, Shi et al. 2016). The resurgence of *Bosmina* around ~1990 (±3 yrs; Figure 5) coincided with the recovery of haplochromines following their decline in the 1980s (Natugonza et al. 2021). This suggests that the increasing abundance of haplochromines may have eased some of the predation by invertebrates on *Bosmina*. *B. longirostris* is generally regarded as being tolerant to environmental stressors (Adamczuk 2016), so this resurgence raises additional questions regarding the potential influence of predation on structuring the small-bodied cladoceran assemblage.

CONCLUSION

Altogether, our findings support the utility of using subfossil assemblages of chironomids and cladocerans to track decadal-scale community composition turnover and lake trophic status (Jeppesen et al. 2001; Brodersen and Quinlan 2006). Our results highlight the spatiotemporal heterogeneity underlying the onset of

anthropogenic eutrophication, as indicated by changes in TChl, and associated shifts in chironomid and cladoceran assemblages throughout the Mwanza Gulf. Evidence for the effects of eutrophication at local sites in Lake Victoria varied by multiple decades along the water depth gradient and indicated that proximity to urbanization has a strong influence on the timing of increased algal production. Chironomid and cladoceran assemblages displayed significant shifts in their responses to increased primary production across all water depths. Yet, while community-wide analyses can effectively capture the impact of large-scale environmental disturbances, individual taxa may exhibit substantial differentiation in occurrence and dominance along natural habitat gradients, most notable perhaps water depth gradients. Ultimately, accounting for pre-disturbance spatial variability will be critical to understanding the detrimental impacts of anthropogenic disturbances on lake ecosystems.

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Supplementary Material

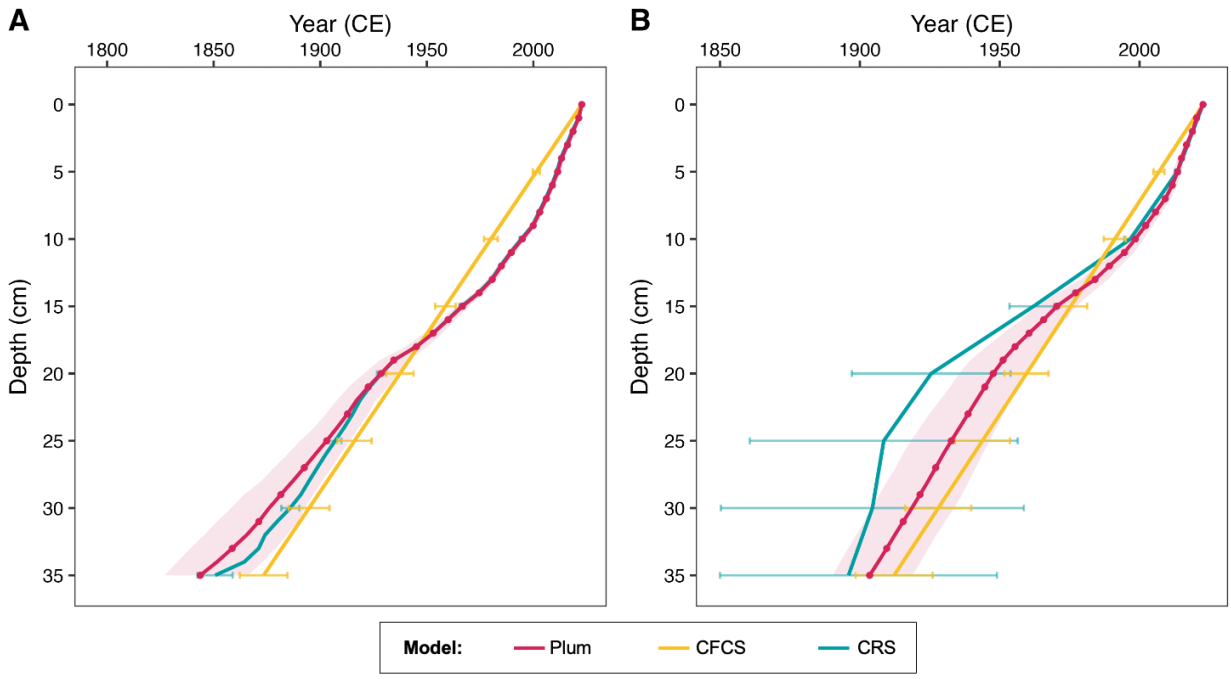

Figure S1. Age-depth relationships of SC35 (A) and SC6 (B) using the *Plum* model (pink; shading indicates the 95% confidence interval), the Constant Flux Constant Sedimentation model (CFCS; yellow), and the Constant Rate of Supply model (CRS; teal).

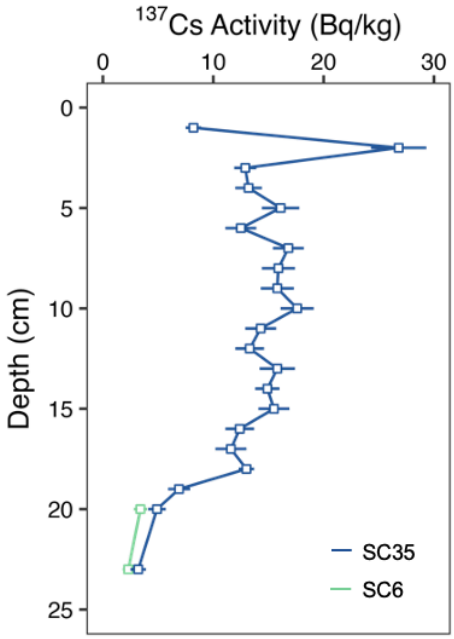

Figure S2. Total ^{137}Cs activity measured in SC35 and SC6.

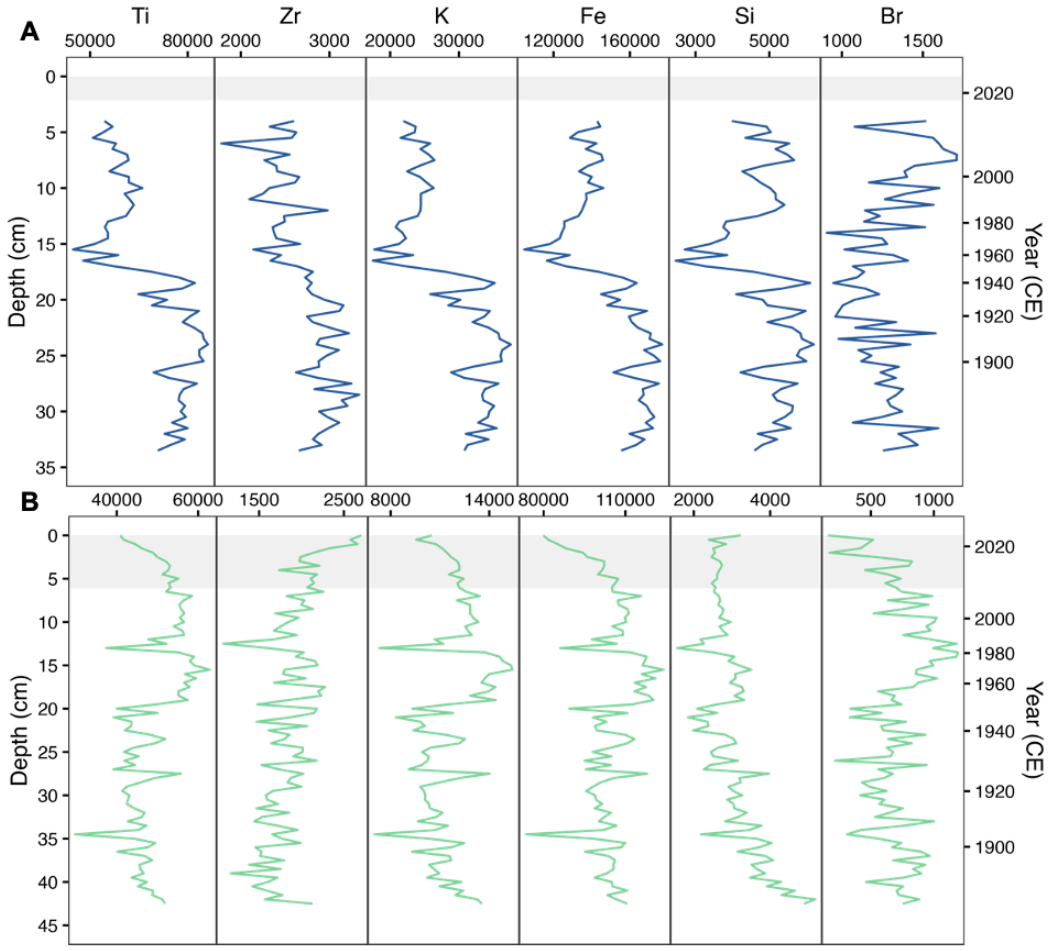

Figure S3. Selected elemental data (total counts) measured using x-ray fluorescence from SC35 (A) and SC6 (B). Gray shading indicates sections of inferred sediment mixing.

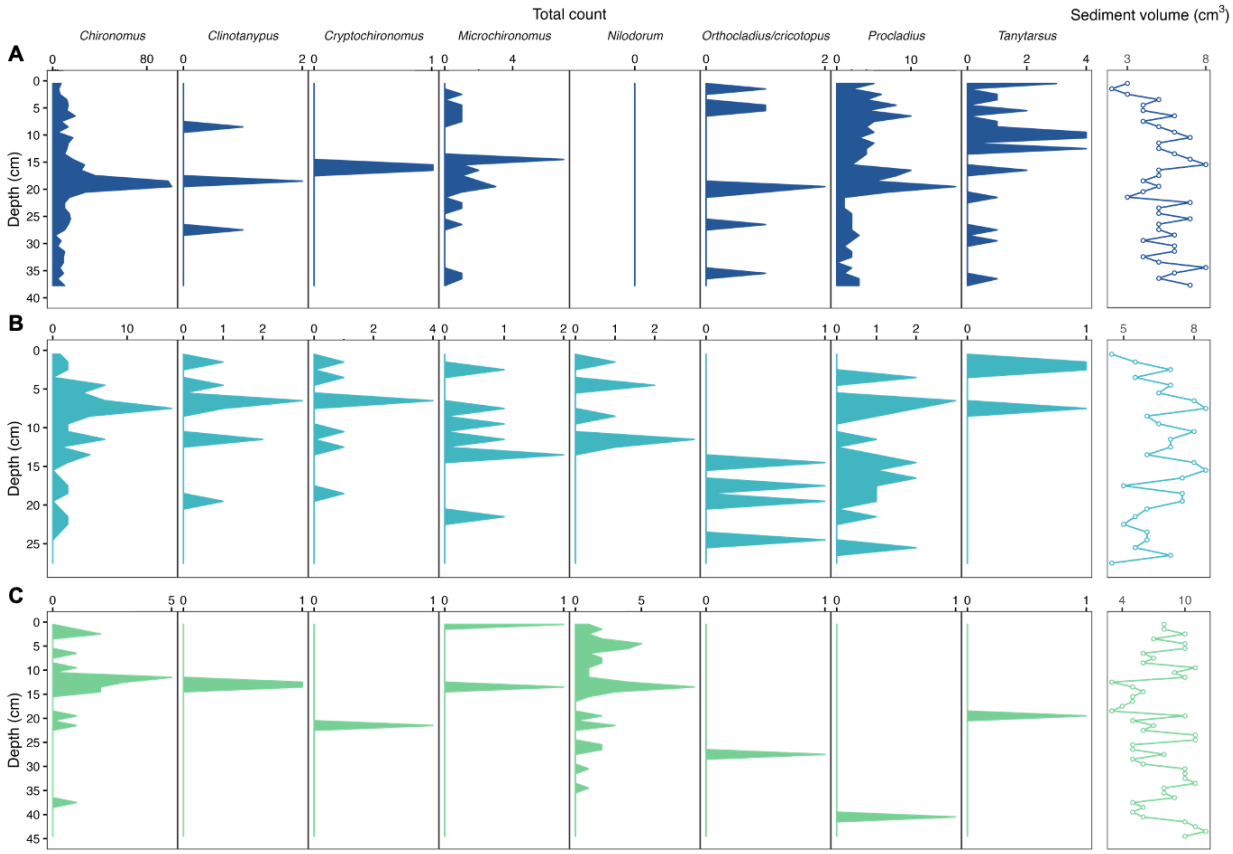

Figure S4. Total counts of chironomids and the total volume of sediment examined in each subsample in SC35 (A), SC14 (B), and SC6 (C).

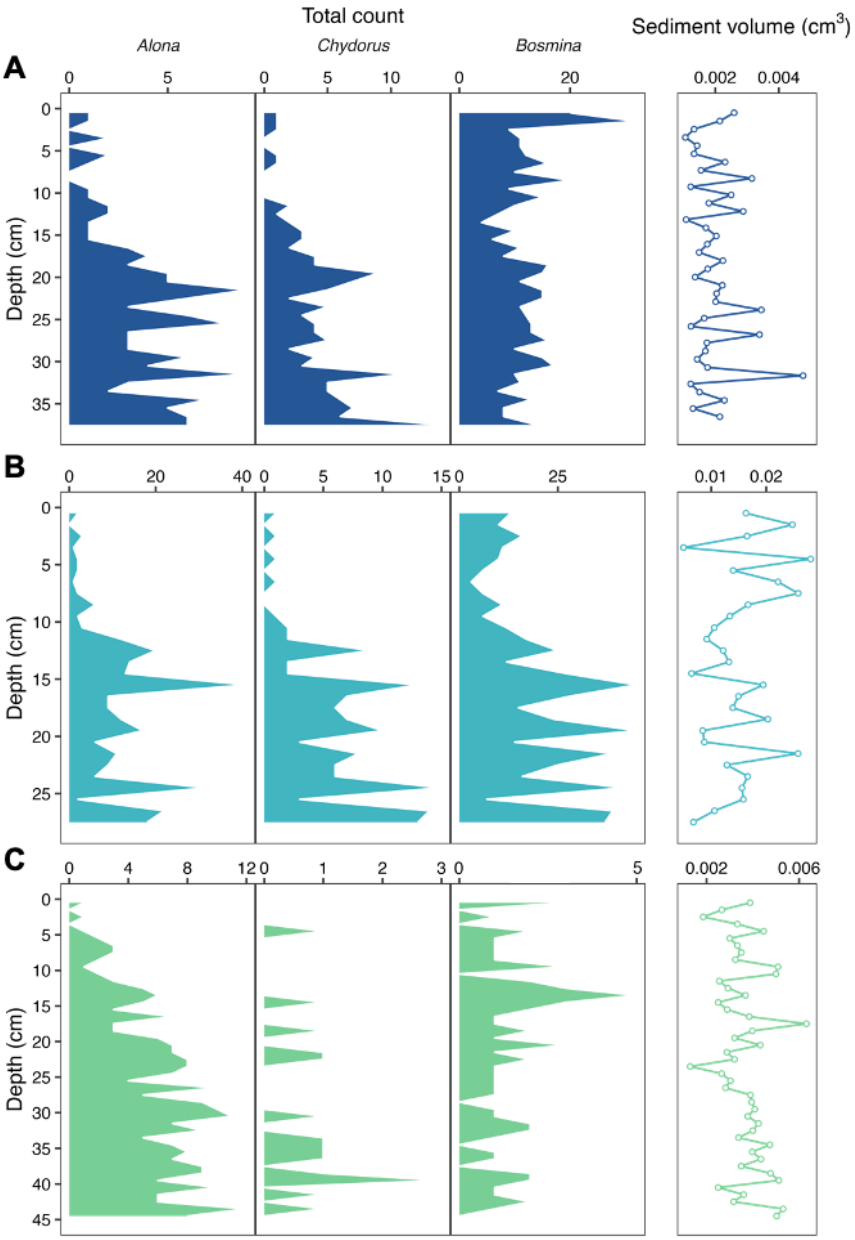

Figure S5. Total counts of Cladocera, determined by the minimum number of individuals possible given the most abundant body part of each taxon, and the total volume of sediment examined in each subsample in SC35 (A), SC14 (B), and SC6 (C).

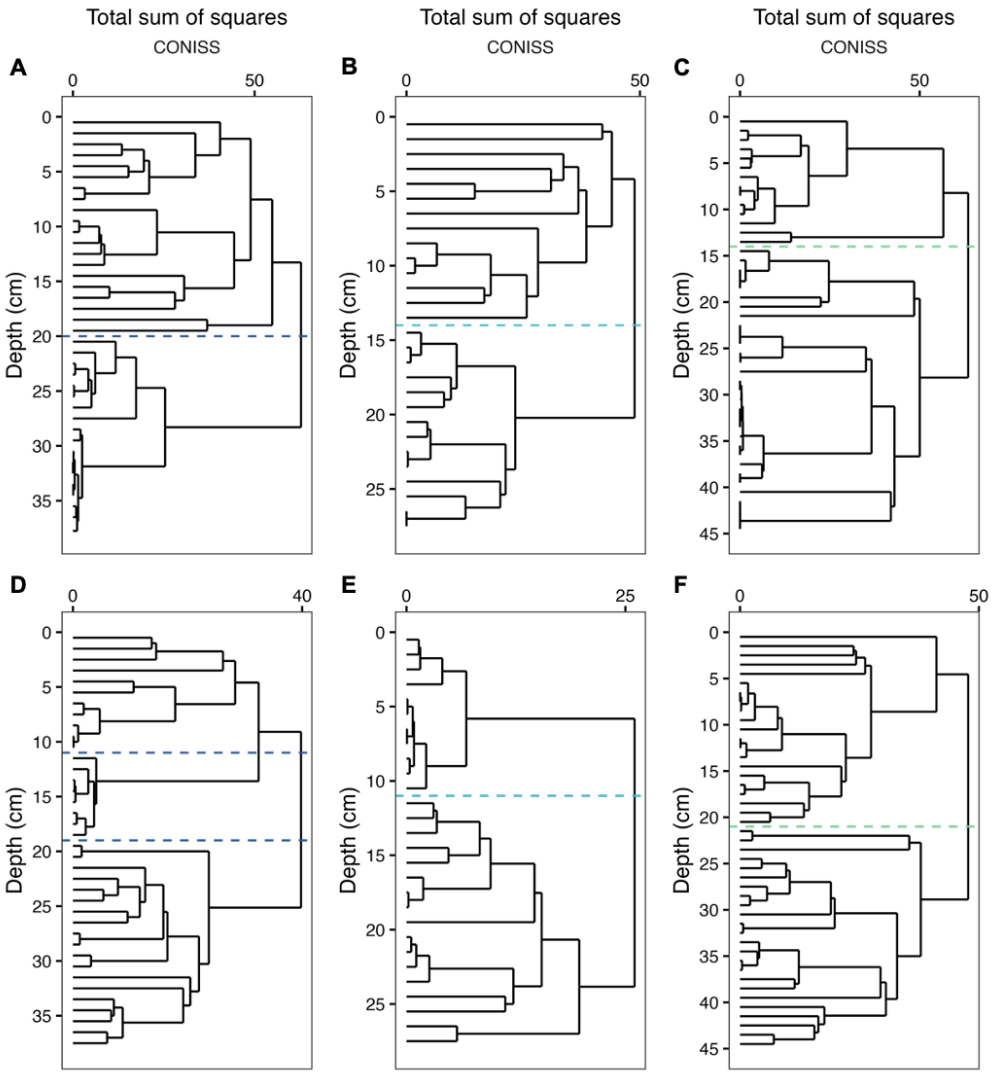

Figure S6. CONISS dendrograms of the chironomid (top; A–C) and cladoceran (bottom; D–F) assemblages of SC35 (A, D), SC14 (B, E), and SC6 (C, F). Dashed lines indicate significant shifts in assemblage.

Chapter 4

Size structure analyses reveal a sustained shift in predation pressure triggered by anthropogenic eutrophication

ABSTRACT

Anthropogenic eutrophication can disrupt ecosystem health and function by altering trophic interactions across all levels of the food web. Size structure analyses of zooplankton assemblages can complement traditional paleolimnological reconstructions and provide valuable insights into changing predation regimes over time. Here, we explore how changes in invertebrate and fish predation pressures associated with eutrophication have influenced the zooplankton assemblage of Mwanza Gulf, Lake Victoria, over the past century. While previous research has demonstrated that the decrease in small-bodied cladocerans coincided with increased primary production, the role of predation in structuring the zooplankton assemblage remains unclear. We analyzed how the size structure of *Bosmina longirostris*, a planktonic cladoceran, changed with the abundance of both *Chaoborus*, a voracious invertebrate predator, and haplochromine cichlids. We found that abundances of *Bosmina* and *Chaoborus* were correlated over the past ~150 years, and a sustained shift to smaller *Bosmina* individuals coincided with increased abundances of *Chaoborus* starting around 1920, potentially attributable to increased hypolimnetic hypoxia. In addition, the recovery of the haplochromine cichlid community in the 1990s coincided with increasing abundances of *Chaoborus* and *Bosmina*, but no significant change in *Bosmina* size structure. Overall, these results suggest a complex interplay between the influence of anthropogenic eutrophication and changes in predation pressures on zooplankton dynamics in the Mwanza Gulf and highlight the need for integrative research that includes multiple trophic levels when investigating the influence of anthropogenic eutrophication.

INTRODUCTION

Predation is widely recognized as a key factor shaping the structure and dynamics of freshwater zooplankton communities (Zaret 1980; Elser and Carpenter 1988). Amid ongoing anthropogenic threats to lake ecosystems, discerning the historical influence of predation on the structure and dynamics of freshwater zooplankton communities is imperative. Sediment core analyses of zooplankton remains can provide critical insight into predation regimes and trophic interactions through time by tracking periods of sustained shifts in size structure (Davidson and Jeppesen 2013; Korosi et al. 2013). Shifts in size-selective predation regimes can lead to changes in the mean body size and morphological defenses of zooplankton communities, both within and across generations (Vanni 1987; Pijanowska 1990). In particular, *Bosmina* is highly susceptible to invertebrate and vertebrate predation and displays cyclomorphosis in response to predation regimes, and their remains are well preserved in lake sediments (Korosi et al. 2013; Adamczuk 2016).

As both fish and invertebrates are typically size-selective predators, changes in the mean size structure of planktonic cladocerans, such as *Bosmina longirostris*, reflects a balance between reducing visibility to fish while developing morphological defenses against invertebrates (Korosi et al. 2013). Zooplanktivorous fish selectively prey on larger individuals, whereas invertebrate predators are gape-limited and thus tend to selectively prey on smaller individuals (Brooks and Dodson 1965). While elongated appendages (*i.e.*, mucro, antennules) provide a defense mechanism against invertebrate predators (Post et al. 1995), these features are unfavorable when fish predation is high due to increased drag while swimming and decreased feeding efficiency (Lagergren et al. 1997). Thus, *B. longirostris* tend to be smaller and/or have shorter appendages in environments with low invertebrate predation and high fish predation (Kerfoot 2006; Kerfoot and McNaught 2010).

Size structure analyses can complement traditional paleolimnological reconstructions, providing a more comprehensive framework to assess zooplankton community response to anthropogenic disturbance (Korosi and Smol 2012; Korosi et al. 2013). For instance, *Bosmina* size structure has been used to reveal a trophic cascade initiated by the introduction of Sockeye salmon, which subsequently reduced copepod predation on *Bosmina*, evident from increased abundances and decreased mean appendage length (Sweetman and Finney 2003). Moreover, this shift in phenotypic structure may contribute to the resilience of *B. longirostris* to environmental stressors (Adamczuk and Mieczan 2019). Comparative analyses across lakes have indicated that *Bosmina* mucro length is a stronger indicator of zooplankton size

structure than antennule length, which generally follows the same directional trend (Alexander and Hotchkiss 2010). However, the interpretation of *Bosmina* size structure can be complicated by anthropogenic eutrophication (Korosi et al. 2013), as eutrophic lakes tend to exhibit smaller individuals (Korosi et al. 2008; Alexander and Hotchkiss 2010).

Renowned for its extraordinary biodiversity, Lake Victoria has undergone unprecedented ecological change over the past century due to anthropogenic pressures within the lake catchment (Verschuren et al. 2002; Hecky et al. 2010). External nutrient enrichment triggered cascading effects throughout the food web, marked by excessive primary production and a decline in small-bodied cladocerans (King and Wienhues et al. *in press*). Furthermore, it contributed to a major collapse in both abundance and diversity, exceeding 40% of documented species, of the endemic haplochromine cichlid community (Seehausen et al. 1997; Ngoepe et al. 2024). Yet, the relative strength of invertebrate to vertebrate predation pressure of the zooplankton community remains a major question to be addressed. In particular, *Chaoborus*, commonly referred to as phantom midges, are a voracious invertebrate predator that is abundant in Lake Victoria. Small-bodied cladocerans, such as *Bosmina*, are favored prey of *Chaoborus* (Lewis 1977; Von Ende and Dempsey 1981) but also common prey for planktivorous fish. Therefore, combining taxa from across levels of the food web is necessary to gain a comprehensive understanding of the trophic interactions underlying both the decline in small-bodied cladocerans and haplochromines.

The main aim of this study was to evaluate the changes in trophic interactions between small-bodied cladocerans, invertebrate predators, and zooplanktivorous fish in response to anthropogenic eutrophication. We used subfossil reconstructions of past abundances of *B.longirostris*, *Chaoborus*, and haplochromine cichlids (validated against contemporary trawling data obtained from Natugonza et al. 2021]). Our specific objectives included: **(1)** to reconstruct past abundances of *Chaoborus* over the past century, **(2)** to assess if changes in *Chaoborus* abundance coincided with shifts in *B. longirostris* size structure, and **(3)** to discuss how changes in predation pressure associated with eutrophication influenced the zooplankton assemblage over the past century.

METHODS

Study site

Situated in Lake Victoria's southeastern region, Mwanza Gulf (Figure 1) serves as a unique site for understanding the interplay between anthropogenic impacts and food web dynamics in one of Africa's largest freshwater ecosystems (surface area = 68,800 km^2, mean depth = 40 m). Located near the city of Mwanza, the gulf has experienced severe water quality and habitat degradation due to exponential population growth within the catchment. More than 70% of the surrounding terrestrial landscape is now characterized as agricultural or urban land use (Cornelissen et al. 2014), which has contributed to an excess of external nutrient loading and associated increase in primary production (King and Wienhues et al. *in press*). The introduction of non-native Nile perch (*Lates niloticus*) in the 1950s (Pringle 2005), which remained at relatively low abundances until the 1980s (Witte et al. 1992), and water hyacinth (*Eichhornia crassipes*) in the 1980s (Witte et al. 1995) further exacerbated the impacts of anthropogenic eutrophication. Additionally, heavy rains in the early 1960s contributed to a ~2m rise in lake levels that was then sustained by the Nalubaale Dam. The culmination of these anthropogenic stressors resulted in the major loss of haplochromine cichlid diversity and biomass in the 1980s (Barel et al. 1985; Witte et al. 1992; Seehausen et al. 1997; Witte et al.2007).

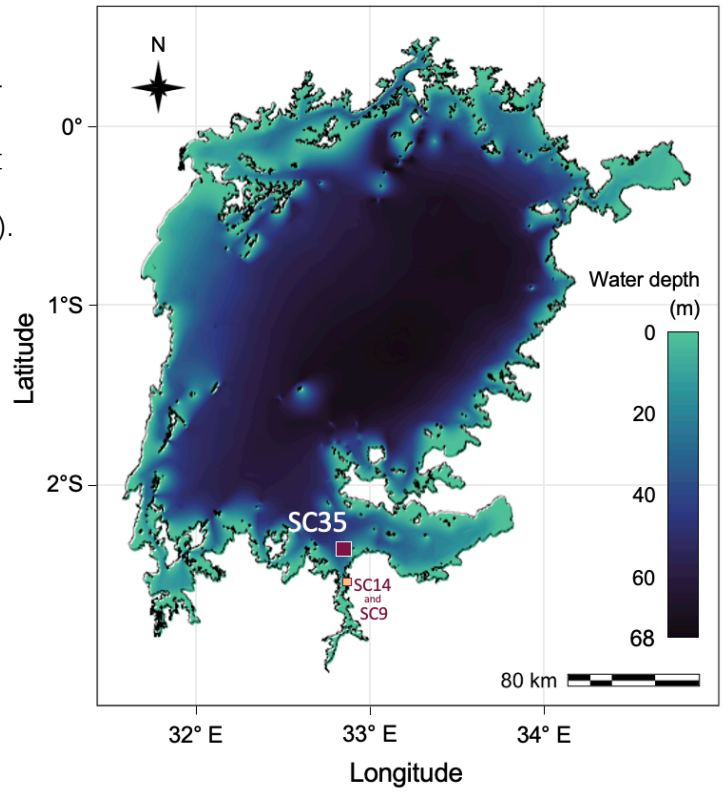

Figure 1.
Bathymetric map of Lake Victoria core sampling sites: SC35 (Chapter 3), SC14 and SC9 (King and Wienhues et al. *in press*; Ngoepe et al. 2024). Bathymetric data was obtained from Hamilton et al. (2022).

Sediment core analyses

In September 2022, a sediment core (SC35; 38.5 cm in length) was collected using a UWITEC gravity corer at a water depth of ~35 m in the southeast of Lake Victoria near the entrance to Mwanza Gulf (Figure 1). Thereafter, the core was split

lengthwise and contiguously subsampled in 1 cm intervals for subsequent analyses. Radioisotope activity was measured throughout the core using gamma-spectrometry (High-Purity Germanium Well Detector, HPGe, Canberra, USA) at the Swiss Federal Institute of Aquatic Science and Technology (Eawag; Dübendorf, Switzerland). The core chronology (Figure 2; obtained from Chapter 3) was developed using Bayesian statistics (*Plum*; Aquino-López et al. 2018).

Chaoborus and cladoceran abundance were reconstructed through the identification and enumeration of subfossils. *Chaoborus* remains were isolated from lake sediments by passing subsample material through a 100-μm mesh. Mandibles were tabulated separately while sorting through the retained material under a stereomicroscope (~25x). We did not distinguish remains beyond the genus level due to the quality of remains in other Lake Victoria cores. Influx was calculated by dividing the minimum number of individuals per volume of sediment (2–8 cm^3) by the number of years per cm of depth. Cladoceran influxes were obtained from Chapter 3, and photographed remains were used to examine the size structure of *B. longirostris* over the past century. Mucro length was measured along the ventral side of the carapace (Sweetman and Finney 2003; Korosi et al. 2013). Antennule length could not be measured given the low preservation quality of remains.

Data Analyses

Stratigraphically constrained cluster analysis (CONISS, Grimm 1987) was conducted using tidypaleo (version 0.1.3, Dunnington et al. 2022) to delineate distinct zones of cladoceran community composition and *Chaoborus* abundance independently. Prior to clustering, influxes were scaled to a mean of 0 and variance of 1, and outliers (defined as greater than or less two standard deviations from the mean length) were omitted. Subsequently, we applied an analysis of variance (ANOVA) test to assess differences in mean mucro length before and after significant changes in *Chaoborus* abundance identified by CONISS. Pearson correlation coefficients were calculated in R (version 4.3.3, R Core Team 2024) to examine the relationships between *Chaoborus* and *Bosmina* abundance. Significance was evaluated using a permutation test (wPerm package, version 1.0.1; Weiss 2022). A confidence level of 95% was applied to all analyses.

RESULTS

The SC35 age-depth model (Figure 2; modified from Chapter 3) represented ~1820–2022 CE, although estimates prior to 1900 exhibit large uncertainties. Sediment

disturbance in the uppermost ~5 cm was inferred from inconsistencies in the expected ^{210}Pb activity profile. Fe:Ti ranged from 1.98–2.63, with values generally increasing and indicating increasing hypoxia after ~1920.

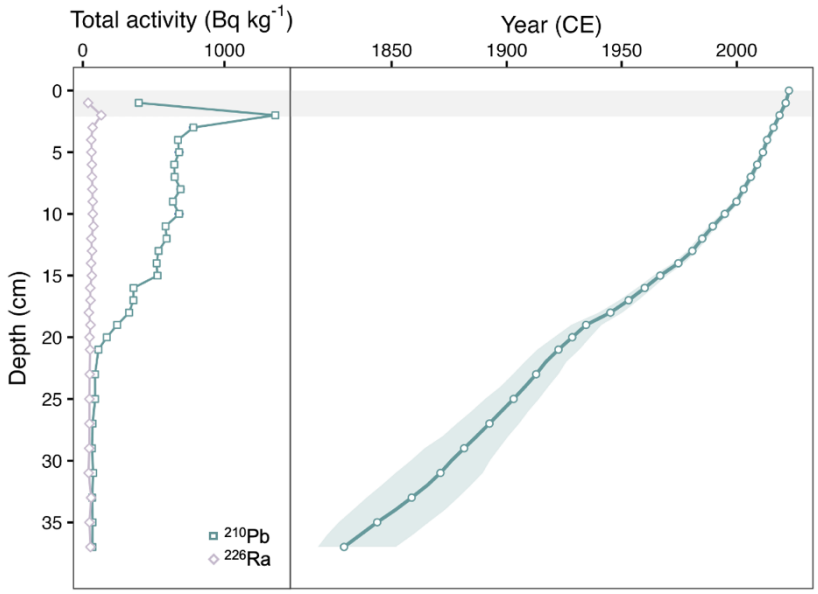

Figure 2. Age-depth model for SC35, based on total measured ^{210}Pb and ^{226}Ra activity, developed using Bayesian statistics.

The minimum number of *Chaoborus* individuals ranged from 1–32, and the number of *Bosmina* mucros measured ranged from 4–39 (Figure 3). Total influxes of *Bosmina* and *Chaoborus* in SC35 ranged from 277–5,973 and 0.02–2.12 individuals cm^{-2} yr^{-1}, respectively (Figure 4). The mean length of *Bosmina* mucro ranged from 29.3 µm to 52.9 µm.

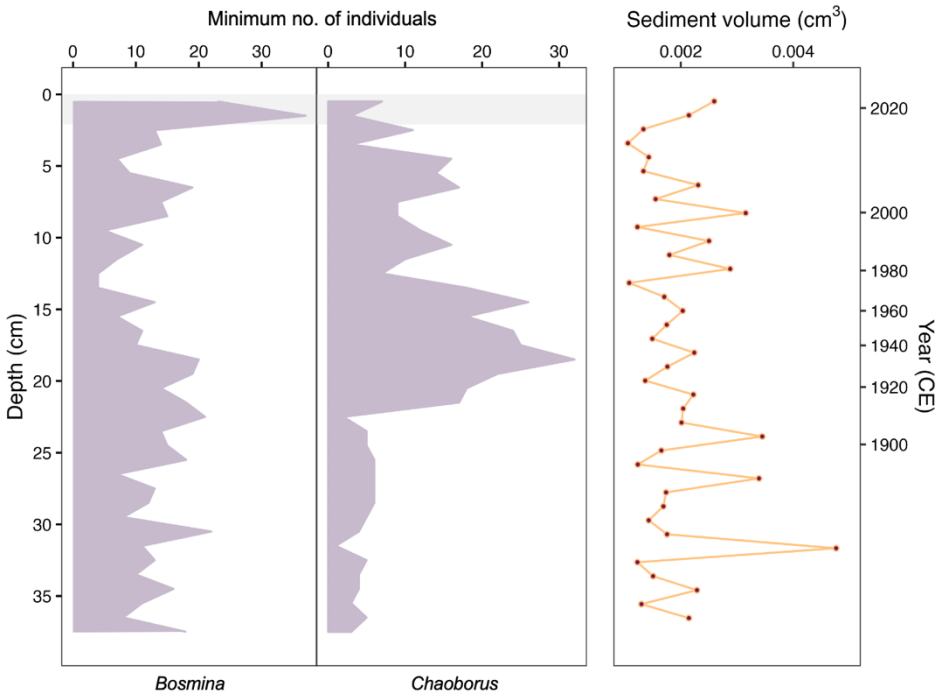

Figure 3. Total counts of *Bosmina* mucro measured and *Chaoborus* individuals, and total volume of sediment examined per subsample, in SC35.

The ANOVA and permutation test indicated a moderate correlation over the whole time series between *Bosmina* and *Chaoborus* abundances ($r = 0.28$, $p = 0.1$). CONISS identified a significant change in the cladoceran assemblage at a core depth of 11 cm and 19 cm (~1934 ± 7 yrs and ~1990 ± 3 yrs, respectively; Chapter 3), whereas for *Chaoborus* it occurred at 21 cm (~1917 ± 9 yrs). The significant shift in *Chaoborus* abundance coincided with a significant decrease in the mean mucro length of *Bosmina* from 41.8 µm to 38.1 µm ($p < 0.001$).

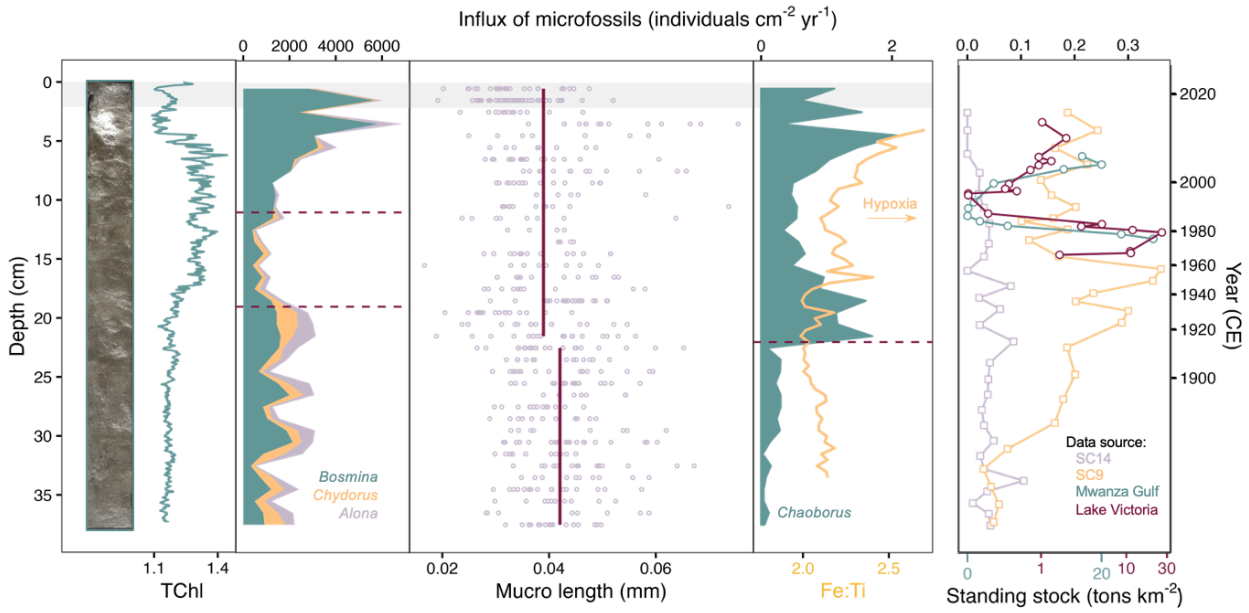

Figure 4. Compilation of paleoproxies depicting total algal chloropigments (TChl), relative abundances of small-bodied cladocerans, *Bosmina* mucro length, *Chaoborus* abundance, Fe:Ti as an indicator of hypolimnetic hypoxia, and haplochromine abundance. With the exception of haplochromines, all data was measured throughout SC35. Haplochromine data was obtained from Natugonza et al. (2021; trawling data from Mwanza Gulf and wider Lake Victoria) and Ngoepe et al. (2024; fossil records from SC14 and SC9). Dashed horizontal lines indicate significant changes in assemblage identified with CONISS, and solid vertical lines indicate significant shifts in mean mucro length. Grey shading represents the sections of core with potential sediment disturbance inferred from radioisotopes. TChl and cladoceran abundances were modified from Chapter 3.

DISCUSSION

The onset of anthropogenic eutrophication in Mwanza Gulf during the early 20th century had major implications on zooplankton abundance and trophic interactions. Nutrient enrichment and excessive primary production (King and Wienhues et al. *in press*) coincided with increased abundances of predatory *Chaoborus* and a decrease in the mean size of *B. longirostris*. This shift in size structure was sustained over the

following decades despite substantial changes in both *Bosmina* and *Chaoborus* abundance. Our findings suggest that eutrophication had major implications on environmental conditions (*e.g.*, hypolimnetic oxygen) and trophic interactions, and these factors have played a crucial role in shaping zooplankton dynamics over the past century.

Changes in *Chaoborus* abundance are commonly attributed to changes in hypolimnetic oxygen concentrations (Liljendahl-Nurminen et al. 2002; Quinlan and Smol 2010; Ursenbacher et al. 2020). Reduced oxygen levels in Lake Victoria have been observed since at least the 1950s (Hecky et al. 1994; Verschuren et al. 2002). However, the rise in *Chaoborus* abundance in SC35 dates back to around ~1917 (± 9 yrs; Figure 4), indicating that oxygen depletion likely began earlier than previously reported. Decreased oxygenation of bottom waters is further corroborated by Fe:Ti profiles at this site (modified from Chapter 3), in which elevated upcore Fe:Ti indicates increased precipitation of pyrite (FeS_2) due to geochemical focusing and reducing conditions (Scholtysik et al. 2022). *Chaoborus* are known to tolerate low oxygen conditions due to their ability to regulate their oxygen metabolism (Jager and Walz 2002), which allows them to migrate vertically through the water column to optimize predator avoidance and foraging opportunities (Dawidowicz et al. 1990; Dodson 1990; Irvine 1997). Thus, the creation of a hypoxic refuge in the bottom waters of Lake Victoria (Figure 4, Fe:Ti ratio increase) may have had a positive impact on *Chaoborus* populations. Rising lake-levels in the early 1960s may have further exacerbated hypolimnetic hypoxia, but the effects would have been minimal as this coring site would have only exhibited a ~5% increase in water depth.

As meroplanktonic ambush predators, increased abundances of *Chaoborus* can profoundly impact lake food webs (Swift and Fedorenko 1975; Black and Hairston 1988). A trophic connection likely exists between *Chaoborus* and *Bosmina*, likely regulated by a bottom-up supply of resources, as indicated by their correlated abundances ($r = 0.28$, $p = 0.1$) over the past century. Thus, the major decline in *Bosmina* abundances following the onset of anthropogenic eutrophication (Chapter 3) may have contributed, at least in part, to declining abundances of *Chaoborus* beginning in the ~1940s, as well as its subsequent resurgence at the turn of the century.

The increase in *Chaoborus* abundance in ~1917 (± 9 yrs) coincided with a significant decrease in *Bosmina* mucro length (Figure 4). Although increased invertebrate predation typically lead to elongated appendages (*e.g.,* copepods; Brooks and Dodson 1965; Kerfoot 1975), *Chaoborus* predation does not consistently

result in pronounced changes in appendage length as observed with other invertebrates considering that even large bosminids are still relatively easily ingested (Korosi et al. 2013). Thus, increased *Chaoborus* abundances may still have prompted a sustained shift in *Bosmina* size structure, either through size-selective predation favoring larger individuals or heightened predation pressures leading to a prevalence of younger, hence smaller, individuals. Abiotic factors, such as increased nutrient loading, may have further contributed to the pervasiveness of smaller *Bosmina*. Comparative analyses of lake systems indicate eutrophic lakes tend to contain smaller *Bosmina* than oligotrophic lakes (Korosi et al. 2008; Alexander and Hotchkiss 2010). Alternatively, the decrease in mean mucro length may be indicative of intensified fish predation; however, changes in the fish community during this period remain unclear. Trawling data does not extend beyond ~1970, and fossil records display contrasting patterns, with abundances increasing in the more littoral SC9 but decreasing in SC14.

Chaoborus both competes with, and is highly vulnerable to predation by, zooplanktivorous fish, thus changes in its abundance can also reflect fluctuations in the fish community (Wissel et al. 2003; Sweetman and Smol 2006). The decline in haplochromines preceded the Nile perch introduction, evident from fossil records and trawling surveys (Figure 4; Natugonza et al. 2021; Ngoepe et al. 2024). This decline likely manifested in an overall reduction in zooplanktivore biomass during the 1970s–1980s, and coincided with a shift towards cyclopoid copepods, a small-bodied cladoceran predator (Wanink et al. 2000, 2002). Although the abundance of *Rastrineobola argentea* (locally known as dagaa), a pelagic zooplanktivorous cyprinid, increased in the mid-1980s, they unlikely had strong impacts on *Chaoborus* and Cladocera abundances directly as their diet primarily consists of copepods (Branstrator et al. 2003). However, morphological remains of copepods are not typically preserved in lake sediments, which limits insights into their competitive interactions with Cladocera and *Chaoborus*. As haplochromine abundances began to recover in the 1990s due to overfishing of Nile perch (Witte et al. 2000), Cladocera and *Chaoborus* exhibited concurrent increases in abundance (Figure 4). The rapidly resurging zooplanktivore community exhibited ecological and morphological adaptations (Katunzi et al. 2003; Witte et al. 2007, 2008; van der Meer et al. 2012; van Rijssel and Witte 2013), potentially altering their interactions with *Chaoborus* and *Bosmina*. Although no significant change was observed in the mean length of Bosmina mucro, this may be due to the limited number of subsamples that span the post-collapse period (Figure 4). Furthermore, increased resource availability does not explain increased cladoceran or *Chaoborus* abundances as primary productivity, still

dominated by diatoms and cyanobacteria, stabilized rather than exhibiting further increases after the 1990s (Deirmendjian et al. 2021; Frank et al. 2023; King and Wienhues et al. *in press*)

Overall, our results help reconstruct over a century of history of the Mwanza Gulf ecosystem, through the lens of food-web interactions and anthropogenic eutrophication. In the early stages of eutrophication, there were near-simultaneous responses in the planktonic community that preceded any detectable changes in the fish community. Specifically, the zooplankton community became increasingly dominated by *Bosmina*, compared to *Chydorus* and *Alona*, and the average body size of the *Bosmina* population decreased. With increasing hypoxia, suggested by increased Fe:Ti, *Chaoborus* abundances also increased dramatically. These shifts in abundance preceded any evidence, both trawling and subfossil records, for the collapse of the haplochromine community. The decline in haplochromine abundance seemed to have little impact on either the abundance and size structure of *Bosmina*, nor on the abundance of *Chaoborus*. However, with such sparse data, and missing species in the reconstruction (*e.g.*, copepods) it is difficult to disentangle the complex trophic interactions in the Mwanza Gulf on the basis of our compiled dataset. Nevertheless, our results provide new insight into how changes in predation pressure due to anthropogenic eutrophication influenced the zooplankton assemblage over the past century.

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Synthesis and Concluding Remarks

Anthropogenic eutrophication remains one of the foremost issues threatening the structure and function of freshwater ecosystems despite decades of research (Schindler 2006). In this thesis, I have investigated the ecosystem development of Lake Victoria, with a focus on the invertebrate assemblages, using paleoecological reconstructions. My aim was to provide valuable insight into the food web dynamics underlying environmental change over both decadal and millennial timescales. First, I evaluated the temporal dynamics of invertebrate community assembly over the modern history of the lake (Chapter 1, King et al. 2024) to provide long-term context of ecological variability prior to the cumulative anthropogenic impacts of the past century. The chapters that followed then focused on the ecological changes observed in a eutrophic embayment, Mwanza Gulf, over the past ~150 years. I used a combination of biogeochemical proxies and zooplankton subfossils to determine the timing and magnitude of change in both the phytoplankton and zooplankton assemblages (Chapter 2, King and Wienhues et al. *in press*). Building upon that, I examined the spatiotemporal heterogeneity of observed changes in the cladoceran and chironomid assemblages along a nearshore to offshore transect of the Mwanza Gulf (Chapter 3). Last, I used size structure analyses to explore the influence that invertebrate and fish predation may have had in structuring the zooplankton assemblage throughout this period of intensive eutrophication (Chapter 4). Such retrospective analyses of sediment archives are crucial for understanding the interplay between biodiversity, food web dynamics, and environmental change over time.

Ecosystem dynamics across millennia

In Chapter 1, I presented the first multi-millennial record of Cladocera, Chaoboridae, and Chironomidae over the dynamic modern history of Lake Victoria (King et al. 2024). To date, there has been a disproportionate focus on temperature rather than

tropical lakes throughout the field of paleolimnology (Escobar et al. 2020). Yet, the East African Rift lakes offer some of the longest records of climatic and environmental variation alongside high levels of biodiversity (Hampton et al. 2018). Our findings offer one of the most extensive datasets documenting changes in invertebrate assemblage in a tropical lake, spanning from lake formation to present and encompassing multiple taxonomic groups. We revealed four distinct phases of invertebrate assemblage that co-varied with environmental changes. First, as the lake-refilled following its relative desiccation during the Late Pleistocene, *Procladius* and *Chironomus* were quick to colonize (~13.7ka), whereas *Chaoborus* were not consistently present until a deep-water lacustrine environment was established (as indicated by a lake-level reconstruction; Wienhues et al. 2023). Notably, all cladoceran taxa were absent during this early phase of the lake. Second, a rise in Chironomidae and *Chaoborus* (~9.1 ka) occurred concurrently with gradually increasing temperatures and decreased diatom productivity compared to the early Holocene. We attributed this increase in dipteran larvae to a change in wind-driven water column mixing during the African Humid Period (AHP; Stager and Johnson 2000; Berke et al. 2012). For instance, the rise of *Procladius*, which is less tolerant to anoxia than *Chironomus* (Verschuren et al. 2002), near the end of the AHP can be linked to increased oxygenation of the hypolimnion due to increased mixing. Third, the establishment of *Alona* (~4.7ka), a first in the lake's modern history, coincided with increased aridity and the late Holocene peak in biogenic silica resulting from resumed wind-mixing. Potential shifts in predation pressure present an alternative explanation but require further investigation. Last, the major increase in cladocerans (~1.3ka), including the establishment of *Chydorus* and *Bosmina*, in the late Holocene marked a change in lake conditions favoring cladocerans, particularly planktonic taxa. However, it remains difficult to disentangle trophic interactions and limnological conditions as potential drivers due to the limited temporal resolution (± 500 years) during this time. Overall, the observed changes in invertebrate assemblages occurred concurrently to changes in diatom productivity and major climatic oscillations and provides valuable context to the ecological changes observed over the past century.

The findings discussed in Chapter 1 complement the insights of other sedimentary proxies into the development of Lake Victoria over the past ~17ka (Figure 1), as they align with those investigated within the broader Sinergia consortium and earlier paleolimnological studies. Following widespread desiccation of Lake Victoria ~18–17ka, regional paleoclimate and lake-level reconstructions suggest that shallow ponds and wetlands were interspersed across the savanna-dominated landscape until ~14–13.5ka,

when lake-levels rose rapidly and inundated the LV1 coring site around ~13.7ka (Temoltzin-Loranca et al. 2023a,b; Wienhues et al. 2023). *Chironomus* and *Procladius* quickly colonized the emerging benthic habitat, and as lake-levels rose to establish a deepwater lacustrine environment, planktonic *Chaoborus* appeared and *Procladius* disappeared as deeper water would have facilitated reduced mixing and hypolimnetic hypoxia. Decreased abundances of haplochromines and cyprinoids further support the interpretation of a transition away from wetland and/or shallow littoral conditions at this site (Ngoepe et al. 2023). The interpretation of reduced mixing from the decline in *Procladius* is consistent with a peak of cyanobacteria and of the diatom *Nitzschia fonticola* around this time (Stager and Johnson 2000; Wienhues et al. 2024). Elevated Rb:K and diatom productivity indicate increased humidity and strong monsoonal activity that enhanced water column mixing around ~11ka, as recorded throughout eastern Africa (Johnson et al. 1998; Stager and Johnson 2000; Gasse 2000; Tierney et al. 2011; Berke et al. 2012; Temoltzin-Loranca et al. 2023a,b; Wienhues et al. 2024). Despite this, *Procladius* did not exhibit an associated increase in abundance during this time, suggesting that other factors may be limiting its abundance. Diatom production then decreased from ~9–7ka, reflecting increased lake stratification and N limitation (inferred from the high C:N ratio), possibly due to nutrient retention by the dense rainforest at that time (Talbot and Lærdal 2000; Temoltzin-Loranca et al. 2023a,b; Wienhues et al. 2024). The subsequent period of enhanced mixing from monsoonal wind activity between ~7–4ka (inferred from increasing diatom deposition; Wienhues et al. 2024), however, does display a simultaneous increase in both *Procladius* and *Chironomus* abundance.

A widespread shift in ecosystem structure occurred around ~5ka, marked by significant changes in terrestrial vegetation as well as algal, invertebrate, and fish assemblages. Consistent with previous paleoclimate reconstructions, the terrestrial vegetation surrounding Lake Victoria exhibited a re-expansion of savanna, as well as increased fire activity and declining lake levels (Gasse 2000; Stager et al. 2003; Shanahan et al. 2015; Temoltzin-Loranca et al. 2023; Wienhues et al. 2024). Diatom production began to steadily decline suggesting lake stratification with seasonally-restricted mixing, whereas total aquatic primary production (TChl) remained relatively high and was characterized by green algae, dinoflagellates, other siliceous algae, cyanobacteria, and sporadic cryptophytes (Stager and Johnson 2000; Wienhues et al. 2024). This facilitated the sustained appearance of small-bodied cladocerans, particularly *Alona*, for the first time in the history of the modern lake (King et al. 2024), which indicates the magnitude of ecological change at this time compared to the previous millennia. This was followed by

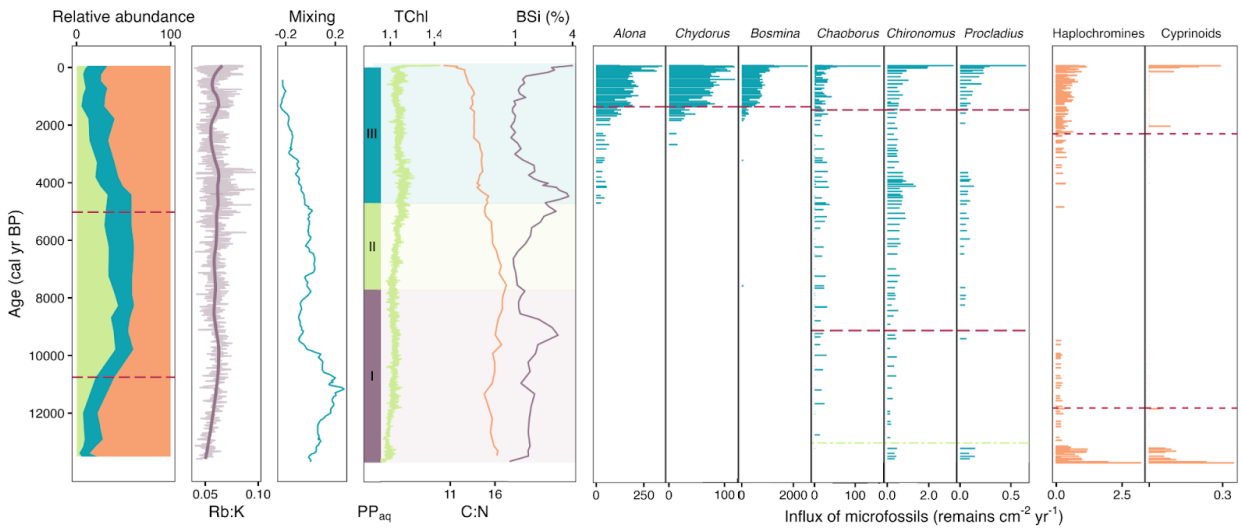

Figure 1. Selected paleoproxies from LV1 modified from Temoltzin-Loranca et al. (2023, vegetation), and Wienhues et al. (2024, biogeochemistry and primary production), King et al. (2024, invertebrates), and Ngoepe et al. (2023, fish). Pink dashed lines and aquatic primary production (PP_{aq}) zones indicate significant shifts in assemblage, and the green dot-dash line represents the transition to a deepwater lacustrine environment.

the appearance of *Chydorus* and *Bosmina longirostris* during the Iron Age around ~2ka, in which increased anthropogenic activity enhanced nutrient inputs to the lake through more intensive land use (Bayon et al. 2012; Temoltzin-Loranca et al. 2023; Wienhues et al. 2024). Subsequently, all invertebrate taxa displayed significant increases in abundances (King et al. 2024). Furthermore, increased invertebrate taxa, particularly planktonic *Bosmina*, coincided with increased abundances of haplochromines and a return of cyprinoids to offshore waters (Ngoepe et al. 2023), indicating a shift that favored the dominance of pelagic taxa.

Overall, the research conducted as part of the interdisciplinary Sinergia project aimed to reconstruct past ecosystem dynamics of Lake Victoria, showcases the interdisciplinary nature of the research. By successfully integrating data from across disciplines, we provided a more comprehensive understanding of ecosystem development and food web dynamics in a real ecosystem context over eco-evolutionary timescales. Furthermore, the millennial-scale reconstruction of ecosystem dynamics reveals the unprecedented magnitude of recent ecological change in Lake Victoria over the past century (observed in the marked increases in primary and secondary production within the uppermost core intervals).

Ecosystem dynamics over the past century

After disentangling the covariation between millennial-scale environmental change and the invertebrate assemblage, in Chapter 2 I shifted to focus on reconstructing the timing and extent of anthropogenic eutrophication and associated changes in food web dynamics of Mwanza Gulf (King and Wienhues et al. *in press*). The Mwanza Gulf, which receives among Tanzania's highest pollution loading (Juma et al. 2014), is the only area of the lake where fish abundances have been monitored, albeit irregularly (Natugonza et al. 2021). This provided a unique opportunity to explore changes in phytoplankton and zooplankton assemblages in relation to changes in the fish community, including the introduction of Nile perch and collapse (and subsequent recovery) in haplochromine abundance (Barel et al. 1985; Pringle 2005; Witte et al. 2007). Biogeochemical analyses indicated that anthropogenic nutrient enrichment began in ~1920 and led to elevated primary production, particularly diatoms and cyanobacteria. Notably, this increase in production was unprecedented within the entire modern history of the lake (Wienhues et al. 2024), consistent with previous diatom evidence from the northern extent of the lake (Stager et al. 2009). Additionally, our findings suggest that eutrophication began earlier in Mwanza Gulf compared to northern inshore areas that began increasing until 1940 (Hecky et al. 2010). Based on the core examined in this study (SC14), the decline in cladoceran taxa occurred in ~1960, clearly preceding any major changes in the fish community, and was likely driven by the cumulative impact of reduced food quality and altered habitat conditions due to lake level rise. Interestingly, the phytoplankton assemblage did not exhibit a coinciding increase in abundance around this time, suggesting that nutrient enrichment was likely the main factor controlling abundance rather than cladoceran grazing pressure. Primary production subsequently stabilized in ~1990, consistent with monitoring data (Silsbe et al. 2006; Frank et al. 2023), potentially due to silica-depletion (which occurred at offshore locations, Verschuren et al. 1998) and/or light-limitation (observed in both shallow and deep water, Cornelissen et al. 2014). At this same time, abundances of *Bosmina* and haplochromines, particularly zooplanktivores, began to recover, indicating that the role of predation pressures as a structuring factor of Cladocera should be explored further (see Chapter 4).

In Chapter 3, I explored the spatiotemporal (dis)similarity of cladoceran and chironomid assemblages along a large-scale nearshore to offshore transect in relation to anthropogenic disturbances. Given the earlier onset of eutrophication in Mwanza Gulf compared to northern inshore regions from the previous chapter (Hecky et al. 2010; King and Wienhues et al. *in press*), I surmised that there may also be variation in both the

timing of eutrophication and invertebrate community structure between nearshore and offshore regions. Similar to other large lakes (*e.g.*, Rowland et al. 2020; Xu et al. 2020), spatial variation in water quality parameters (*e.g.*, chlorophyll *a*, water clarity) has been observed previously in neoecological studies of Lake Victoria, and even within the confines of Mwanza Gulf (Mugidde 1993; Gikuma-Njuru et al. 2013; Cornelissen et al. 2014). Further underscoring the importance of accounting for depth gradients, many invertebrate taxa are known to segregate by water depth (Eggermont et al. 2007; Nevalainen 2011). Moreover, I wanted to explore the possibility that littoral Cladocera had migrated to shallower waters following the rise in lake levels, which would have shifted the extent of the littoral zone (as speculated as a possibility in King and Wienhues et al. *in press*). Thus, the zooplankton results from the preceding chapter were used to represent an intermediate water depth (~14.5 m), which I then paired with a shallow water core (~6.5 m) and a deeper water core (~35 m).

The intermediate and deepwater cores displayed increased algal productivity, inferred from total chloropigment profiles, starting around ~1920–1930, whereas in shallower waters minor increases began in ~1940 with the major increase not occurring until ~1980. In regard to the invertebrate assemblages, Cladocera and Chironomidae exhibited substantial variation in community structure across water depth, consistent with other large lakes (*e.g.*, Hayford et al. 2015). For instance, *Nilodorum* dominated in shallow water, whereas it was completely absent in deeper waters. Moreover, concurrent shifts in both assemblages coincided with increased primary production, indicating that anthropogenic eutrophication is likely the main factor driving these changes, with other anthropogenic disturbances playing a contributing role. Chironomids displayed increased abundances following eutrophication, as expected (Brodersen and Quinlan 2006), whereas abundances of cladoceran taxa declined. Notably, *B. longirostris*, which is typically considered an indicator of eutrophication (Adamczuk 2016), decreased in abundance, suggesting that the decline was likely influenced by altered habitat conditions associated with eutrophication (*e.g.*, turbidity, food quality). Overall, this chapter highlights that the impact of anthropogenic eutrophication on invertebrate assemblages is dependent on pre-disturbance community structure, although community-level analyses can capture the impact of large-scale disturbances.

While the preceding two chapters delved primarily into consumer-resource interactions, Chapter 4 aims to investigate the influence of invertebrate and fish predation on shaping the cladoceran assemblage. Complementing traditional subfossil analyses, size

structure measurements of *Bosmina* (*i.e.*, mucro length) provides the opportunity to infer past changes in predation pressures (Korosi et al. 2013). Given that *Bosmina* are preyed upon by both invertebrates and zooplanktivorous fish, *Bosmina* size structure was examined alongside changes in abundance of both *Chaoborus*, a planktonic predator of small-bodied cladocerans, and haplochromine cichlids. The deepwater core (~35 m) was the only core that had a sufficient amount of *Chaoborus* mandibles to produce a reliable estimate of past abundances (Quinlan and Smol 2010). A secondary advantage of using the deepwater core was its comparable water depth to LV1 (presented in Chapter 1), which provides millennial-scale context to the changes observed over the past century (Figure 2). Similar to chironomids (Chapter 3), abundances of *Chaoborus* increased following the onset of eutrophication in ~1920. Tolerant of low oxygen environments, *Chaoborus* likely benefited from the creation of a hypoxic refuge in bottom waters (Liljendahl-Nurminen et al. 2002; Quinlan and Smol 2010), indicated by concurrent increases of Fe:Ti. Increased *Chaoborus* abundances also coincided with a significant decrease in *Bosmina* mucro length, suggesting a sustained shift to smaller individuals in response to heightened *Chaoborus* predation. This decrease in mean mucro length constituted more than 30% of the total variation observed over the past two millennia, emphasizing the magnitude of ecological change over the past century.

Changes in the fish community would in turn have influenced *Chaoborus* abundance through both competition and predation. Evident from the sediment record and modern trawling surveys, anthropogenic eutrophication has been implicated as the primary driver of the collapse in haplochromine abundance and diversity, as well as the overall reduction in zooplanktivore biomass (Seehausen et al. 1997; Wanink et al. 2000; Natugonza et al. 2021; Ngoepe et al. 2024). While zooplanktivores constituted only 10–20% of haplochromines preceding their collapse, they dominated the community upon their recovery in the 1990s (Witte et al. 2007). Thus, the concurrent increase in abundances of *Bosmina* and *Chaoborus* with the recovery of haplochromines indicate a probable trophic link between them. Altogether, this chapter contributes valuable insight into our understanding of temporal changes in food web dynamics in response to anthropogenic eutrophication.

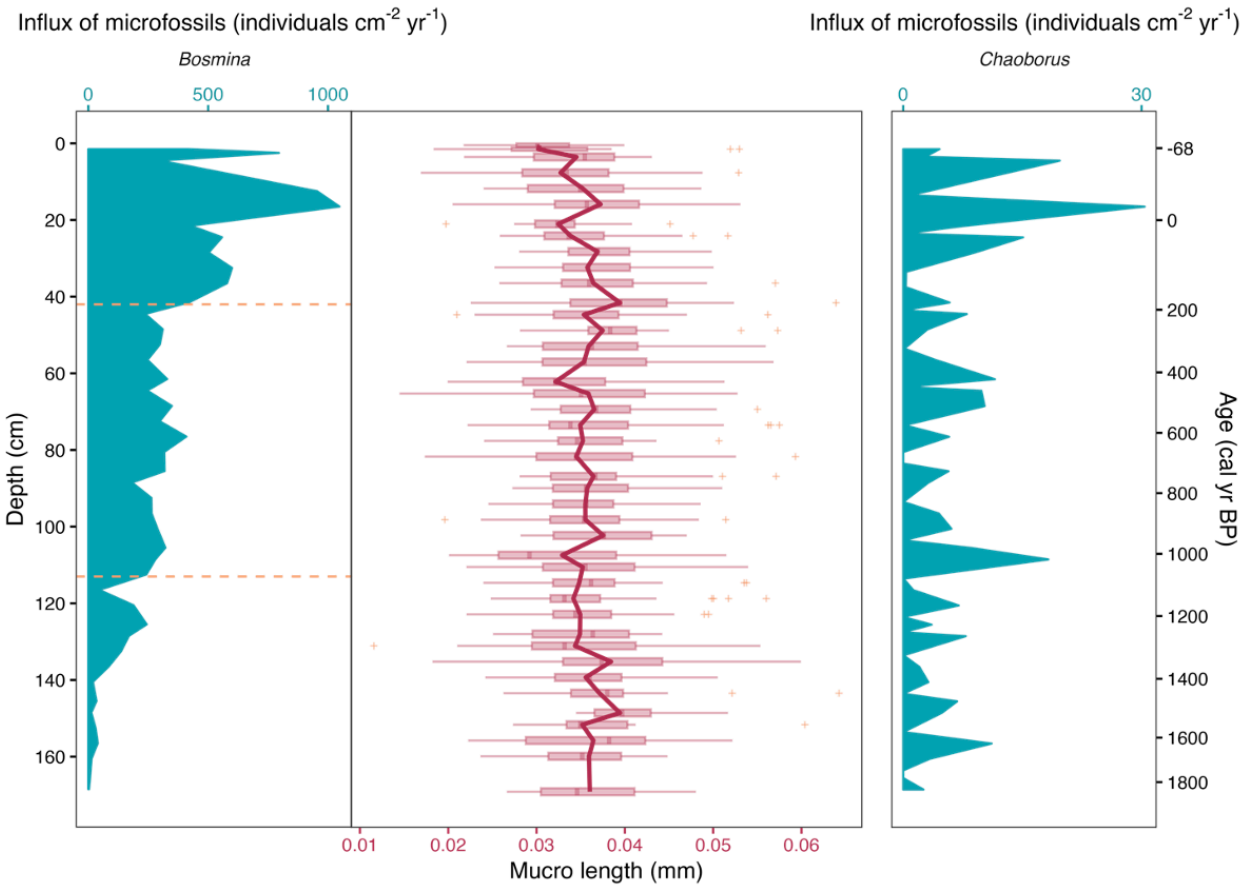

Figure 2. Influx of *Bosmina longirostris* and *Chaoborus* individuals to the sediment observed throughout LV1 (outliers were omitted; modified from King et al. 2024) alongside box plots displaying the distribution of mucro length within each subsample analyzed. The solid line represents the mean mucro length, and the dashed lines indicate the core depth of significant changepoints of individual taxa identified with CONISS. The absence of *Bosmina* below 170 cm in LV1 restricts the size structure analyses to the past ~2ka.

Future Directions

One major question that persisted throughout each of my chapters was the lack of insight into changes in copepod abundance and how this would have shaped the zooplankton community through both competition and predation. This remains a fundamental topic throughout the field of paleoecology given that morphological remains of copepods, as well as larger-bodied cladocerans (*e.g.*, *Daphnia*), are not typically preserved in lake sediments (Rautio et al. 2000). Although they do produce diapausing eggs that are preserved (*e.g.*, Chan et al. 2008), these are of limited use in paleolimnological studies because they lack any clear diagnostic features. Copepods often constitute major portions of zooplankton biomass, including Lake Victoria. Contemporary studies have suggested that copepods have become increasingly dominant in Mwanza Gulf over the

past century, particularly cyclopoid copepods, which have increased in abundance alongside decreased cladoceran abundances (Wanink et al. 2000, 2002; Ngupula et al. 2010). While sedimentary DNA (sedDNA) has emerged as a promising genetic tool aimed at tracking temporal changes in biological communities of lake ecosystems (Crump 2021), studies of invertebrate assemblages, including copepods (*e.g.*, Nakane et al. 2023), have lagged behind (Gregory-Eaves et al. 2023). Furthermore, such reconstructions are not always successful if environmental conditions do not facilitate the preservation of sedDNA (as was the case in Lake Victoria). Thus, the development of novel copepod biomarkers would represent a significant advancement in paleoecological research. Without such progress, understanding the role of copepods in past ecosystem dynamics will remain a mystery.

Alternatively, initiating experimental studies or monitoring efforts to investigate trophic interactions (*i.e.*, competition, predation) between copepods and the invertebrate taxa within the Lake Victoria ecosystem context could yield valuable insight into the past. Consistent monitoring over the coming decades could reveal how changes in abundance of various taxa coincide with changes in environmental conditions and improve identification of tropical taxa but may not be feasible given the resources required for its implementation. On a smaller scale within a laboratory or mesocosm setting, one could experimentally examine interspecific competition and predation by recording changes in abundance and feeding over time. However, trophic interactions are further complicated by abiotic factors (*e.g.*, temperature; Sakamoto and Hanazato 2009) and can also be species specific (Chang and Hanazato 2005). Consequently, additional experimental setups would be required to address these complexities, ultimately making it difficult to apply observations from a lab setting to a real ecosystem context. Observed patterns can also vary between ecosystems, with some studies suggesting increased copepod abundance and others indicating reduced abundances following increased *Chaoborus* predation (MacKay et al. 1990; Arcifa et al. 2015), highlighting the need for studies specifically within the ecosystem context of Lake Victoria. Nonetheless, such experiments could serve as a starting point for understanding the influence of copepods on shaping the zooplankton community of Lake Victoria.

Additional research should also delve deeper into the widespread shift in ecosystem structure that occurred around ~5–3ka in Lake Victoria. While considerable attention has been given to both the early developmental history of the modern lake (Stager and

Johnson 2008; Muschick et al. 2018; Temoltzin-Loranca et al. 2023; Wienhues et al. 2023) and its most recent history (Verschuren et al. 2002; Stager et al. 2009; Hecky et al. 2010; King and Wienhues et al. *in press*), the major changes observed across much of the food web following the termination of the African Humid Period remain relatively unexplored. While the connection between increased nutrient delivery to the lake, driven by the transition back to savanna and the onset of the Iron Age, and increased primary production is logical, the consumer-resource and predator-prey interactions throughout the rest of the food web remain unclear. In particular, one question that remains is whether the timing of changes in the food web around this time coincided with any key events in the adaptive radiation of haplochromine cichlids. For instance, the establishment of abundant small-bodied cladocerans, especially planktonic *Bosmina*, may have facilitated a new ecological opportunity for a previously constrained haplochromine species to diversify to exploit the novel resource. In contrast, the emergence of pelagic zooplanktivores around this time may have indirectly released some of the controls that had previously limited small-bodied cladocerans.

Lessons from the past

The research presented and synthesized throughout this thesis sheds light on the past ecosystem dynamics of Lake Victoria and provides crucial context for understanding its current state, which is essential for preserving the function and resilience of this unique ecosystem into the future. This is especially important given the socioeconomic importance of Lake Victoria at both regional and global scales. Paleoecological reconstructions provide the opportunity to contextualize anthropogenic impacts on lake ecosystems within the broader framework of natural climate and environmental variability. Furthermore, integrating changes observed across multiple levels of a food web contributes to a more comprehensive understanding of the dynamic nature of biological communities in the face of environmental change. Invertebrates, in particular, play a vital role in lake food webs, linking primary producers to top consumers and are thus important to include in paleoecological reconstructions given the complexity of ecosystem responses.

While my research is primarily motivated by understanding how the structure and function of lake ecosystems respond to anthropogenic pressures, multi-millennial records provide critical insight into ecosystem development prior to the unprecedented degradation observed in recent centuries. Exploring ecosystem dynamics through a retrospective lens can be used to inform evidence-based conservation and

management decisions, as well as to develop tools to predict how an ecosystem will respond in the future through modeling approaches. Such efforts to prevent further loss of biodiversity and preserve ecosystem function will be vital to safeguarding the ecosystem services that freshwater lakes provide into the future.

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Declaration of Consent

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