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Regional diversity, ecology and palaeoecology of aquatic invertebrate communities in East African lakes

Regionale diversiteit, ecologie en paleo-ecologie van aquatische invertebraten-gemeenschappen in Oost-Afrikaanse meren

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Samenvatting

Gezien de wereldwijde toename van het gebruik van land door de mens is het een belangrijke uitdaging voor aquatische ecologen om te bepalen in welke mate deze menselijke activiteiten een invloed hebben op de structuur en de functie van aquatisch ecosystemen. In dit opzicht moet men ook het herstellingsvermogen van de aangetaste waters inschatten (Sutherland et al, 2002). In Afrika wordt verwacht dat klimaatveranderingen en de klimaatschommelingen extra druk zullen plaatsen op zowel de beschikbaarheid van en de toegang tot (zoet) water als op de vraag ernaar (Boko *et al.*, 2007). Een grondige kennis over de respons van zoetwaterecosystemen op vroegere variaties in klimaat en menselijke invloed is essentieel om een beter inzicht te verwerven in de veerkracht van deze ecosystemen. Dit laat ons toe om een inschatting te kunnen maken van hun veerkracht ten opzichte van de voorspelde klimaatverandering en de verwachte toename van intensief landgebruik. Hetgeen op zijn beurt noodzakelijk is voor het opstellen van een beheersstrategie die het behoud van de functies en de diensten van het ecosysteem op lange termijn weet te handhaven.

Deze doctoraatsstudie wil de respons en het herstelvermogen van Oost-Afrikaanse meren op veranderingen in het milieu nagaan. De nadruk wordt hierbij gelegd op de gevoeligheid van lokale aquatische gemeenschappen voor abiotische veranderingen in hun omgeving alsook op de snelheid en de wijze van het herstel na een periode van verstoring. In dit onderzoek werden de natuurlijke klimaatsgedreven veranderingen in het aquatisch milieu (variatie in habitat gerelateerd aan veranderingen in meerniveau en saliniteit) onderzocht evenals de veranderingen door menselijke verstoring van het meer en het omringend terrestrisch ecosysteem. Methodologisch gezien hebben we ons hierbij geconcentreerd op het potentieel van een aantal tot nog toe weinig gebruikte zoölogische groepen uit het sedimentarchief van Afrikaanse meren als indicatoren voor omgevingsveranderingen.

In een eerste onderzoeksluik werden de hedendaagse ongewervelde zoetwatergemeenschappen uit West-Oeganda (hoofdstuk I, II en IV) en Zuid-Kenia (hoofdstuk III) bestudeerd. Op deze manier werd nagegaan welke omgevingsparameters de soortensamenstelling bepaalt. De verspreiding van Cladocera (watervlooien; Crustacea: Branchiopoda) in Oegandese meren werd het sterkst beïnvloed door de beschikbaarheid van nutriënten (totaal fosforgehalte, TP), de aanwezigheid en diversiteit van waterplanten, pH, de gemiddelde jaartemperatuur en het gedeelte van het meerbekken dat als landbouwgrond wordt gebruikt. De soortenrijkdom van de Cladocera was het grootst in ondiepe, eutrofe zoetwatermeren met een relatief lage pH (6,5-7) en dichte begroeiing van waterplanten. De samenstelling van de Ostracoda gemeenschap (mosselkreeftjes; Crustacea: Ostracoda) in zoete (<1500 µS/cm) Oegandese kratermeren werd het sterkst beïnvloed door het beschikbare littorale habitat, saliniteit en aquatische productiviteit. Dezelfde omgevingsparameters bepalen tevens de samenstelling van andere aquatische ongewervelde groepen zoals aquatische insecten (Arthropoda: Insecta), mosmijten (Acari: Oribatida), mosdiertjes (Bryozoa: Plumatellidae) en testate amoeben (Protista: Rhizopoda) in deze meren.

De mate waarin de samenstelling van deze fauna varieert volgens belangrijke omgevingsgradiënten illustreert hun potentieel als indicatoren. Enerzijds kunnen ze gebruikt worden om vroegere omgevingsparameters te reconstrueren. Anderzijds kan men deze groepen gebruiken als indicatoren voor de waterkwaliteit en de gezondheid van het ecosysteem in West-Oegandese kratermeren. Analyse van de Ostracoda fauna in ondiepe Keniaanse meren en vijvers bood ons de mogelijkheid om de omgevingsgradiënten uit te breiden om tot efemere zoetwaterhabitats. In deze ecosystemen werd de ostracodengemeenschap voornamelijk gestructureerd volgens gradïenten van temperatuur, oevervegetatie en de aan- of afwezigheid van vis.

Om op accurate wijze vroegere aquatische ecosystemen te reconstrueren is het noodzakelijk om het verband tussen de levende en de fossiele collecties te begrijpen (Frey, 1986) (Hoofdstuk IV). De samenstelling van een fossiel assemblage in meersedimenten wordt beïnvloed door verschillende factoren zoals de morfometrie van het meerbekken, de transport-sedimentatieprocessen, het oplossen en verbrokkelen van resten, bioturbatie en tijdelijke en ruimtelijke variaties in de levende fauna (Korhola & Rautio, 2001). Van 61 West-Oegandese kratermeren werd de samenstelling van de assemblage aan aquatische ongewervelden uit oppervlaktesedimenten vergeleken met de samenstelling van de levende fauna. Dit om te bepalen hoe goed individuele taxa bewaard bleven en in welke mate de samenstelling van de resten in de oppervlaktesedimenten uit het midden van het meer de hedendaagse (levende) fauna weerspiegelde. Het verband tussen de soortensamenstelling van Cladocera, Ostracoda en andere aquatische biota (zoals verschillende aquatische insecten, mosmijten, mosdiertjes, testate amoeben, weekdieren, …) en de omgevingsvariabelen werd onderzocht met behulp van indirecte en directe ordinatietechnieken. Hieruit bleek dat dezelfde omgevingsparameters zowel de levende gemeenschappen als het fossiele assemblage beïnvloeden, naast het feit dat de samenstelling van deze laatste groep ook sterk afhangt van de grootte en de diepte van het meer. Dit laatste illustreert het belang van de morfometrie van het meerbekken op de ruimtelijke integratie van de resten voor dat ze bedolven worden.

De methodologie die werd ontwikkeld in het eerste deel van deze studie werd vervolgens toegepast op het sedimentarchief van twee zoetwater kratermeren in West-Oeganda (Wandakara en Katinda; Hoofdstuk V). Het fossiel archief van dansmuglarven (Diptera: Chironomidae), watervlooien, mosselkreeftjes en andere aquatische ongewervelden werd gebruikt om, over de periode van de laatste 4000 jaar, de langetermijn-respons van aquatische gemeenschappen op lokale veranderingen in het milieu te reconstrueren. Onze analyses geven aan dat de aquatische biota in West-Oegandese meren onderhevig zijn geweest aan sterke natuurlijke schommelingen in omgevingsparameters. Vanaf ~2150 (in Katinda) en ~900 (in Wandakara) jaar geleden hebben menselijke invloeden de samenstelling van de aquatische ongewervelde fauna gewijzigd. De aquatische ongewervelde fauna heeft hiervan zich slechts deels kunnen herstellen toen de mens de streek voor meer dan 150 jaar verliet. In beide meren waren de effecten op het aquatisch leven ten gevolge van de natuurlijke veranderingen in het milieu ondergeschikt aan de veranderingen te wijten aan veranderingen in landgebruik door de mens.

Het potentieel van deze paleo-ecologische methodologie werd verder geïllustreerd aan de hand van reconstructies van vroegere veranderingen in klimaat en milieu in gebieden buiten de studiezone van West-Oeganda (Hoofdstuk VI-VII). In een eerste studie (Hoofdstuk VI - Ryner *et al.*, 2007) werd de samenstelling van de fossiele Ostracoda- en Chironomidae-fauna uit het sedimentarchief van Emakat, Empakaai Krater (Noord-Tanzania), onderzocht als onderdeel van een multidisciplinair onderzoek naar de lokale respons van het meersysteem op streekgebonden klimatologische en hydrologische instabiliteit tijdens de periode van de post-glaciale opwarming (c. 14.8–9.3 kyr BP). In de tweede studie (Hoofdstuk VII - Eggermont *et al.*, 2008) werden langetermijnsveranderingen in de zoöbenthos- en zoöplanktongemeenschappen van het Yoa meer (Ounianga regio, Noordoost-Tsjaad) gereconstrueerd om de hydrologische evolutie van dit, door grondwater in stand gehouden, aquatisch systeem te documenteren gedurende de uitdroging van de Sahara in het Midden- en Laat-Holoceen. De kwantitatieve reconstructies van het zoutgehalte gebaseerd op fossiele chironomidengroepen werd vergeleken met verschuivingen in de samenstelling van andere aquatische biota om na te gaan hoe de Vroeg-Holocene zoetwaterhabitaten veranderden naar de huidige hypersaliene omstandigheden. In beide gevallen werd bewezen dat een snelle biologische doorlichting (‘Rapid Biological Screening’ - RBS) van de fossiele groepen van relatief grote (> 150 µm) resten van verschillende aquatische ongewervelden erg waardevol is om vroegere veranderingen in meerniveau, nutriëntenrijkdom en zoutgehalte te reconstrueren en is daarenboven ook een belangrijk hulpmiddel bij de interpretatie van reconstructies gebaseerd op Chironomidae.

Een analyse van de relatie tussen de algemene diversiteit van de bestudeerde huidige ongewervelde fauna in West-Oegandese kratermeren en het landgebruik in deze meerbekkens, duidde aan dat het aangeraden is landbouwactiviteiten op steile kraterwanden van het meerbekken te vermijden (Hoofdstuk VIII). Daarenboven onthulde de analyse van het sedimentarchief van twee meren (Katinda en Wandakara) slechts een gedeeltelijk herstel van de aquatische ongewervelde fauna na afname van de menselijke druk op het ecosysteem hetgeen erop wijst dat het herstel van het ecosysteem een relatief traag proces is. Grote, diepe meren zijn minder gevoelig voor antropogene eutrofiëring (cf. Szeroczyńska, 2002). Gecombineerde maatregelen ten bevordering van duurzaam landbeheer en voor het behoud van de aquatische biodiversiteit zijn nodig als garantie voor het langdurig behoud van de ecosysteemfuncties en -diensten in West-Oegandese kratermeren, vooral met het oog op een explosieve populatiegroei en de natuurlijke en de door de mens veroorzaakte klimaatverandering.

Summary

As anthropogenic land disturbance continues to increase worldwide, aquatic scientists are faced with the challenge of determining how human activities influence the structure and function of aquatic ecosystems, and of assessing the potential for restoration of impacted waters (Sutherland et al, 2002). In Africa, climate change and variability are likely to impose additional pressures on water availability, accessibility and demand (Boko *et al.,* 2007). Knowledge of the response of freshwater ecosystems to past variability in climate and anthropogenic impacts is essential in order to better understand and predict their resilience to projected climate change and increasing land-use intensification. This in turn is crucial to devise strategies for management and conservation which can guarantee long-term maintenance of ecosystem functions and services.

This PhD project was conceived to determine the resilience of East African lakes to environmental change, with particular focus on the sensitivity of local aquatic communities to changes in their abiotic environment, and on the tempo and mode of their recovery after a period of disturbance. In this study we considered both natural, climate-driven changes in the aquatic environment (habitat changes linked to lake-level and salinity variation) and changes caused by human disturbance of the lake itself and the surrounding terrestrial ecosystem. Methodologically, we focused on the potential of a number of previously underexploited zoological indicators preserved in African lake-sediment records as indicators of environmental change.

Here, we first studied present-day aquatic invertebrate communities in western Uganda (Chapter I-II, IV) and southern Kenya (Chapter III) to identify which environmental conditions determine their species composition. Cladocera (water fleas; Crustacea: Branchiopoda) species distribution among the Ugandan lakes appeared to be most strongly determined by nutrient availability (total phosphorus, TP), the presence and diversity of aquatic macrophyte habitat, pH, mean annual temperature, and the fraction of the crater catchment used for agriculture. Cladocera species richness was highest in shallow, fresh eutrophic waters, with relatively low pH (6.5-7) and dense aquatic macrophyte growth. Ostracoda (seed shrimps; Crustacea: Ostracoda) faunal composition in fresh (<1500 µS/cm) Ugandan crater lakes was influenced most strongly by the structural diversity of aquatic macrophyte habitat, salinity and aquatic productivity. These same environmental parameters also determined the faunal composition of other aquatic invertebrate groups (including aquatic insects, mites, bryozoa and testate amoebae) in these lakes. The significant turnover of these groups in relation to important environmental gradients demonstrates their potential as palaeoenvironmental indicators, indicators for water quality and ecosystem health of western Uganda crater lakes. Analysis of the ostracod communities in shallow Kenyan lakes and ponds allowed us to extend our environmental gradient to also include ephemeral

freshwater habitats. In these systems, ostracod community composition was structured by temperature, the abundance of littoral vegetation and fish.

It is essential to understand the relationship between living and fossil assemblages in order to accurately reconstruct past aquatic ecosystems (Frey, 1986) (Chapter IV). The composition of fossil assemblages in lake sediments is influenced by various factors such as basin morphometry, transport-sedimentation processes, dissolution and fragmentation of remains, bioturbation, and temporary and spatial variations in the living communities (Korhola & Rautio, 2001). We compared the composition of aquatic invertebrate assemblages from the surface sediments of 61 western Uganda crater lakes with live samples in order to determine the preservation potential of individual taxa and the extent to which the surface-sediment assemblages from the centre of the lake reflected the modern (live) fauna. Using indirect and direct ordination methods, we related species composition of Cladocera, Ostracoda and other aquatic biota (including various groups of aquatic insects, oribatid mites, freshwater bryozoans, testate amoebae, molluscs, …) to existing environmental gradients which revealed that the same environmental parameters influenced both live communities and fossil assemblages, although the latter are also strongly influenced by lake size and depth, reflecting the impact of basin morphometry on pre-burial spatial integration.

Methods developed in the first part of this thesis were then applied to the sediment records of two currently fresh crater lakes in western Uganda (Lake Wandakara and Lake Katinda; Chapter V). Fossil assemblages of chironomid larvae, cladocerans, ostracods and other aquatic invertebrates were used to reconstruct long-term response of aquatic communities to regional environmental change over the past 4000 years. Our analyses indicate that the aquatic biota in western Ugandan lakes have been subject to strong natural fluctuations in environmental parameters. Human impact starting ~2150 (for Katinda) and ~900 (for Wandakara) years ago severely changed the composition of the aquatic invertebrate fauna and the former only partly recovered when humans vacated the area for over 150 years. In both lakes, the effects of natural environmental changes on the aquatic biota were subordinate to those of changes in anthropogenic land use.

We further illustrated the potential of our palaeoecological methods in the reconstruction of past climate and environmental change in regions outside the main study region of western Uganda (Chapter VI – VII). In a first study (Chapter VI - Ryner *et al.*, 2007), the composition of ostracod and chironomid fossil assemblages in the sediment record of Lake Emakat, Empakaai Crater (northern Tanzania) was used to further support a multi-proxy palaeoenvironmental reconstruction of local lake-system response to regional climatic and hydrological instability during the period of post-glacial warming (c. 14.8–9.3 kyr BP). In the second study (Chapter VII - Eggermont *et al*., 2008), long-term changes in the zoobenthos and zooplankton communities of Lake Yoa (Ounianga region, northeastern Chad) were reconstructed to document the hydrological evolution of this groundwater-fed aquatic ecosystem during mid- and late-Holocene desiccation of the Sahara. The results of quantitative salinity inferences based on fossil chironomid assemblages were compared with shifts in the composition of the other aquatic biota to determine how their early-Holocene freshwater habitat changed into the hypersaline conditions prevailing today. In both cases, rapid biological screening (RBS) of the fossil assemblages of various relatively large (> 150 µm) aquatic invertebrate remains proved very valuable in reconstructing past changes in lake level, trophic state and salinity, and our technique also aided interpretation of chironomid-based reconstructions.

Analysis of the overall diversity of the studied present-day invertebrate fauna in western Uganda crater lakes in relation to anthropogenic land use indicated that it is advisable to avoid agricultural activities within the (steep) crater basins of small lakes (Chapter VIII). In addition, downcore analysis in two lakes (Katinda and Wandakara) revealed only partial recovery of the aquatic invertebrate fauna when anthropogenic pressure was removed, pointing to relatively slow recovery of the ecosystem. Large, deep lakes on the other hand are generally less sensitive to anthropogenic eutrophication (cf. Szeroczyńska, 2002). A collaborative effort of both sustainable land management and measures to conserve aquatic biodiversity will be needed to ensure long-term maintenance of ecosystem functions and services in western Uganda crater lakes, especially in the face of explosive population growth and natural and human-induced climate change.

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I

Introduction

As we come to the end of the first decade of the 21st century, it is becoming increasingly difficult to ignore the fact that there is a human contribution to climate change. Physical and biological systems on all continents and in most oceans are already being affected by recent climate changes (IPCC 2007). In Africa, climate change and variability are likely to impose additional pressures on water availability, accessibility and demand (Boko *et al.*, 2007). In addition, increasing human usage of freshwaters through expanding agriculture is inevitable, and in the next 50 years the global effects thereof may rival those of climate change (Tilman *et al.*, 2001). In densely populated arid and semi-arid regions such as tropical East Africa, large inter-annual and decadal changes in precipitation can have a dramatic impact on water resources available for natural ecosystems and human society (Verschuren *et al*, 1999). Knowledge of the response of freshwater ecosystems to past variability in climate and anthropogenic impacts is essential in order to better understand and predict their resilience to projected climate change and intensifying land use. This in turn is essential to devise strategies for management and conservation which can guarantee long-term maintenance of ecosystem functions and services.

Sediments that accumulate on the bottom of (climate-sensitive) lakes in tropical Africa chronicle the response of the aquatic biota to both natural and human-induced environmental changes. Various sedimentological, biological and geochemical climate-proxy data extracted from these sediment archives have frequently been used to reconstruct past variations in the regional water balance (ratio of precipitation to evaporation) of East Africa with high reliability (Verschuren, 2003). This PhD project was conceived to determine the resilience of East African lakes to environmental change, with particular focus on the sensitivity of local aquatic communities to changes in their abiotic environment, and on the tempo and mode of their recovery after a period of disturbance. In this study, we considered both natural, climate-driven changes in the aquatic environment (habitat changes linked to lake-level and salinity variation) and changes caused by human disturbance of the lake itself and the surrounding terrestrial ecosystem. Methodologically, we focused on a number of previously underexploited zoological indicators preserved in African lake-sediment records.

Environmental history of western Uganda in recent millennia

In tropical Africa, climate during the late Holocene (the last ~5000 years) has been characterized by a succession of wet and dry periods (Gasse, 2000; Verschuren, 2004; Russell & Johnson, 2005). Evidence of prolonged droughts concurrently affecting the entire East African region are known from the sediment record of several African Great lakes (Figure 1), including Lake Edward (Russell & Johnson, 2005), Lake Turkana (Halfman *et* al., 1994; Ricketts & Johnson, 1996), Lake Victoria (Stager *et al.*, 1997) and Lake Tanganyika (Cohen *et al.,* 2005; Stager *et al.*, 2009) as well as from smaller lakes and swamps, including Lake Naivasha (Verschuren *et al.,* 2000), Empakaai Crater (Ryner *et al.,* 2008) and several crater lakes in western Uganda (Ssemmanda *et al*., 2005; Ryves *et al.*, in review). About 2000 years ago and during the Medieval Climate Anomaly (MCA = ~1000-1300 AD), drought was broadly synchronous across East Africa, but during the past millennium a contrasting climate evolution was recorded for the eastern and western parts. For example, during the main phase of the Little Ice Age (LIA= ~1500-1800 AD) relatively wet conditions were found in the easternmost part of the region, whereas studies based on lakes in the westernmost part of the region indicate prolonged and severe drought in this period (reviewed by Verschuren & Charman, 2008). Although the exact geographical pattern of these multi-decadal to century-scale droughts has yet to be established, it is clear that in the relatively recent past all regions of equatorial East Africa (i.e. from sub-humid western Uganda to semi-arid northern Kenya) have experienced substantial water-resource variability that is not immediately evident from 20th-21st century historical instrumental data. Consequently, the modern-day hydrological balance (rainfall minus evaporation) is a poor guide to evaluate the long-term functioning and resilience of regional aquatic ecosystems, even in the absence of anthropogenic disturbance.

An improved understanding of past climate variability in the region will not only increase the understanding of natural tropical climate dynamics, but will also facilitate more precise analysis of the interaction between climate, environment and human societies (Ryner, 2007). Droughts have contributed to human migration in tropical Africa, caused major societal transitions, and have significantly altered human-environment interrelationships (Robertshaw *et al.*, 2004). The question therefore arises whether the dynamics and health of African lake ecosystems have also been impacted by a long history of more or less intense exploitation of the lakes and surrounding terrestrial ecosystems by indigenous people, well before the 20th-century increase in demographic pressure led to rapidly intensifying human impact. Characteristically, the cultural history of western Uganda does not fit the simple model of initially modest, and gradually increasing anthropogenic impact. Historical linguistics and archaeological studies offer evidence of the onset of an ‘Early Iron Age’ ~2500 BP, with Sudanic-speaking peoples who herded cattle and grew grain (Schoenbrun, 1993; Taylor & Marchant, 1995; Taylor *et al.*, 2000). The Later Iron Age developed in the second millennium AD with multiple social, political and economic changes (Robertshaw, 1987), including migration of Bantu-speaking people (Schoenbrun, 1993; Sutton, 1993). Large-scale settlements appear to have been abandoned in a shift to small dispersed homesteads with emphasis on mobile cattle-keeping, around 1400 AD in the southern part of western Uganda and in the AD 1600s to 1700s in the northern part, (Robertshaw, 1994). This evolution led to the emergence of the pre-colonial Kingdom states (Figure 1) described by the first European visitors to the region in the late 1800s. From about 1890, grasslands in the south of the study region used by Basongora pastoralists were abandoned when first a devastating local war broke out (Stanley, 1891, in Osmaston, 1998) followed by an outbreak of rinderpest. This was followed in the early 20th century by an epidemic of sleeping sickness (Hall and Langlands, 1968). In the latter half of the 20th century, a country-wide growth rate of 3.4% has caused the Ugandan population to grow five-fold, from 5 million in 1948 to 24.4 million in 2002 (Wakabi, 2006) and to circa 35 million today (United Nations, 2008). This is putting additional pressure on both terrestrial and aquatic ecosystems as people are forced to exploit more marginal land for crop cultivation (Republic of Uganda, 2002). The clearly non-linear history of human impact on the western Uganda landscape, together with significant climate fluctuations, forces us to probe the sediment record of our study lakes for specific and independent proxies of these two major drivers of aquatic ecosystem change through time.

Figure 1: Study area of western Uganda, showing the location of archaeological sites and locations of late-Holocene environmental reconstructions. (boundaries of pre-colonial kingdoms are based upon Posnansky, 1963). The eastern shoreline of Lake Albert and the southern bank of the (White) Nile River effectively form the western and northern boundaries of Bunyoro. (Adapted from Robertshaw *et al.*, 2004).

Aims & objectives of the thesis

The overall aim of this PhD project is to determine the response of aquatic ecosystems in tropical East Africa to historical climate-driven and anthropogenic environmental change, in order to improve predictions of the resilience of these natural systems to present-day and future anthropogenic impacts. Since little is known about the biodiversity and ecology of the aquatic communities presently inhabiting these lakes, and their resilience to ongoing environmental change, we were first required to conduct a survey of the contemporary aquatic communities to provide modern baseline data. The main study area, consisting of four crater lake districts in western Uganda was selected because it offered the opportunity to study the distribution of aquatic taxa along a wide range of environmental conditions (Figure 2).

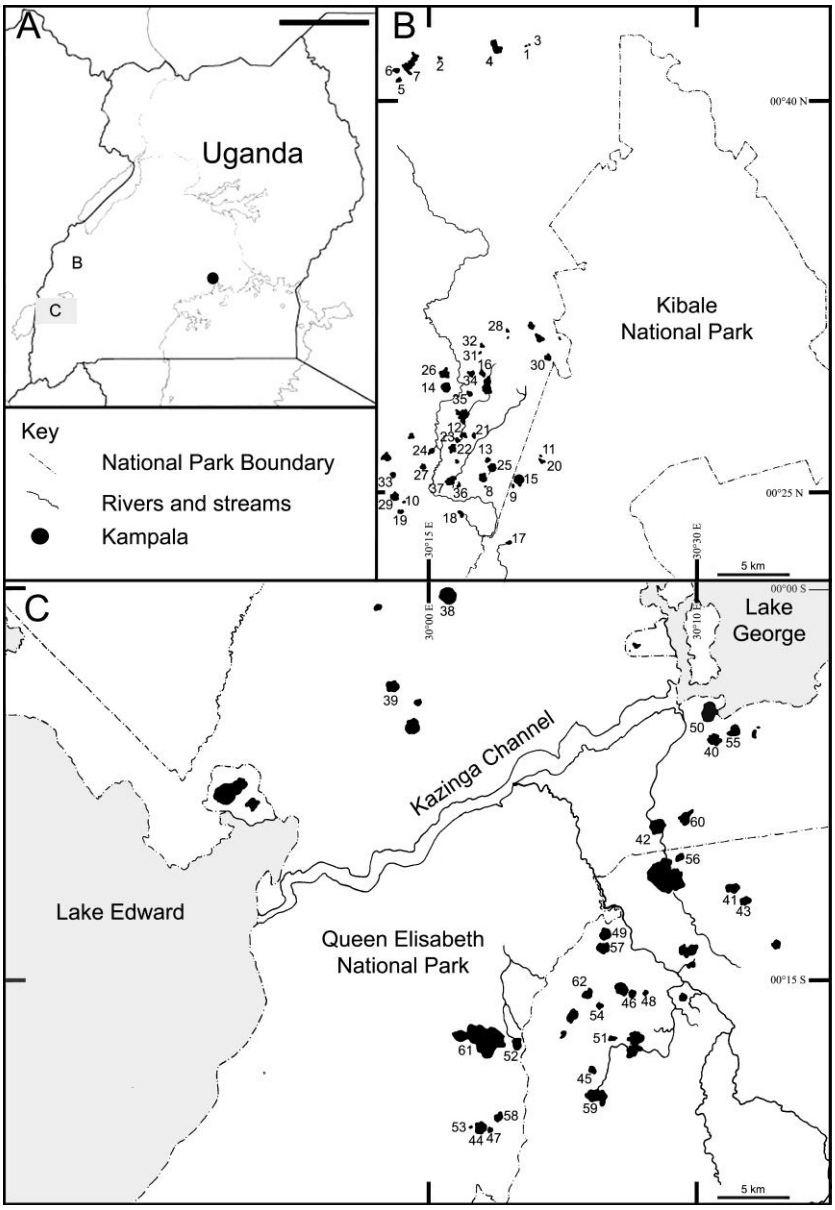

Figure 2: Map of the study region in western Uganda showing the locations of 62 crater lakes where live samples and surface sediments were studied, to determine whether the latter reflect the biological communities which inhabited these lakes at the time of deposition. Names of numbered lakes: see Appendix.

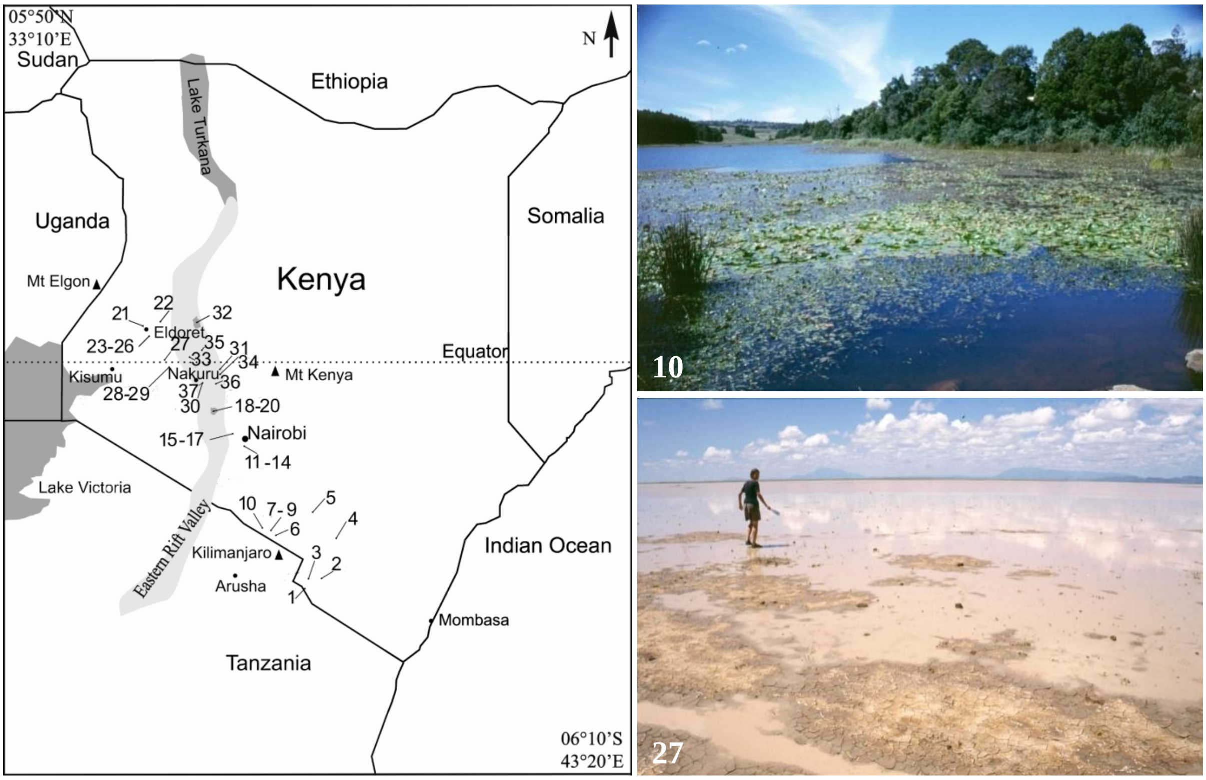

Figure 3: Map of the study region in Southern Kenya with indication of the study sites (left; adapted from Mergeay *et al.*, 2006). Lake Amboseli (top right) and Lake Narasha (bottom right). Names of numbered lakes: see Appendix. (2001, photographs by J. Mergeay)

The great variation in basin morphometry, mixing regime, salinity, trophic level and the intensity of land use in the catchment area of the different study lakes has resulted in highly varied aquatic invertebrate communities. We extended our study area with 37 shallow lakes and ponds in southern Kenya in order to obtain a picture of ostracod distribution in fresh waters experiencing very strong seasonal fluctuations (Figure 3). Previous work on biological material collected during this survey has focused on the Chironomidae (Insecta: Diptera), with the purpose to construct calibration data sets for reconstruction of climate-driven changes in lake-water salinity (Eggermont *et al*, 2006). This effort included production of identification guides to African subfossil chironomid remains (Eggermont & Verschuren, 2004a; b). However, incomplete auto-ecological information on specific taxa hampered their use in lake-history reconstructions focusing on aquatic ecosystem response to anthropogenic rather than climate change.

Remains of most aquatic groups are preserved in the sediment (Frey, 1964). These include, but are not limited to: diatom valves, seed and stems of macrophytes, fungal spores, tests of testate amoebae, various types of remains of aquatic insects, cladoceran carapaces and ephippia, ostracod valves, … Most of these groups have previously been used in paleo-environmental studies in northern and temperate climates where they were used to trace various environmental changes (see Warner, 1990; Smol *et al.*, 2001a, b for an overview). In an exploratory study (Rumes *et al.*, 2005), we analyzed subfossil death assemblages of aquatic invertebrate communities in a salinity series of 35 western Ugandan crater lakes. A first evaluation of their potential as biological indicators of past habitat conditions in palaeo-environmental research was made and illustrations of the non-chironomid aquatic invertebrate remains were provided. The results from this study indicated that analysis of relatively large (>150 µm) remains of a wide variety of aquatic invertebrates (Diptera, Ephemeroptera, Cladocera, Ostracoda, Bryozoa, Rhizopoda, ...) would yield vital information on aquatic ecosystem conditions, but that a more thorough study was required to determine the indicator value of the various groups. A combination of insufficient auto-ecological information on the African species and problems with regard to the identification of fossil remains hampered the application of the aforementioned taxa in palaeoenvironmental research in the tropics.

Furthermore, it is essential to understand the relationship between living and fossil assemblages in order to accurately reconstruct past aquatic ecosystems (Frey, 1986). The composition of fossil assemblages in lake sediments is influenced by various factors such as basin morphometry, transport-sedimentation processes, dissolution and fragmentation of remains, bioturbation, and temporary and spatial variations in live assemblages (Korhola & Rautio, 2001). Part of the differences in the occurrence of species in the live and fossil assemblages may result from the different time periods that are represented by the assemblages (Frey, 1988). Whereas fossil assemblages from surface sediments are usually expected to integrate species composition from at least one whole year, live assemblages are a momentary recording of the living fauna. Also, caution should be taken when trying to transplant methods that are routinely used in temperate and northern lakes to the tropics. For example, the ratio of planktonic to benthic cladocera, which has often been used to indicate historical fluctuations in lake levels (e.g. Whiteside & Swindoll, 1988; Hofmann, 1998), is only applicable when concentrations of pelagic fossil remains are deposited in the sediments in direct proportion to the density of live pelagic cladocera and not influenced by other biotic and abiotic factors.

In sum, the main objectives of this PhD are

- to study present-day aquatic invertebrate communities in western Uganda crater lakes and identify which environmental conditions determine the species composition of important faunal groups
- to determine the preservation potential and ecological indicator value of the fossil remains of various groups and taxa of aquatic invertebrates in East African lakes
- to assess the extent to which fossil aquatic invertebrate assemblages reflect the biological communities which inhabited these lakes at the time of deposition, and how lake characteristics affect this relationship

- to develop a technique of rapid biological screening (RBS) which uses relatively large (> 150 µm) fossil remains of aquatic invertebrates to document the general nature of the aquatic ecosystem at the time of deposition
- to document and interpret the long-term functioning of aquatic ecosystems in western Uganda, with emphasis on their response to natural long-term climate variability and the history of human impact

In order to determine how the aquatic ecosystem of these Ugandan crater lakes responded to past climatic and anthropogenic impacts, reconstructions of the abiotic lake environment based on sedimentological and geochemical analyses will be integrated with reconstructions of the long-term dynamics of their aquatic communities, based on both Chironomidae and various other biological proxies.

Outline of the dissertation

Chapter I focuses on the environmental regulation of the distribution and faunal richness of Cladocera in western Uganda crater lakes in order to determine their potential as biological indicators for the water quality and ecosystem health. More specifically, we analyzed the distribution and species richness of Cladocera in 62 western Uganda crater lakes spread across the climatic gradient between the sub-humid shoulder and semi-arid floor of the Rift Valley.

In Chapter II, the species composition of present-day ostracod communities was studied in the same set of 62 Ugandan crater lakes in relation to environmental and hydrochemical characteristics of their aquatic habitat. In addition, we provide scanning electron microscopy (SEM) images of the valve morphology of all encountered taxa to aid their identification in palaeolimnological applications.

Chapter III focuses on the species composition of ostracod communities in 37 shallow lakes and ponds in southern Kenya. As in Chapter II, we provide SEM images of the valve morphology of all encountered ostracod taxa.

In Chapter IV, the composition of aquatic invertebrate assemblages from the surface sediments of 61 western Uganda crater lakes was compared with live samples in order to determine the preservation potential of individual taxa and the extent to which the surface sediment assemblages from the center of the lake reflected the encountered live fauna. Using indirect and direct ordination methods, we related species composition of assemblages of Cladocera, Ostracoda and other aquatic biota to existing environmental gradients and determined which environmental parameters influenced both fossil and live assemblages.

The methods developed in chapters I-IV were then applied in Chapter V. More specifically, we used fossil assemblages of chironomid larvae, cladocerans, ostracods and other aquatic invertebrates preserved in the sediment records of two currently fresh crater lakes in western Uganda (Lake Wandakara and Lake Katinda) to reconstruct long-term changes in aquatic communities to regional environmental change over the past 4000 years.

Chapters VI (Ryner *et al.*, 2007) and VII (Eggermont *et al.*, 2008) are two applications of our palaeoecological methods in regions outside the main study region (western Uganda). In Chapter VI, the composition of ostracod and chironomid fossil assemblages in the sediment record of Lake Emakat, Empakaai Crater (northern Tanzania) was used as part of a multi-proxy palaeoenvironmental reconstruction of local lake-system response to regional climatic and hydrological instability during the period of post-glacial warming (c. 14.8–9.3 kyr BP). In Chapter VII, long-term changes in the zoobenthos and zooplankton communities of Lake Yoa (Ounianga region, northeastern Chad) were reconstructed to document the hydrological evolution of this groundwater-fed aquatic ecosystem during mid- and late-Holocene desiccation of the Sahara. The results of quantitative salinity inferences based on fossil chironomid assemblages were compared with shifts in the composition of the other aquatic biota to determine how their early-Holocene freshwater habitat changed into the hypersaline conditions prevailing today.

Finally, Chapter VIII provides a global assessment of how the work conducted in this thesis has moved us closer to the objectives set out above, and assesses a number of opportunities for future research. The individual chapters of this dissertation are structured as a series of manuscripts, which are published or are in preparation for submission.

The co-authorship of Chapters I-VIII:

The idea to work on various zoological indicators in lake sediments from western Uganda crater lakes was proposed by Prof. dr Dirk Verschuren and dr Hilde Eggermont, who helped me planning and designing the study, in addition to aiding interpretation and discussion of the data. Kay Van Damme, Prof. dr Koen Martens and Prof. dr. Dirk Van Damme, assisted with the identification of cladocerans (Chapter I), ostracods (Chapter II-III) and mollusks (Chapter IV), respectively. Générose Kabihogo identified the majority of other aquatic invertebrates in the Lake Katinda and Lake Wandakara sediment records (Chapter V). Dr Ilse Bessems and dr Hilde Eggermont provided sedimentological data and chironomid-based salinity inferences, respectively (Chapter V). In Chapter VI, I provided ostracod and chironomid data, and contributed to interpretation and discussion of the data. In Chapter VII, I provided aquatic invertebrate data (excluding chironomid data) and aided interpretation of results.

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Appendix

Lake names from Figure 2

N°	Lake/District	N°	Lake/District
	Fort Portal		**Kikorongo**
1	Ekikoto	38	Kikorongo
2	Kaitabarago	39	Kitagata
3	Kayihara		**Bunyaruguru**
4	Kyaninga (South)	40	Bagusa
5	Kyegere	41	Bugwagi
6	Nyabikora	42	Chibwera
7	Saka (crater)	43	Ibamba
	Kasenda	44	Karolero
8	Kanyabutetere	45	Kako
9	Kanyamansira	46	Kamweru
10	Kanyamukali	47	Kacuba
11	Kanyanchu	48	Kasirya
12	Kanyango	49	Katinda
13	Kasenda	50	Kibengo
14	Katanda	51	Kigezi
15	Kerere	52	Kyasunduka
16	Kifuruka	53	Kyogo
17	Kisibendi	54	Mafura
18	Kitere	55	Maseche
19	Kyanga	56	Mbugo
20	Kyerbwato	57	Mirambi
21	Lugembe	58	Murabio
22	Mahuhura	59	Nkugute
23	Mbajo	60	Nshenyi
24	Mubiro	61	Nyamusingere
25	Murusi	62	Nyungu
26	Mwengenyi		
27	Njarayabana		
28	Nkuruba		
29	Ntambi		
30	Nyabikere		
31	Nyahirya		
32	Nyamswiga		
33	Nyamugosani		
34	Nyantonde		
35	Rukwanzi		
36	Wandakara		
37	Wankenzi		

Lake names from Figure 3

N°	**Lake**
1	Lake Jipe
2	temp.pond Taveta-Taita 1
3	temp.pond Taveta-Taita 3
4	perm.pond Voi-Nairobi 1
5	perm.pond Voi-Nairobi 2
6	Amboseli Olokenya swamp
7	Amboseli Serena Lodge
8	Amboseli Enamishera
9	Amboseli Lake Kioko
10	Amboseli Lake Amboseli
11	Nairobi Nat. Park Narogomon dam
12	Nairobi Nat. Park Hyena Dam
13	Nairobi Nat. Park 3
14	Nairobi Nat. Park Hyrax valley
15	Semiperm. pond Limuru 1b
16	Perm. lake Limuru 2
17	Perm. Lake Limuru 3
18	Lake Naivasha main
19	Lake Naivasha Crater
20	Lake Oloidien
21	Eldoret Sigawet Dam
22	Lake Katalin
23	Perm. pond Eldoret Nakuru 1a
24	Perm. pond Eldoret Nakuru 1b
25	Perm. pond Eldoret Nakuru 2
26	Perm. pond Eldoret Nakuru 3
27	Lake Narasha
28	Perm. pond Eldoret Nakuru 5
29	Perm. pond Eldoret Nakuru 6
30	Perm. pond Nakuru Naivasha 2
31	Lake Ol Bolossat
32	Lake Baringo
33	Mogotio Kapchelukung Dam
34	Kanga Reservoir
35	Bogoria
36	Elementea
37	Nakuru

1

Environmental regulation of the distribution and faunal richness of Cladocera in western Uganda crater lakes

Abstract

Cladocera (Crustacea: Branchiopoda) play an important role in aquatic food webs, and as such, contribute to the ecological integrity of aquatic ecosystems. Understanding the environmental controls underlying their distribution thus provides valuable information on aquatic ecosystem functioning. This is particularly true for the tropical crater lakes in western Uganda, where increasing human pressure on the lakes and their catchments threatens natural ecosystem functioning. In this study, we analyse the distribution and species richness of Cladocera in 62 western Uganda crater lakes, spread across the climatic gradient between the sub-humid shoulder and semi-arid floor of the Rift Valley. As a result, they cover large environmental gradients with salinity ranging from 56 to 135,400 µS/cm, trophic status (primary productivity) from oligotrophic to hyper-eutrophic, and depth from shallow and mixing daily to deep and permanently stratified. Only a single species, *Moina belli*, was found in the true saline lakes (> 10 000 µS/cm), whereas 36 species were encountered in the freshwater lakes (< 1500 µS/cm). Local species richness was found to be determined primarily by the presence of a well-developed littoral belt of submerged and emergent aquatic macrophytes, pH, and conductivity. The highest species richness occurred in fresh but eutrophic shallow waters, with relatively low pH (6.5-7) and dense aquatic macrophyte growth. Cladocera species distribution among the Ugandan lakes is most strongly determined by nutrient availability (total phosphorus, TP), the presence and diversity of aquatic macrophyte habitat, pH, mean annual temperature, and the fraction of the crater catchment used for agriculture (presumably through its effect on transparency and aquatic macrophyte development). The significant turnover of cladoceran species along these environmental gradients demonstrates their potential as biological indicators for water quality and ecosystem health of western Uganda crater lakes.

Keywords: Cladocera – Uganda – crater lakes – aquatic macrophytes - habitat - environmental control – species distribution

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1.1 Introduction

The Lake Edward-George branch of the African Rift Valley and adjacent uplands in western Uganda contain about 80 volcanic crater lakes (Melack, 1978) and several other small permanent water bodies displaying strong variations in morphometry, mixing regime, conductivity and trophic level. Dramatic population increase in recent decades (UNEP, 2006) has resulted in a growing need for arable land (Wakabi, 2006), forcing people to exploit more marginal land (especially on steep slopes) for crop cultivation, which in turn has resulted in increased soil erosion (Republic of Uganda, 2002). When these form the catchment basin of a lake, increased soil erosion and nutrient export to the lake can enhance both lake turbidity and productivity. Studies investigating human impact on the lakes of western Uganda are still scarce. Crisman *et al*. (2001) showed how clearance of forest for agriculture and firewood in the drainage basin of Lake Saka, and concurrent introduction of Nile perch *(Lates niloticus*), resulted in an increase in trophic state in western Uganda. Similarly, Green (1976) attributed the disappearance of several pelagic Cladocera species from lakes Mutanda and Bunyoni (Uganda) to three possible factors: eutrophication, pollution and grazing by introduced zooplanktivorous fish. In the absence of historical data, the individual impacts of these factors on aquatic ecosystems are difficult to assess (Smol, 2002). With limited knowledge of pre-impact conditions, impacted lakes are commonly compared to reference lakes that are believed to be unaffected. Lakes situated within the boundaries of Queen Elisabeth National Park, for example, have been used as references to determine the impact of fisheries on nearby, unprotected lakes (Bwanika *et al.*, 2004).

Cladocera have proven to be effective biological indicators reflecting a wide range of environmental variables (Tremel *et al.*, 2000). Both living communities and their fossil remains preserved in lake sediments reflect their environment in similar ways (Davidson *et al.*, 2007). As a consequence, they are widely used as biological indicators, both for modern monitoring practices and for reconstruction of past environments (Bigler *et al.*, 2006; DeSellas *et al.*, 2008). Previous studies on cladoceran communities in Ugandan lakes have focused on the Great Rift lakes (Green, 1971; Burgis *et al.*, 1973; Lehmann, 2002; Mutune *et al.*, 2006), swamps (Thomas, 1961) or the open-water community only (Green, 1976; Kizito *et al*., 1993; Green, 1995). An initial palaeolimnological analysis of the environmental regulation of tropical African cladoceran communities in a fluctuating lake in Kenya (Verschuren *et al.*, 2000) indicated that cladoceran community composition was influenced by salinity, depth, and availability of submerged vegetated substrates.

We analysed the distribution and species richness of Cladocera in 62 crater lakes (and a few other permanent waters) in western Uganda to assess the relationships of both pelagic (open-water) and littoral (benthic/epibenthic) taxa to the physical and chemical nature of the abiotic environment, and associated biological habitat characteristics.

1.2 Methods

1.2.1 Study Area

Our study sites are located in one of the four main maar crater lake districts of Fort Portal, Kasenda, Katwe-Kikorongo and Bunyaruguru (Melack, 1978) in southwestern Uganda (Fig. 1). These small lakes are spread along the regional Rift Valley gradient from 914 to 1566 m elevation and from semi-arid to subhumid climate regimes. The lakes range from 56 to 135,400 µS/cm in surface-water conductivity, from oligotrophic to hyper-eutrophic in aquatic productivity, and from shallow and unstratified to deep and permanently stratified (Table 1). Lakes on the moist shoulder of the Rift Valley are fed mainly by rain and surface runoff (and an occasional small inflowing stream), and are hydrologically open with outflow to the regional groundwater table through porous upper crater walls. Lakes on the dry Rift Valley floor are hydrologically closed, often saline, and maintained against the local moisture deficit by substantial groundwater inputs. Water depth ranges from 0.1 to 180 m, and surface area from 0.01 and 3.84 km^2. The water level of all lakes undergoes seasonal fluctuations, modest in the hydrologically open lakes and stronger in the closed lakes. Some of the salt lakes are known to dry up seasonally or intermittently.

The natural vegetation surrounding the lakes mainly reflects the local rainfall regime, and varies from dry grass savannah on the floor of the Rift Valley (Katwe-Kikorongo and the northern part of Bunyaruguru) to semi-deciduous lowland forest on its shoulders (Fort Portal, Kasenda, and the southern part of Bunyaruguru) (White, 1983). In most of the wetter, more densely populated areas, natural vegetation around the crater basins has now been replaced by an agricultural landscape. Routine burning of secondary vegetation and intense subsistence agriculture inside gently sloping crater basins has augmented their phosphorus loading, often causing eutrophication (Kizito, 1993). Some lakes are situated within the boundaries of Kibale and Queen Elisabeth National Park, where human activities are limited to fishing and low-intensity exploitation of the surrounding forest (Fig. 1).

Table 1: Study lakes in western Uganda ordered by district, with data on lake surface area in km² (SA), maximum depth in m (Z_{max}), Elevation (Elev) in m asl, Mean Annual Temperature (MAT, in °C), surface-water conductivity (Scond) in µS/cm at 25°C, Surface water pH (pH-surf), littoral habitat types (Type), Secchi- depth in m (Secchi), Total phosporous (TP) in measurements in mg/l, Calcium (Ca) and Magnesium (Mg) in mg/l, and the fractional area of land-cover types Stable (forest, savannah and plantation), Agriculture and Fallow, Cladoceran species richness (Ntaxa). The habitat types are sandy or rocky shores, including those with submerged parts of terrestrial vegetation (S), emergent reed-like vegetation (R), submerged aquatic macrophytes with considerable floating parts (N), submerged aquatic macrophytes with little or no floating parts (C), and swampy littoral vegetation (W).

	Lake/District	SA	Z_{max}	Elev	MAT	Scond	pH-surf	Type	Secchi	TP	Ca	Mg	Stable	Agri	Fallow	Ntaxa
	Fort Portal															
1	Ekikoto	0.02	74	1537	20.02	497	8.29	SR	1.80	0.01	36.0	21.2	0.35	0.25	0.40	5
2	Kaitabarago	0.02	70	1548	19.93	489	8.03	SRC	0.75	0.07	21.6	41.1	0.70	0.00	0.30	4
3	Kayihara	0.01	66	1537	20.02	498	8.07	S	1.60	0.01	30.2	15.7	0.70	0.00	0.30	5
4	Kyaninga (South)	0.24	58	1531	20.07	420	8.34	SR	5.85	0.01	36.6	27.5	0.40	0.00	0.60	9
5	Kyegere	0.12	53	1566	19.79	250	8.31	SRC	2.15	0.01	13.6	5.0	0.01	0.40	0.59	9
6	Nyabikora	0.07	7.7	1561	19.83	188	8.31	SRL	1.20	0.02	23.2	9.1	0.15	0.50	0.35	8
7	Saka (crater)	0.01	8.5	1566	19.79	612	7.59	SRL	0.45	0.08	58.0	36.4	0.45	0.40	0.15	10

	Lake/District	SA	Z_{max}	Elev	MAT	Scond	pH-surf	Type	Secchi	TP	Ca	Mg	Stable	Agri	Fallow	Ntaxa
	Kasenda															
8	Kanyabutetere	0.01	5	1188	22.85	401	8.62	SRC	0.78	2.38	42.7	12.2	0.00	0.80	0.20	6
9	Kanyamansira	0.02	30	1177	22.94	394	8.96	SRC	0.82	0.03	19.9	27.8	0.90	0.00	0.10	3
10	Kanyamukali	0.02	11	1150	23.16	920	8.60	SR	0.65	0.40	40.3	48.7	0.10	0.70	0.20	6
11	Kanyanchu	0.01	4.8	1233	22.48	568	8.26	SRCLW	0.93	0.07	21.8	23.2	1.00	0.00	0.00	7
12	Kanyango	0.12	58	1259	22.27	493	8.75	SRL	0.45	0.02	42.2	40.6	0.25	0.65	0.10	3
13	Kasenda	0.09	13.5	1244	22.39	312	7.63	SR	0.83	0.04	29.7	12.3	0.40	0.05	0.45	4
14	Katanda	0.37	152	1340	21.62	419	8.51	SR	2.00	0.04	10.1	20.0	0.35	0.50	0.15	3
15	Kerere	0.27	68	1184	22.88	263	8.04	RC	3.63	0.02			0.80	0.00	0.20	9
16	Kifuruka	0.13	3.7	1403	21.11	411	8.33	SRCLW	0.82	0.08	44.4	27.1	0.45	0.45	0.10	9
17	Kisibendi	0.04	4.5	1126	23.35	277	9.30	SR	0.03	0.30	30.5	13.0	0.80	0.00	0.20	0
18	Kitere	0.10	51	1160	23.07	711	8.97	SR	0.83	0.13	34.8	51.1	0.33	0.07	0.60	0
19	Kyanga	0.12	54	1146	23.19	1112	9.11	SRC	1.40	0.11	14.5	84.0	0.80	0.15	0.05	1
20	Kyerbwato	0.01	12.5	1233	22.48	411	8.47	SRCL	1.65	0.02	24.9	16.5	0.90	0.00	0.10	11
21	Lugembe	0.08	15	1281	22.09	407	8.30	SR	1.35	0.05	22.4	22.7	0.20	0.60	0.20	5
22	Mahuhura	0.19	154	1254	22.31	600	8.97	SRC	5.60	0.23	35.6	47.4	0.38	0.02	0.60	6
23	Mbajo	0.08	35	1234	22.47	504	8.64	SRL	1.30	0.02	40.0	39.8	0.30	0.10	0.60	5
24	Mubiro	0.16	70	1208	22.69	718	9.02	SRC	3.20	0.02	24.0	85.4	0.40	0.15	0.45	4
25	Murusi	0.21	57	1226	22.54	382	8.54	SR	1.40	0.01	29.8	26.2	0.35	0.25	0.40	2
26	Mwengenyi	0.29	140	1397	21.15	352	8.43	SRCLW	3.35	0.10	15.1	10.0	0.40	0.40	0.20	13
27	Njarayabana	0.12	38	1179	22.92	857	8.84	SR	1.20	0.81	61.6	79.4	0.35	0.15	0.50	0
28	Nkuruba	0.01	34.5	1480	20.48	370	8.31	S	1.01	0.06	43.3	24.6	0.80	0.00	0.20	2
29	Ntambi	0.32	111	1158	23.09	5820	9.75	SC	0.40				0.90	0.05	0.05	0
30	Nyabikere	0.39	47.3	1376	21.32	271	7.89	SRC	0.61	0.11	36.0	12.3	0.84	0.01	0.05	7
31	Nyahirya	0.01	79	1444	20.77	379	8.18	SL	0.97	0.11	24.8	21.2	0.60	0.10	0.30	3
32	Nyamswiga	0.03	43	1447	20.75	330	7.76	SRCL	1.10	0.21	39.5	17.4	0.35	0.20	0.45	8
33	Nyamugosani	0.11	37	1234	22.47	988	8.94	SR	1.52	0.34	49.3	58.3	0.10	0.35	0.55	1
34	Nyantonde	0.12	180	1387	21.24	501	8.76	SR	3.10	0.01	29.1	46.0	0.15	0.60	0.25	6
35	Rukwanzi	0.08	169	1332	21.68	425	8.33	S	5.02	0.05	29.2	34.1	0.92	0.02	0.06	5
36	Wandakara	0.03	10.5	1158	23.09	1125	8.76	SR	0.70	0.06	22.8	42.8	0.02	0.65	0.33	2
	Wandakara - swamp	0.01	0.4	1146	23.19	1452	8.21	W	0.10	0.39			0.10	0.80	0.10	1
37	Wankenzi	0.16	59	1158	23.09	496	8.65	SR	0.36	0.06	25.4	12.0	0.10	0.50	0.40	2
	Kikorongo															
38	Kikorongo	0.92	9.8	915	25.06	22400	9.58	S	1.20		7.7	5.7	1.00	0.00	0.00	1
39	Kitagata	0.62	8.9	914	25.07	135400	9.63	S	0.05				1.00	0.00	0.00	0
	Bunyaruguru															
40	Bagusa	0.33	0.9	905	25.14	61100	10.62	S	0.24		9.6	70.7	1.00	0.00	0.00	0
41	Bugwagi	0.60	85	1048	23.98	441	9.02	SR	2.45	0.02	20.5	37.7	0.45	0.40	0.15	4
42	Chibwera	0.76	10.5	971	24.60	457	8.91	SCW	1.35	0.06	15.3	24.3	1.00	0.00	0.00	11
43	Ibamba	0.01	1.2	1073	23.78	104	6.55	RLW	0.35	0.15	9.0	7.1	0.10	0.75	0.15	21
44	Karolero	0.51	35	1103	23.54	181	8.05	SL	3.80	0.24	12.7	7.6	1.00	0.00	0.00	8
45	Kako	0.17	29	1396	21.16	89	8.18	S	2.30	0.01	6.5	6.0	0.08	0.85	0.07	3
46	Kamweru	0.20	43	1232	22.49	170	9.59	S	0.55	0.07	16.7	13.5	0.05	0.65	0.30	3
47	Kacuba	0.05	14.5	1102	23.54	148	8.75	SRCL	1.49	0.05	12.6	7.8	1.00	0.00	0.00	13
48	Kasirya	0.09	43	1251	22.34	302	8.72	SR	2.35	0.02	22.8	24.1	0.15	0.50	0.35	0
49	Katinda	0.44	17	1024	24.18	743	9.48	SR	0.53	0.04	12.0	27.7	0.01	0.70	0.29	1
50	Kibengo	0.88	4.8	914	25.07	264	9.92	SR	0.20	0.09	25.8	11.1	1.00	0.00	0.00	5
51	Kigezi	0.39	29	1302	21.92	265	8.49	SRC	0.99	0.11	27.3	19.6	0.11	0.47	0.41	4
52	Kyasunduka	0.50	2.1	1004	24.34	269	8.69	SR	0.30	0.46	19.9	15.3	0.60	0.20	0.20	1
53	Kyogo	0.02	3.4	1113	23.45	56	6.87	RCLW	3.00	0.59	4.8	2.0	1.00	0.00	0.00	20
54	Mafura	0.16	29	1255	22.30	259	9.29	SR	0.65	0.02	27.6	19.7	0.00	0.80	0.20	2
55	Maseche	0.32	0.2	908	25.12	68200	10.19	S	0.02		7.8	6.0	1.00	0.00	0.00	0
56	Mbugo	0.36	2.6	978	24.55	214	9.63	SR	0.51	0.10	8.2	29.8	0.20	0.70	0.05	1
57	Mirambi	0.53	22	1077	23.75	642	9.83	SR	0.90	0.04	9.9	27.0	0.00	0.70	0.30	2
58	Murabio	0.27	15	1098	23.58	141	8.42	SRCL	2.03	0.02	11.9	8.3	1.00	0.00	0.00	7
59	Nkugute	0.89	58	1409	21.06	121	8.72	SRL	0.90	0.05	11.3	7.6	0.21	0.64	0.15	5
60	Nshenyi	0.44	0.05	966	24.65	11230	10.05	S	0.02		7.5	2.0	1.00	0.00	0.00	0
61	Nyamusingere	3.84	4.3	978	24.55	681	9.40	SR	0.36	0.06	11.0	30.9	0.99	0.00	0.00	2
62	Nyungu	0.14	25	1172	22.98	430	9.40	SR	0.08	0.26	27.2	41.3	0.02	0.85	0.13	0

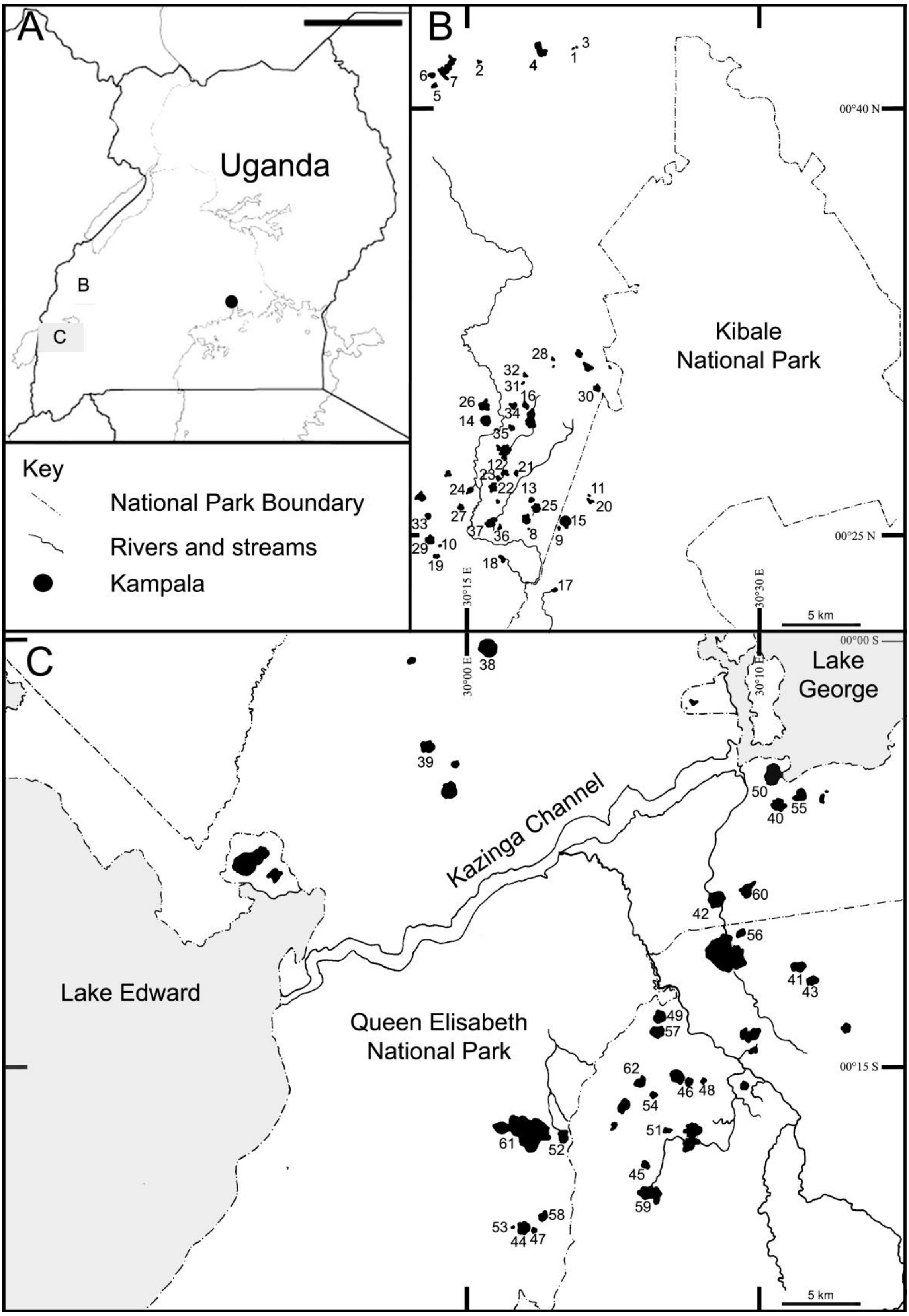

Figure 1: Map of the study region in western Uganda showing the locations of (A) the crater lake districts in the Edward-George branch of the Rift Valley, (B) the Fort Portal (lakes 1 to7) and Kasenda (lakes 8 to 37) districts, and (C) the Kikorongo (lakes 38 to 39) and Bunyaruguru (lakes 40 to 62) districts.

1.2.2 Fieldwork

In the course of 2007-2008, we conducted four dry-season (January-February or August-September) field campaigns in southwestern Uganda, surveying a total of 62 crater lakes. Latitude, longitude and elevation (in meter above sea level) were recorded by GPS (Garmin Csx 60). Mean annual air temperature (MAT) was estimated using a region-specific linear relationship between elevation and temperature ($p<0.001$, RMSE: 0.95°C) derived from the Global Historical Climatology Network (GHCN-Monthly) data base (time series from the 1930s to 2006; four stations) and the Global Summary of the Day (GSOD) data base (time series from 1957 to 2006; 10 stations). Maximum lake depth (Z_{max}) was determined by GPS-guided echo-sounding. Lake surface area (SA) was calculated using either field-measured diameter and/or circumference (small, circular crater lakes) or by analysis of topographical maps (larger lakes, often irregular in shape). We distinguished the following types of land use: stable ground cover (which included natural or secondary forest, savannah, and tree plantations), fallow land, habitation, and (subsistence and commercial crop) agriculture. Habitation constituted a significant fraction of total land cover in two crater basins only (Kasenda and Nyabikere) and was therefore not included in statistical analyses. The other three represent broad categories in runoff and soil erosion rates, ranging from low (stable) to intermediate (fallow land) and high (agriculture).

Surface-water temperature (SWT), surface and bottom pH (pH-surf, pH-bot), dissolved oxygen (DO) at 0.5m depth (or surface when $Z_{max} < 0.5$m) and specific conductance at 25°C (Scond, a proxy for salinity) were measured at the time of sampling with a Hydrolab Quanta multiprobe. Transparency (Secchi) was measured using a 22 cm diameter Secchi disk. The following parameters were determined: cations (Ca, Mg, Na, K, Ba, Sr, Fe, Mn), anions (F, Cl, Br, NO_3, SO_4), dissolved silica (Si), dissolved phosphorus (P), dissolved organic carbon (DIC), total organic carbon (TOC), total phosphorus (TP) and total nitrogen (TN). Collection of water samples and analysis for cations, anions, dissolved phosphorus (P), and dissolved inorganic carbon (DIC) followed the procedures described in Eggermont *et al.* (2007). Nutrients were analysed the same day using a Hach Lange DR2800 spectrophotometer. Total phosphorus (TP, in mg/l) and total nitrogen (TN, in mg/l) concentrations were determined using quartz-cuvette tests following hydrolysis. Dissolved silica (Si, in mg/l) was analysed upon return to Belgium, using inductively coupled plasma atomic emission spectrometry. Chlorophyll a (Chl a, in µg/l) concentrations were measured at the surface. Between 400 and 700 ml of water was filtered using a Nalgene filtration unit and GF5 Macherey Nagel glass fiber filters (45 mm diameter). The filter was extracted by placing it for 24 hours in a tube containing 5 ml of 90% acetone, at 4 °C. The extracted solution was filtered using a syringe with encapsulated filter into a 5-cm spectrophotometric cell. The Chl a concentration is the absorption value at 665 nm in a DRELL 2800 spectrophotometer after zeroing with pure acetone.Using Secchi-disk depth and surface-water chlorophyll a (Chl a), lakes were classified according to their primary productivity using a trophic level index (TLi: Chl a/Secchi) (Plisnier *et al.*, in prep).

The presence of fish was recorded in all 56 study lakes with Scond values < 1500 µS/cm; fish can be assumed absent in the true saline lakes (> 10,000 µS/cm) and in Lake Ntambi (5820 µS/cm). Many lakes contain indigenous fish populations (Sato *et al.*, 2003), but in most cases non-indigenous fish were introduced to increase available protein resources (Kizito, 1993; Crisman, 2001; Bwanika *et al.*, 2004). We did not include the relative intensity of fishing per se in this study, as even inside national parks fish poaching is a common practice and no trustworthy information on fishing pressure is available.

Cladocera were sampled by repeatedly sweeping a 50-µm mesh net across planktonic and epibenthic habitat in near-shore (littoral) environments, and in the off-shore planktonic (pelagic) environment. If habitats contained aquatic macrophytes, these were removed from the water and rinsed above the net to adequately sample the attached invertebrate fauna. Samples were instantly fixed in either formalin (5% formaldehyde) neutralized with powdered calcite, or in 40% ethanol. Concurrent sampling and identification of aquatic macrophytes was carried out along transects from the lake shore to the depth limit of aquatic plant growth. Submerged macrophytes in deeper water were sampled using a 4-m long rake. For this study (compare with Lebrun *et al*., in prep) we differentiated between five main types of littoral habitat (HA): sandy or rocky shores including those with submerged parts of terrestrial vegetation (HA-sand); emergent reed-like vegetation such as *Phragmites*, *Cladium* and *Typha* (HA-emer); submerged vegetation with few or no floating parts, such as *Ceratophyllum*, *Potamogeton* and *Chara* (HA-subm); submerged vegetation with considerable floating parts, mostly *Nymphea nouchali* (HA-float); and a swampy vegetation occurring at the edge of some lakes with *Cyperus papyrus* and *Miscanthidium violaceum* (HA-swamp). The total number of aquatic macrophyte habitat types present in a lake (#Macrophytes) was used as a macrophyte habitat diversity measure.

1.2.3 Laboratory analyses

Samples were rinsed using a 50-µm mesh sieve, and retained residues were scanned with a binocular microscope at 30× magnification under a combination of incident and transmitted light. Except for some readily identifiable species, most specimens were picked and mounted in glycerine on microscope slides. Dissection of specimens was carried out when necessary. Identifications were done with a compound microscope at 100-400× magnification, by comparison with Korovchinsky (1992) for the Sididae; Kořínek (1984) and Rey & Saint-Jean (1968; 1969) for the Daphniidae; Smirnov (1976) and Dumont *et al.* (1981) for the Moinidae; Smirnov (1992), Kořínek (1984) and Dumont *et al.* (2002) for the Macrothricidae; Fryer (1968) and Kotov & Štifter (2006) for the Ilyocryptidae; and Smirnov (1996), Kořínek (1984), Rajapaksa & Fernando (1987), Dumont & Silva-Briano (2000), Smirnov *et al.* (2006) and Van Damme & Dumont (2008) for the Chydoridae. A sizable fraction of currently-recognised widespread species may harbour cryptic species diversity (Forró *et al.*, 2008). We used the designation ‘cf.’ to distinguish between species described from Europe or South America and the morphologically similar, yet distinct, African specimens encountered in our samples.

1.2.4 Data analyses

Three water-chemistry variables (Br, NO_3, SO_4) were removed because their concentrations were below detection limit (MDL) at more than half of the study sites. The remaining variables were tested for normality using Shapiro-Wilks tests (Shapiro *et al.*, 1968). Fifteen variables were normalized using either logarithmic (SA, Scond, TP, TN, Chl a, TOC, Na, Mn, P, S and Cl) or squared-root transformation (K, Sr, F and #Macrophytes). Relationships among the environmental variables were assessed using a Pearson’s correlation matrix (Appendix 1). Correlation matrices and normality tests were generated using the software package STATISTICA 5.5 (Statsoft, 2000).

Presence of a species in a sample was recorded when at least two specimens were encountered. For multivariate statistical analysis samples were pooled per lake, across habitat types in order to obtain a representative presence-absence dataset of each lake. We retained species which occurred in only one lake as even rare species contribute ecological information to the data set (Birks, 1995). For freshwater lakes (Scond < 1500 µS/cm), we calculated a Spearman rank correlation matrix to quantify the relationships between environmental variables and species richness, using pairwise deletion where data on environmental parameters was incomplete. To allow meaningful comparison between lakes species richness was evaluated using the raw number of species rather than a diversity index, because even with similar sampling effort among sites, the number of individuals collected varied by three orders of magnitude. We estimated total species richness in the study area using Chao’s formula and two resampling estimators (Colwell & Coddington, 1994; Appendix 2).

Multivariate analyses were conducted only for the subset of 51 out of the 56 sampled freshwater lakes where cladocerans were actually found. Chl a data for Lake Mafura are lacking and were replaced by the average based on the remaining freshwater lakes. The same principle was applied for the missing water chemistry data from Kerere. The final set of 35 environmental variables, including five categorical variables representing the various types of littoral habitat, from 51 lakes was centred and standardized to allow comparison of disparate variables (ter Braak & Šmilauer, 2002).

A principal components analysis (PCA) on a matrix of correlations was used to identify the principal environmental gradients that may structure the faunal data set. Given a gradient length of 2.76 in a detrended correspondence analysis (DCA; Hill & Gauch, 1980), we consequently used canonical correspondence analysis (CCA; ter Braak & Šmilauer, 2002) to explore the relationships between the presence-absence of species and environmental variables. Rare species were down-weighted and forward selection of environmental variables was used to identify which variables explained the greatest amount of variance in the species assemblages. In case of similar contributions, priority was given to variables with known ecological relevance. In order to determine whether the observed effect of cations and anions was not due to their correlation to other environmental parameters, a supplementary correspondence analysis was performed without cation and anion data. We used a Monte Carlo permutation test with 499 permutations to test whether the first axis significantly explained part of the variation in the species data (ter Braak & Verdonschot, 1995). Multivariate statistics were performed using the package CANOCO v. 4.5 (ter Braak & Šmilauer, 2002).

1.3 Results

1.3.1 Environmental gradients

We found a number of correlations between MAT (as elevation) and SWT, conductivity, pH, lake depth, and local vegetation (see correlation matrix), describing the climatic gradient between the often large, shallow and more saline lakes of the dry, warm Rift Valley floor and the smaller, deeper freshwater lakes of the wetter uplands. Transparency (Secchi) is positively correlated with maximal lake depth and negatively with the productivity indicators TN, Chl a, and TOC. Scond and pH-surf are positively correlated with most cations and anions and negatively with #Macrophytes. Negative correlations between the different types of land use are due to the quantification of land use in the crater basin as percentage land cover. The various indicators of aquatic productivity (TP, TN, TOC, and Chl a) are all positively mutually correlated.

Our dataset of freshwater lakes with Cladocera covers a number of environmental gradients (Fig. 2). The first two PCA axes together account for 30.1% of the environmental variance in the dataset ($\lambda_1 = 0.209$ and $\lambda_2 = 0.092$; Fig. 2; Table 3). PCA axis 1, which explains 20.9% of the total variation, mainly captures gradients of aquatic macrophyte habitats, conductivity and surface pH. To a lesser extent, it also reflects gradients in DIC, dissolved Si, Cl and Mg. Several types of aquatic macrophyte habitat show a strong inverse relationship with pH, reflected by their opposite positions in the ordination plot (Fig. 2; see also correlation matrix). Surface-water pH in pristine freshwater lakes ranges from slightly acidic to alkaline (6.55-9.92), with the slightly acidic lakes containing diverse aquatic macrophyte habitats and the alkaline lakes dominated by algae. PCA axis 2, which explains 9.2% of the total environmental variance, is mainly determined by gradients in MAT, lake depth, land use and Ca. To a lesser extent it also reflects gradients in SWT, TP, and P. The plot also illustrates the strong inverse relationship between transparency, and both Chl a and TOC.

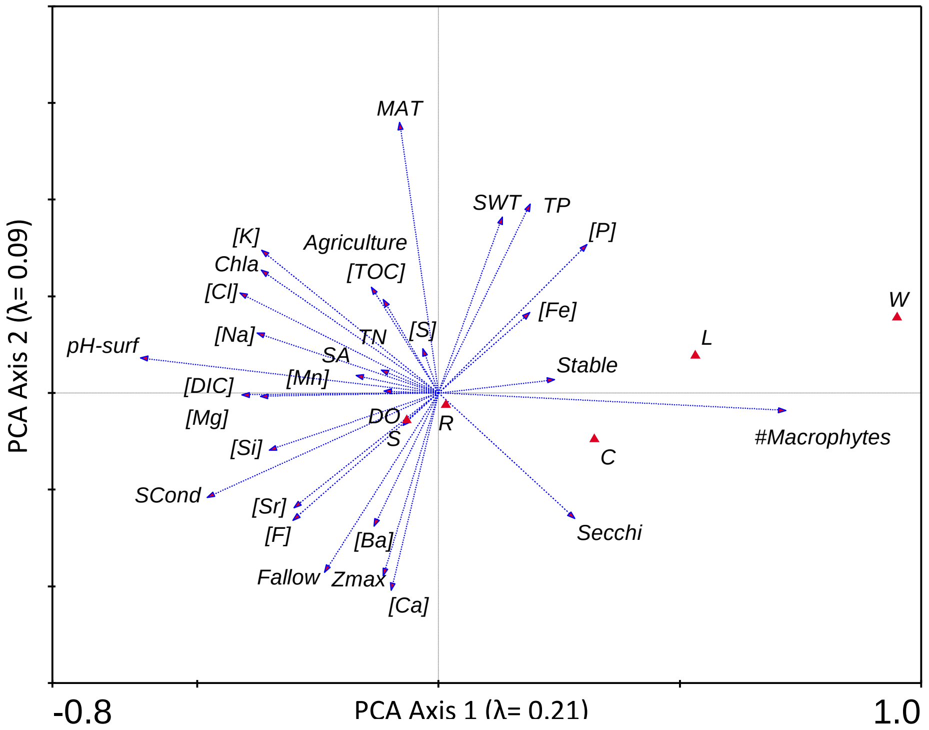

Figure 2: Principal components analysis (PCA) of all measured environmental variables from 51 study sites, freshwater lakes with Cladocera, in Western Uganda.

Table 2: Weighted correlation coefficients of environmental variables for PCA analysis.

	Axis 1	Axis 2	Axis 3	Axis 4
#Macrophytes	0.72	-0.04	-0.35	0.03
W	0.65	0.11	0.11	0.12
L	0.62	0.09	-0.21	-0.05
pH-surf	-0.62	0.07	-0.10	-0.22
Scond	-0.48	-0.22	-0.11	0.02
C	0.43	-0.13	-0.35	-0.11
[Mg]	-0.41	0.00	-0.21	0.12
[Cl]	-0.41	0.21	0.13	-0.14
S	-0.39	-0.33	-0.19	-0.24
[Na]	-0.38	0.12	0.10	0.01
[K]	-0.37	0.30	0.06	-0.07
Chl a	-0.37	0.25	0.15	0.05
DIC	-0.37	-0.01	-0.06	0.03
[Si]	-0.35	-0.12	-0.09	0.05
[P]	0.31	0.31	0.17	0.02
[Sr]	-0.30	-0.24	-0.21	0.04
[F]	-0.30	-0.26	-0.19	0.10
Secchi	0.28	-0.26	-0.18	-0.19
Stable	0.24	0.03	-0.11	-0.33
Fallow	-0.24	-0.37	-0.17	0.24
LogTP	0.19	0.39	0.15	0.03
[Fe]	0.19	0.17	0.31	0.28
SA	-0.17	0.04	0.13	-0.22
Agriculture	-0.14	0.22	0.22	0.25
SWT	0.13	0.36	0.13	-0.11
[Ba]	-0.13	-0.28	-0.16	0.00
TN	-0.12	0.05	0.14	-0.13
[Mn]	-0.11	0.00	0.16	0.22
[TOC]	-0.11	0.19	0.25	0.02
Z_{max}	-0.11	-0.38	-0.06	-0.02
[Ca]	-0.10	-0.41	-0.06	0.08
MAT	-0.08	0.56	0.13	-0.09
DO	-0.07	-0.07	0.02	-0.12
R	0.06	-0.09	-0.12	0.16
[S]	-0.03	0.09	0.17	-0.01

1.3.2 Faunistics

A total of 37 Cladocera species from 26 genera were found in 52 of the 62 study lakes (Table 2). *Chydorus parvus, Macrothrix triserialis, Ceriodaphnia cornuta*, *Pseudochydorus* cf. *globosus*, *Alona cambouei* and *Moina micrura* were the most widely distributed, being present in 30, 29, 28, 27, 18 and 17 lakes, respectively. Species richness per lake was highly variable ranging from 0 (see below) to 21 (Lake Ibamba). Several species, such as *Scapholeberis kingi*, *Pseudosida szalayi*, *Moinodaphnia macleayi, Ilyocryptus spinifer* and *Kurzia longirostris* were found only in the shallow, swamp-like lakes Ibamba and Kyogo. Other rare taxa that were found in only one or two lakes include *Alonella exigua, Coronatella* cf. *rectangula, Bosmina longirostris, Daphnia barbata, Diaphanosoma excisum, Graptoleberis testudinaria, Moina belli, Simocephalus mesorostris* and *S. serrulatus* (Table 2). *Bosmina longirostris* was encountered only in a shallow temporary swamp near Lake Wandakara. *Daphnia barbata* was found in Lake Kibengo (a satellite basin of Lake George) and in the Kazinga channel which connects lakes George and Edward (Fig. 1). No cladocerans were found at five freshwater lakes: Kasirya, Kitere, Kisibendi, Njarayabana and Nyungu. Both Nyungu and Kisibendi are hyper-eutrophic, while Kasirya, Kitere and Njarayabana lack significant submerged or floating aquatic macrophytes.

Only three cladoceran species were found at Scond values above 1000 µS/cm: *Alonella excisa* was found in Lake Kyanga (1112 µS/cm) and *Macrothrix* sp. in Wandakara (1158 µS/cm). *Moina belli* is the only truly halophilic cladoceran in our dataset, occurring at conductivities up to 22400 µS/cm (Lake Kikorongo).

In the set of 56 freshwater lakes, species richness was positively correlated with the diversity of aquatic macrophyte habitat (#Macrophytes: $r= 0.733$, $P< 0.001$), and negatively with pH-surf ($r= -0.662$, $P< 0.001$), Chl a ($r= -0.369$, $P= 0.006$) and Scond ($r= -0.448$, $P= 0.001$). Chao’s formula suggests a regional species richness of 42 species; the first- and second-order jackknife estimates are 44 and 47 species, respectively. This indicates that the present survey may have missed between five to ten species (12-21%) of the total regional species pool.

Table 3: Taxonomic overview of identified Cladocera with indication of the number of lakes in which the species were encountered (number of additional lakes where only a single specimen was found indicated between brackets) and the total number of specimens found**.** See Appendix 3 for an overview of the changes in nomenclature since Verschuren *et al.* (2000).

	#lakes	#specimens
Sidoidea		
Ctenopoda		
Sididae Baird, 1850		
Pseudosida Herrick, 1884		
Pseudosida szalayi Daday, 1898	2	53
Diaphanosoma Fischer, 1850		
Diaphanosoma excisum Sars, 1886	2	19
Daphnioidea		
Anomopoda		
Bosminidae Sars, 1865		
Bosmina Baird, 1845		
Bosmina longirostris Muller, 1785	1	6
Chydoridae Dybowski & Grochowski, 1894		
Alona Baird, 1843		
Alona cambouei Guerne & Richard, 1893	18	97
Alona guttata G. O. Sars, 1862	8	196
Alona cf. *verrucosa* Sars, 1901	11	186
Alonella Sars, 1862		
Alonella exigua Lilljeborg, 1853	1	10
Alonella excisa Fischer, 1854	5	19
Chydorus Leach, 1816		
Chydorus eurynotus Sars, 1901	4(1)	177
Chydorus parvus Daday, 1898	30	1649
Coronatella Dybowki & Grochowski, 1894		
Coronatella cf. *rectangula* Sars, 1861	1	28
Disparalona Fryer, 1968		
Disparalona hamata Birge, 1879	11	128
Dunhevedia King 1853		
Dunhevedia crassa King, 1853	11	51
Dunhevedia serrata Daday, 1898	3	10
Ephemeroporus Frey, 1982		
Ephemeroporus barroisi Richard, 1894	4	59
Euryalona Sars, 1901		
Euryalona orientalis Daday, 1898	4	17
Graptoleberis Sars, 1862		
Graptoleberis testudinaria Fischer, 1848	2	7
Karualona Dumont and Silva-Briano, 2000		
Karualona iberica Alonso & Pretus, 1989	14	198
Kurzia Dybowski and Grochowski, 1894		
Kurzia longirostris Daday, 1898	1	2
Notoalona Rajapaksa and Fernando, 1987		
Notoalona globulosa Daday, 1898	3	85
Oxyurella Dybowski and Grochowski, 1894		
Oxyurella singalensis Daday, 1898	6	75
Pleuroxus Baird, 1843		
Pleuroxus cf. *varidentatus* Frey, 1993	14	199
Pleuroxus toumodensis Brehm 1933	5	42
Pseudochydorus Fryer, 1968		
Pseudochydorus cf. *globosus* Baird, 1843	26(1)	90

	#lakes	#specimens
Daphniidae Straus, 1820		
Ceriodaphnia Dana, 1853		
Ceriodaphnia cornuta Sars, 1885	28	1142
Ceriodaphnia dubia Richard, 1894	14	880
Daphnia Müller, 1785		
Daphnia barbata Weltner, 1898	1	2
Daphnia laevis Birge, 1879	3(1)	67
Scapholeberis Schoedler, 1858		
Scapholeberis kingi Sars, 1888	1	7
Simocephalus Schoedler, 1858		
Simocephalus mesorostris Orlova-Bienkowskaja, 1995	2	69
Simocephalus vetulus Muller, 1776	11	162
Simocephalus serrulatus Koch, 1841	1	67
Ilyocryptidae Smirnov, 1976		
Ilyocryptus G. O. Sars, 1862		
Ilyocryptus spinifer Herrick, 1882	1	40
Macrothricidae Norman & Brady, 1867		
Macrothrix Baird, 1843		
Macrothrix triserialis group Brady, 1886	29	970
Moinidae Goulden, 1868		
Moina Baird, 1850		
Moina belli Gurney, 1904	1	24976
Moina micrura Kurz, 1874	17(1)	2192
Moinodaphnia Herrick, 1887		
Moinodaphnia macleayi King, 1853	2	125

1.3.3 Species-environment relationships

CCA with forward selection retained the following variables, which together explain 21.7% of the total faunal variance: TP, MAT, #Macrophytes, pH-surf, % agriculture and Mg (Table 4). The Monte Carlo permutation test on the first CCA axis was highly significant (axis 1: F=3.55, P= 0.002). TP, MAT, pH-surf and #Macrophytes are the most important predictors of cladoceran assemblage composition on CCA axis 1 (Fig. 3). Besides the diversity of aquatic macrophyte habitats, the fraction of the crater basin used for agriculture and TP explain the most variance along CCA axis 2. This reflects a gradient in both aquatic macrophyte diversity and lake productivity, as determined by Z_{max} and %agriculture. Lakes situated in the lower quadrants have an extensive littoral zone with several types of submerged, floating or emergent aquatic macrophytes. They are often located in national parks (Fig. 1), and/or have crater basins with steep, uncultivated slopes. The upper quadrants include lakes located in crater basins with intensive agriculture, as well as several shallow, naturally eutrophic lakes. *Diaphanosoma, Moinodaphnia, Ilyocryptus* and *Pseudosida* seem to be associated with dilute, swampy lakes with low pH (Fig. 3B). *Ceriodaphnia*, *Alona cambouei*, *Macrothrix triserialis* and *Chydorus parvus* were encountered in a wide variety of lakes, while *Simocephalus latirostris*, *Dunhevedia crassa*, *Alona guttata,* and *Pleuroxus toumodensis* seem restricted to lakes with diverse aquatic macrophyte habitat. Removal of cation and anion data did not drastically alter the resultant CCA as forward selection retained the same remaining variables, which, due to the exclusion of Mg, explain only 18.8% of the total faunal variance (Table 5).

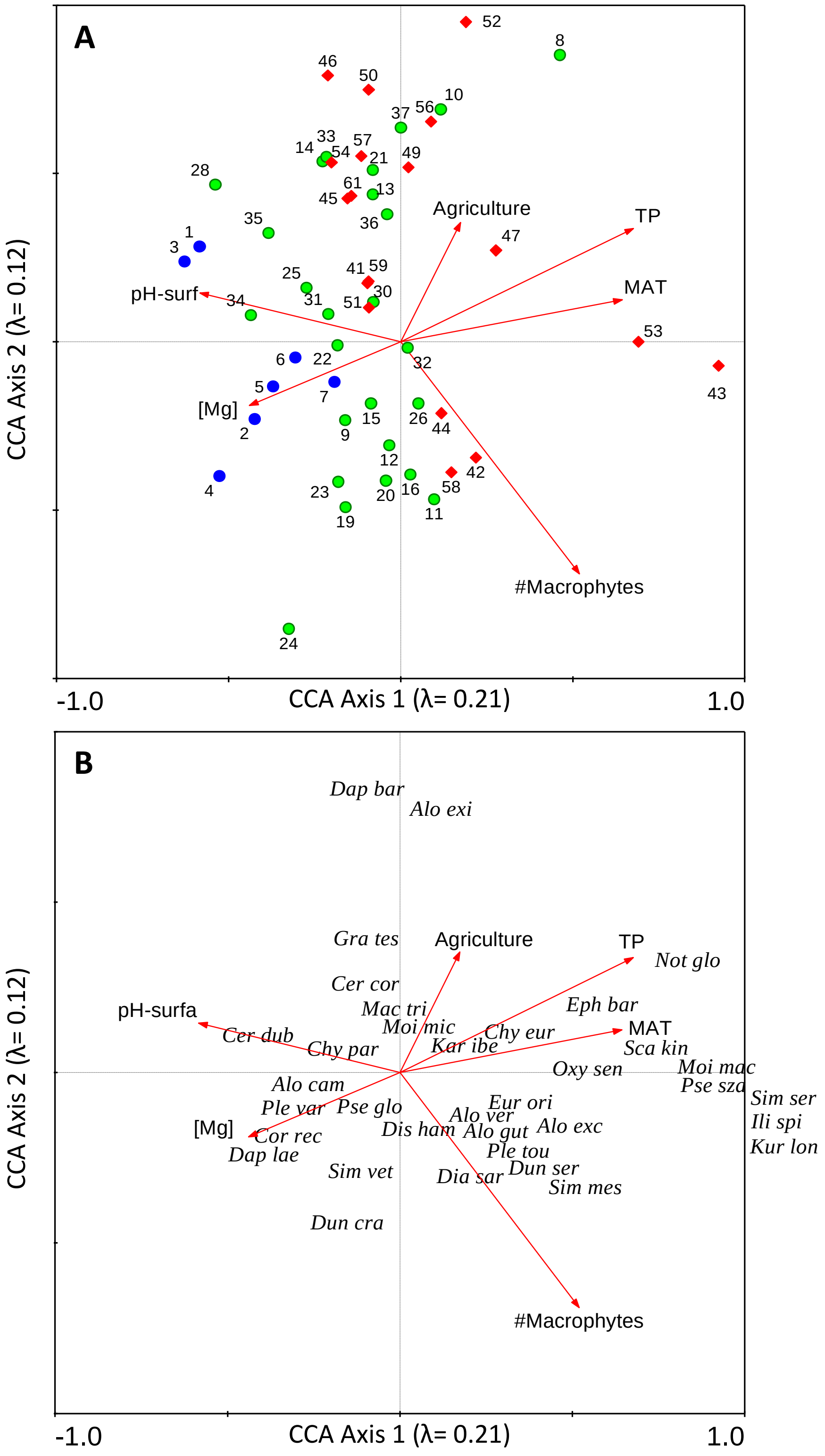

Figure 3: Ordination diagram (canonical correspondence analysis, CCA) of A) the 51 sample sites and B) cladoceran Presence-Absence data in relation to selected environmental variables. Sites are classified as follows: Fort Portal (cross), Kasenda (circle) and Bunyaruguru (diamond) lake clusters. Site and taxon codes are found in Tables 1 and 2, respectively. Three species (*Sim ser*, *Ili spi* and *Kur lon*) have identical scores due to a uniform distribution.

Table 4: CCA (summary) based on presence-absence of 36 Cladocera species from 51 lakes.

Canonical correspondence axes:	1	2	3	4	
Eigenvalues	0.21	0.12	0.09	0.08	
Species environment correlations	0.86	0.76	0.69	0.71	
Cumulative percentage of variance					
of species data	7.5	12	15.3	18.2	
of species-environment relationship	34.3	55	70.4	83.6	
Sum of all eigenvalues					2.74
Sum of all canonical eigenvalues					0.59
Weighted correlation coefficients of selected environmental variables					
TP	0.58	0.26	-0.09	0.01	
MAT	0.55	0.10	0.08	0.50	*
pH-surf	-0.50	0.11	0.11	0.34	*
#Macrophytes	0.44	-0.53	-0.21	-0.14	*
Mg	-0.38	-0.14	0.48	0.25	*
Agriculture	0.15	0.27	0.43	-0.42	*

* Environmental variable significantly explains part of the variation after variance partitioning

Table 5: CCA (summary) based on presence-absence of 36 Cladocera species from 51 lakes. Anion and cation data removed from the dataset.

Canonical correspondence axes:	1	2	3	4	
Eigenvalues	0.20	0.12	0.08	0.07	
Species environment correlations	0.85	0.75	0.70	0.69	
Cumulative percentage of variance					
of species data	7.4	11.7	14.7	17.2	
of species-environment relationship	39.6	62.5	78.2	91.8	
Sum of all eigenvalues					2.74
Sum of all canonical eigenvalues					0.52

1.4 Discussion

1.4.1 Environmental gradients

The limited number of lakes with intermediate salinities (1500-10,000 µS/cm) in our current dataset reflects the true scarcity of such lakes in tropical Africa (Talling & Lemoalle, 1998). In our dataset, saline to hypersaline lakes are concentrated in the southern (Kikorongo and Bunyaruguru) lake clusters, and are typically rather shallow and eutrophic. The freshwater lakes display a wide range of depths and trophic levels, with the shallower lakes often being polymictic and eutrophic, whereas deeper lakes are oligomictic or meromictic, and oligo- to mesotrophic (Plisnier *et al.*, in prep.). Pronounced interannual and interseasonal differences in measured surface-water TP is due to cycles of stratification and mixing, as often a quite strong depth gradient in TP (and TN) occurs with nutrients accumulating in the hypolimnion during stratification (Plisnier *et al.*, in prep.). A single surface-water TP, TN, DOC or Chl a measurement will therefore not always be a good measure for the average trophic status of a lake. In the PCA, the fraction of land used for agriculture points in the same direction as both

TOC and Chl a, suggesting a relationship between lake trophic status and land use intensity. This relationship is neither straightforward nor universal, however, since there is no significant positive correlation between %agriculture and the various indicators of lake trophic status (see Correlation Table). Land-use intensity influences aquatic ecosystem functioning by impacting on aquatic macrophyte development, as suggested by the negative correlation of #Macrophytes with %agriculture (r=-0.318, P=0.016) and its positive correlation with stable types of land cover (r=0.396, P=0.002) in freshwater lakes. In our dataset, transparency (Secchi) is positively correlated with maximal lake depth and negatively with MAT, since most deep lakes are situated in the northern (Fort Portal and Kasenda), more elevated and thus colder lakes. This also explains the inverse relationship between MAT and transparency.

1.4.2 Faunistics

The species richness of Cladocera in the 62 western Uganda crater lakes studied here (37 species) is comparable to that found in a set of lowland lakes and ponds in Cameroon (35 species, Chiambeng, 2004). Due to the large number of species recorded from only one (9 species) or two (5 species) lakes, Chao’s formula indicated that between five to ten species were missed by this survey. A more comprehensive study, with extensive sampling conducted over a longer period of time, would probably reveal more species. Green (1993) found that in East African freshwater lakes the long-term number of zooplankton species found could be two to three-and-a-half times the momentary number of species sampled. We suspect that the currently missing species are to be found mainly in either swamp or planktonic habitats. Swamp habitats are represented in the dataset from only seven locations, and we did not encounter several of the species previously recorded from Ugandan swamps (Thomas, 1961). The pelagic zone is subject to marked seasonal dynamics in algal composition (Kizito, 1993) which in turn is likely to result in seasonal changes in zooplankton composition.

Several cladoceran species such as *Scapholeberis kingi, Pseudosida szalayi* and *Moinodaphnia macleayi* were found only in dilute, but eutrophic, swampy lakes. *Pleuroxus toumodensis* and *Dunhevedia serrata* were found almost exclusively in pristine lakes with (abundant) aquatic macrophytes. Several other species, such as *Karualona iberica, Moina micrura* and *Macrothrix triserialis* did not exhibit clear responses to any of the measured environmental parameters, indicating a eurytopic nature. Indeed, *Moina micrura* is considered by some to be the most successful cladoceran of Africa for its wide distribution and fast adaptation to changes in ecological conditions (Saint-Jean & Bonou, 1994). In this study, we found it in a wide diversity of lakes, ranging from shallow, eutrophic lakes with abundant macrophytes to very deep, oligotrophic lakes without significant littoral zone. *Alona cambouei* was often found in lakes with sandy or muddy littoral zones, while *A.* cf. *verrucosa* and *A. guttata* were more common in lakes with submerged or floating macrophytes. Different representatives of this genus are known to prefer different habitats (Tremel *et al.*, 2000) or environmental conditions (Verschuren *et al.*, 2000; and primary references therein). *Simocephalus vetulus* was found almost exclusively in oligo- or mesotrophic lakes with submerged or emergent macrophytes. The two exceptions are Lake Ibamba and Lake Nyabikere, two eutrophic lakes with a broad reed fringe along the shore and other aquatic macrophytes in the littoral. *S. vetulus* has previously been noted to live between dense vegetation of submerged macrophytes (Alonso, 1996, Hann & Zrum, 1997). *Simocephalus mesorostris* was found in two shallow, pristine lakes with abundant vegetation, which corresponds with previous records of this species in the vegetation of warm, unpolluted water bodies with low pH and low oxygen concentrations (Orlova-Bienkowskaja, 1995). *Graptoleberis testudinaria*, a phytophilic chydorid that while feeding glides over surfaces of aquatic macrophytes like a minute snail (Fryer, 1968), was found in lakes Nyabikere and *Kanyamukali*. In the latter lake, we assume it must be feeding on epiphytic algae on submerged parts of reeds as there were no other aquatic macrophytes present. *Pseudochydorus* cf. *globosus* was found to be most common in oligo- to mesotrophic lakes, but it also occurred in one shallow, hyper-eutrophic lake. This species is a scavenger feeding on dead crustaceans and organic detritus (Fryer, 1968; Van Damme & Dumont, 2007). In Europe it occurs in oligo- to slightly eutrophic waters, in association with submerged macrophytes (Flössner, 2000), but can also be the dominant cladoceran in turbid water containing little or no vegetation (Van Damme & Dumont, 2007).

1.4.3 Environmental regulation of Cladocera distribution

When considering the entire dataset, lake-water salinity (Scond) seems to be a major factor in determining Cladocera distribution among lakes, with only one species (*Moina belli*) found in the saline lakes. *Moina belli* has been found at Lake Kikorongo by the authors since 2001 and we suspect that Thomas's (1961) record of *Moina* sp. from there concerns *M. belli* as well. It has also been recorded from Lake Shala, Ethiopia, where it occurs at conductivities up to 21000 µS (Green, 1993). Its absence from lake Nshenyi (11,230 µS/cm) in this study could be related to seasonal desiccation, as two *M. belli* resting eggs were found in the samples from this lake. This low diversity in saline lakes reflects the typically freshwater nature of Cladocera species, most of which are unable to tolerate conductivities above 3000 µS/cm (Frey, 1993). Even within the freshwater range (Scond < 1500 µs/cm) cladoceran species richness was negatively correlated with conductivity, which could be due to the limited salinity tolerance of aquatic macrophytes rather than through direct physiological stress of the Cladocera (Hammer, 1986).

Our CCA-analysis of cladoceran community composition in freshwater Ugandan crater lakes showed that the diversity of aquatic macrophyte habitat in a lake, TP, MAT, pH-surf, land used for crop agriculture and Mg are all important explanatory environmental variables. This result is consistent with observations that cladoceran community composition is influenced by aquatic vegetation (Declerck *et al.*, 2005), nutrients (Jeppesen *et al.*, 2003; Declerck *et al.*, 2005; Taylor *et al*, 2006), pH (Roff & Kwiatkowski, 1977), climate (Gyllström *et al*., 2005; Kamenik *et al.*, 2007) and cations (Kamenik *et al.*, 2007). To a certain extent CCA axis 1 reflects broad regional differences in Mg and TP between the northern (Fort Portal and Kasenda) and southern (Bunyaruguru) lakes (Fig. 3A). CCA axis 2 distinguishes mostly pristine lakes with abundant macrophytes from those with significant human impact. The density of zooplantivorous fish, not measured in this study, may also be an important structuring force as was the case in shallow European lakes (Davidson *et al*., 2007).

Our results match those of studies in Europe where eutrophic shallow waters, densely overgrown with macrophytes, generally support large densities of phytophilous cladocerans, including rare taxa (Gulyás, 1994; Illyová & Némethová, 2005). In this regard it is worth noting that species richness in Lake Kifuruka fell from 14 species in 2002 (Knockaert & Rumes, unpublished data) to 9 in 2008, likely because *Nymphea nouchali* and *Ceratophyllum demersum* were strongly reduced by the introduction of a *Tilapia* species that feeds on aquatic macrophytes. In most tropical lakes, low turbidity, low productivity, abundant aquatic macrophytes, and the associated rich cladoceran faunas, are maintained by wide *Phragmites australis* or *Cyperus papyrus* belts that limit terrestrial nutrient input (Dumont, 1992). Even a small buffer of natural vegetation along the shoreline or in the littoral zone might be beneficial, particularly in shallow lakes with steep crater slopes and high soil-erosion rates. This may explain why species richness in Lake Ibamba, and to a lesser extent in Lake Nyabikora, is higher compared to other shallow lakes with similar land use in the crater basin.

Hoffmann & Dodson (2005) discuss the various ways in which land use can affect zooplankton species richness. In this study, land used for crop agriculture is a proxy for the vulnerability of catchment soils to erosion, and therefore also to cultural eutrophication; TP is an obvious proxy for lake trophic status at the time of sampling. In the pristine lakes we studied, species richness tended to increase with primary productivity as in Hoffman & Dodson (2005), but at the upper end of the productivity gradient cladoceran species richness drastically declined due to the absence of submerged plants. Indeed, the latter results in loss of structural diversity, habitat and food (Jeppesen *et al*., 2003; Declerck *et al*., 2005). In disturbed lakes, the relationship between primary productivity and species richness was less clear, but the decline in species richness at the upper end of the productivity gradient was still obvious. This strong variation in productivity and aquatic macrophytes in shallow lakes may explain why, in contrast to Hofmann (1996), we did not find a positive correlation between cladoceran species richness and lake depth or lake size, even when limiting our dataset to relatively shallow lakes (Zmax < 20m).

While the effect of Ca concentrations on zooplankton species assemblages has been illustrated (Hessen, 2000; Wærvågen *et al.*, 2002), it is unclear how Mg concentrations here affect cladoceran species composition. Variation of calcium and magnesium with total salinity in African lakes is controlled by the precipitation of their carbonates in waters of higher salinity and alkalinity (Beadle, 1932). Magnesium carbonates will precipitate at higher alkalinities than those of calcium (Talling & Talling, 1965; Gorham *et al.*, 1983). In our data there was a significant correlation between Mg and both cladoceran species richness (r= -0.387, P= 0.003) and Scond (r= 0.416, P= 0.001). Additionally, there is also a north-south gradient, in freshwater lakes with Cladocera, with on average higher Mg concentrations and conductivities in northern lakes than in southern lakes (Fig. 3A). The effect of Mg on species composition could be attributed to both Scond and a north-south gradient in bedrock Mg concentrations, rather than a direct effect of Mg itself.

In conclusion, our results demonstrate that Cladocera species distribution among the Ugandan lakes is most strongly determined by a number of quantifiable environmental parameters such as nutrient availability (total phosphorus, TP), the presence and diversity of aquatic macrophyte habitat, pH, mean annual temperature, and the fraction of the crater catchment used for agriculture. The significant turnover of cladoceran species in relation to these critical environmental gradients demonstrates their potential as biological indicators for the water quality and ecosystem health of western Ugandan crater lakes as well as for palaeolimnological reconstructions of both natural and anthropogenic changes in lake systems.

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Appendix 1

Correlation table

	Log(SA)	Zmax	MAT	Scond	Secchi	Stable	Agriculture	Fallow	pH-surf	SWT	O2	TP	TN	Chl a	TOC	Na	K	Ca	Mg	Sr	Ba	Fe	Mn	P	S	Si	F	Cl	DIC
Zmax	0.058																												
MAT	***0.475	**-0.396																											
Scond	0.238	-0.059	**0.392																										
Secchi	0.043	***0.598	*-0.295	-0.240																									
Stable	0.127	-0.110	*+0.307	*0.277	0.035																								
Agriculture	-0.032	-0.026	-0.109	*-0.254	-0.206	***-0.856																							
Fallow	-0.201	0.262	***-0.435	-0.138	*0.266	***-0.599	0.105																						
pH-surf	***0.550	-0.072	***0.552	***0.591	*-0.287	0.073	0.014	-0.152																					
SWT	**0.337	***-0.467	***0.749	**0.390	-0.200	**0.386	-0.212	**-0.418	**0.343																				
O2	0.238	0.107	-0.076	0.050	-0.215	-0.079	*0.282	*-0.292	0.124	-0.066																			
TP	-0.004	*-0.266	**0.402	**0.400	-0.217	0.156	-0.069	-0.187	0.093	**0.387	*-0.270																		
TN	*0.296	-0.240	**0.389	*0.249	**-0.347	0.190	-0.042	*-0.306	*0.271	**0.376	0.158	***0.455																	
Chl a	0.163	**-0.406	***0.462	*0.274	***-0.582	0.098	0.023	-0.233	***0.523	0.189	0.093	*0.341	**0.411																
TOC	0.205	**-0.395	***0.508	***0.551	***-0.534	*0.315	-0.158	**-0.369	**0.420	***0.510	-0.008	**0.437	***0.609	***0.545															
Na	0.242	-0.246	***0.534	***0.872	-0.254	0.156	-0.115	-0.134	***0.624	***0.494	-0.067	**0.429	**0.350	**0.423	***0.643														
K	0.244	-0.187	***0.456	***0.491	-0.169	-0.181	0.225	-0.027	***0.518	0.236	0.041	0.220	0.125	*0.276	0.153	***0.842													
Ca	**-0.378	0.097	**-0.418	0.012	-0.001	-0.214	-0.034	***0.464	-0.192	**-0.368	0.051	0.088	-0.072	0.012	*-0.316	-0.163	-0.047												
Mg	-0.003	0.204	0.085	**0.416	0.081	-0.120	-0.027	*0.282	*0.306	-0.073	-0.072	0.000	-0.246	0.082	-0.055	*0.330	***0.492	**0.374											
Sr	-0.172	***0.467	-0.226	0.242	*0.310	-0.188	-0.085	***0.495	0.027	*-0.322	-0.087	-0.058	*-0.290	-0.167	*-0.310	0.070	0.197	***0.597	***0.783										
Ba	*-0.307	**0.367	*-0.265	*0.277	0.188	0.063	-0.230	0.232	-0.151	-0.243	-0.127	0.134	-0.108	-0.132	-0.025	0.101	-0.040	***0.457	***0.446	***0.769									
Fe	0.080	-0.264	*+0.273	0.244	*-0.286	*0.330	-0.200	*-0.318	-0.036	**0.431	0.097	0.253	0.174	*0.338	***0.591	*0.286	-0.254	-0.163	-0.115	-0.265	-0.031								
Mn	0.051	-0.186	0.175	0.204	*-0.339	0.175	-0.077	-0.224	0.102	0.180	0.025	*0.296	0.166	**0.450	***0.511	0.182	-0.120	0.079	0.046	-0.085	0.112	***0.675							
P	-0.001	-0.203	***0.440	***0.468	-0.107	0.177	-0.037	*-0.272	0.188	**0.402	-0.254	***0.778	0.224	*0.288	***0.540	***0.527	0.116	-0.029	0.057	-0.027	0.152	**0.359	*0.289						
S	0.087	-0.246	**0.376	***0.507	-0.232	0.077	-0.110	0.040	**0.398	***0.486	-0.167	0.232	0.255	0.209	***0.492	***0.609	0.221	-0.194	0.125	-0.085	-0.095	0.250	-0.035	0.260					
Si	0.085	0.058	*0.299	***0.463	-0.113	-0.023	-0.075	0.155	**0.350	0.191	0.090	0.213	0.254	0.152	*0.268	**0.404	0.122	0.243	0.214	0.249	0.240	0.181	0.132	*0.286	0.180				
F	0.107	0.033	*0.267	***0.863	-0.053	0.165	-0.230	0.038	***0.467	*0.270	-0.164	0.252	0.052	*0.279	***0.540	***0.788	0.234	0.010	***0.499	*0.322	**0.391	**0.395	*0.298	***0.552	***0.488	**0.388			
Cl	**0.366	-0.238	***0.597	***0.820	*-0.281	0.115	-0.015	-0.214	***0.688	***0.516	-0.046	***0.5639	***0.5186	***0.452	***0.635	***0.917	***0.829	-0.208	0.264	-0.034	0.029	0.272	*0.293	***0.654	***0.508	**0.367	***0.729		
DIC	0.047	-0.050	0.230	***0.561	-0.112	*-0.294	0.190	0.219	**0.399	0.157	-0.001	0.208	0.164	0.211	0.119	***0.775	***0.789	*0.285	***0.676	**0.448	0.233	*-0.332	-0.099	0.147	0.195	*0.302	***0.580	***0.730	
#Macrophytes	*-0.264	-0.015	-0.245	*-0.303	0.227	*0.272	-0.239	-0.142	***-0.480	-0.083	-0.053	-0.001	*-0.311	*-0.313	*-0.280	**-0.375	*-0.311	-0.025	-0.172	-0.041	0.126	0.007	-0.109	-0.126	-0.190	*-0.320	-0.231	***-0.459	*-0.328

* $P < 0.05$ ** $P < 0.005$ *** $P < 0.001$

Appendix 2

Total species richness was estimated using Chao’s formula and two resampling estimators (Colwell & Coddington, 1994). In this formula S* = number of species; S_{obs} = observed number of species; L= the number of observed species that are represented by in only a single sample (i.e. the no. of “singletons”); M = is the number of observed species present in exactly two samples (i.e. no. of “doubletons”) and n = the number of samples.

- Chao’s formula is given by

$$S^{*} = S_{obs} + \frac{L^{2}}{2M}$$

- The first-order jacknife estimate is given by

$$S^{*} = S_{obs} + L\frac{n-1}{n}$$

- The second-order jacknife estimate is given by

$$S^{*} = S_{obs} + \left[L\frac{2n-3}{n} - M\frac{(n-2)^{2}}{n(n-1)}\right]$$

Appendix 3

Overview of the changes in nomenclature since Verschuren *et al.* (2000).

Alona rectangula	⇨	*Coronatella* cf. *rectangula*
Alona nr *cambouei*	⇨	*Alona cambouei*
Biapertura karua	⇨	*Karualona iberica*
Biapertura verrucosa	⇨	*Alona* cf. *verrucosa*
Pleuroxus aduncus	⇨	*Pleuroxus* cf. *varidentatus*
Pleuroxus nr *laevis*	⇨	*Disparalona hamata*
Pseudochyodorus globosus	⇨	*Pseudochydorus* cf. *globosus*
Ceriodaphnia nr *rigaudi*	⇨	*Ceriodaphnia cornuta*
Ctenodapnia barbata	⇨	*Daphnia barbata*

2

Environmental regulation of ostracod (Crustacea: Ostracoda) communities in western Uganda crater lakes

Abstract

We analyzed the species composition of present-day ostracod communities in 62 lowland crater lakes of western Uganda in relation to environmental and hydrochemical characteristics of their aquatic habitat. These lakes are spread across the climatic gradient between the sub-humid shoulder and semi-arid floor of the Rift Valley, and cover a conductivity (~salinity)[1] gradient from 56 to 135,400 µS/cm, a productivity gradient from oligotrophic to hypertrophic, and a depth gradient from shallow and mixing daily to deep and permanently stratified. We found 33 ostracod taxa, 29 of which had not previously been reported from Uganda and six could not be assigned to known species or subspecies. We provide scanning electron microscopy (SEM) images of the valve morphology of all encountered taxa to aid their identification in palaeolimnological applications. No living ostracods were found in the five lakes with conductivity exceeding 10,000 µS/cm. Multivariate analysis of ostracod species distribution in relation to environmental variables, based conservatively on species occurrence records of at least two live specimens collected at any site, found that ostracod faunal composition in fresh (<1500 µS/cm) Ugandan crater lakes is influenced most strongly by the structural diversity of aquatic macrophyte habitat, salinity, and aquatic productivity. Including species occurrence records of single live specimens and by-catch of sub-recent empty ostracod valves did not significantly alter this result, however it dramatically increased the fraction of lakes in which species were recorded, suggesting significant seasonality in local population development. The distinct distribution of ostracod species in relation to the aquatic habitat characteristics of Ugandan crater lakes indicates that fossil ostracod assemblages preserved in Ugandan lake sediments have high potential as palaeoenvironmental indicators for past climatic and human impacts on aquatic ecosystems in equatorial East Africa.

Keywords: Ostracoda, Uganda, crater lakes, palaeolimnology

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[1] Salinity is measured as the total concentration (mg per liter) of ions dissolved in water. Ions common in fresh water include calcium, magnesium and bicarbonate with lesser amounts of other common ions such as sodium, potassium, sulfate, chloride, nitrate, phosphate, and silicate. Salinity can be measured as specific conductance (also called conductivity). The more ions in water, the better it conducts electricity. Conductivity is measured by the rate of flow of current between two platinum electrodes, and the preferred units of electrical conductance are micro-Siemens (µS). (Dodson, 2005)

Rumes, B., K. Martens & D. Verschuren. Environmental regulation of ostracod (Crustacea: Ostracoda) communities in western Uganda crater lakes. In preparation.

2.1 Introduction

Freshwater ostracods are small to medium-sized (0.3 to 3.5 mm) crustaceans that form a bi-valved carapace impregnated with low-magnesium calcite. They can occur in all types of water ranging from slightly acidic to alkaline, standing or flowing, temporary or permanent, as well as in groundwater and (semi-) terrestrial environments. Their fossilized carapaces or valves are often abundantly found in Quaternary lake sediments, preserving information about the local aquatic environment which occurred at the time of burial (Holmes, 2001). Due to their great ecological diversity and their excellent preservation, ostracod valves are used in palaeolimnology as sensitive indicators of both natural and anthropogenic changes affecting lake environments. The distribution of non-marine ostracod species has been shown to be determined by temperature (Viehberg, 2006; Horne 2007), lake depth (Mourguiart & Carbonel 1994), water chemistry (Cohen *et al.*, 1983; De Deckker, 1988; Bunbury & Gajewski, 2005) and various substrate types (Cohen, 1986; Verschuren et al., 2000; Kiss, 2007). Ostracods have been used to monitor the effects of anthropogenic disturbance (cf. Külköylüoğlu, 2004) and changes in lake trophic state (cf. Namiotko *et al.*, 1993). In our study area, the gap between the potential and actual use of ostracods in these and other ecological applications is the result of the lack of both distributional data and quantitative ecological information on many taxa and the perceived difficulty associated with even rudimentary identification of ostracods As a result, biodiversity assessments of East African freshwater ecosystems (Mutune *et al.*, 1996, Mwebaza-Ndawula, 2005) and environmental studies (Basima *et al.*, 2006) have rarely included ostracods, contributing to skewed biodiversity estimates and preservation efforts being focused on better -studied groups.

Crater lakes and other small surface waters in western Uganda constitute a regionally important water resource (Republic of Uganda, 2002) and are known to have been influenced both by disturbance from historical human activity (Ssemmanda *et al.* 2005; Russell *et al.* 2009) and substantial natural climate variability in the relatively recent past (Bessems *et al.*, 2008; Russell *et al.*, 2007). An analysis of fossil ostracod assemblages in dated lake-sediment records could allow better understanding of how the now rapidly increasing population pressure and land use are impacting the ecological functioning of the Uganda crater lakes in relation to natural long-term ecosystem dynamics, provided that the ecological requirements and tolerances of individual ostracod species is known.

The present study aims to produce a first significant contribution to this goal through multivariate statistical analysis of comprehensive collections of ostracods and a wide range of ecologically relevant environmental parameters from a large number of these lakes. The ostracod fauna of these Uganda crater lakes has never been analysed before, except for the record of one single species (*Oncocypris mülleri, as O. worthingtoni*) in Lake Kigezi by Lowndes (1936). Other historical ostracod distribution records in western Uganda are from the nearby Rift lakes Edward (Lowndes, 1936; Lindroth, 1953) and George (Lowndes, 1936) and from glacial lakes in the Ruwenzori mountain range (Löffler, 1968).

2.2 Methods

2.2.1 Study area

The crater lakes and a few other small surface waters studied here are all located in one of the four main maar crater districts (Fort Portal, Kasenda, Katwe-Kikorongo, and Bunyaruguru; Melack, 1978) in southwestern Uganda (Figure 1). These small lakes (surface area 0.01-3.84 km^2) are spread along the regional Rift Valley gradient between 914 and 1566 m elevation and semi-arid to subhumid climate regimes. The lakes range from 56 to 135, 400 µS/cm in surface-water salinity, from oligotrophic to hyper-eutrophic, and from shallow and unstratified to deep and permanently stratified (Table 1). Lakes on the moist shoulder of the Rift Valley are fed mainly by rain and surface runoff (and an occasional small stream input), and contribute to the regional groundwater through porous upper crater walls. Lakes on the dry Rift Valley floor are hydrologically closed, often saline, and maintained against the local moisture deficit by substantial groundwater inputs. Water levels of all lakes undergo modest to strong seasonal fluctuations, with some of the salt lakes known to dry up seasonally or intermittently. The crater lakes are mostly alkaline at the surface with an average pH of 8.99 (range 6.55-9.92; SD = +/-0.7), while bottom water can be mildly acidic (average pH 7.3, range 5.81-9.64, SD = +/-1.1)(Plisnier *et al.*, in prep.). The freshwater lakes have been classified as sodium-potassium-magnesium-bicarbonate type lakes, which are rich in potassium (K^+), magnesium (Mg^{2+}) and calcium (Ca^{2+}), and strongly reflect the mineralogy of regional volcanic rocks (Kilham, 1971). For most ions, concentrations seem to be determined by the evaporation of inflow water as predicted by simple evaporative concentration models.

The natural vegetation surrounding the Ugandan crater lakes mainly reflects the local rainfall regime, and varies from dry grass savannah on the floor of the Rift Valley (Katwe-Kikorongo and northern part of Bunyaruguru) to semi-deciduous lowland forest on its shoulders (Fort Portal, Kasenda, and southern part of Bunyaruguru) (White, 1983). In most of the wetter, more densely populated areas, natural vegetation around the crater basins has now been replaced by an agricultural landscape. Routine burning of secondary vegetation and intense subsistence agriculture inside gently sloping crater basins has augmented their phosphorus loading, often causing eutrophication (Kizito et al., 1993). Some lakes are situated within the boundaries of Kibale and Queen Elisabeth National Park, where human activities are limited to fishing and low-intensity exploitation of the surrounding forest (Figure 1).

Table 1: Study lakes in western Uganda ordered by district, with data on lake surface area in km² (SA), maximum depth in m (Z_{max}), Elevation (Elev) in m asl, Mean Annual Temperature (MAT, in °C), surface-water conductivity (SCond) in µS/cm at 25°C, Surface water pH (pH-surf), Bottom water pH (pH-bot), surface water temperature (SWT) in °C, littoral habitat types (Type), Secchi- depth in m (Secchi), Chlorophyl a (Chl a) measurements in µg/l, and the fractional area of land-cover types Stable (forest, savannah and plantation), Agriculture and Fallow, Ostracod species richness (Ntaxa). Habitat types as in Fig.7.

	Lake/District	SA	Z_{max}	Elev	MAT	SCond	pH-surf	pH-bot	SWT	Type	Secchi	Chl a	Stable	Agri	Fallow	Ntaxa
	Fort Portal															
1	Ekikoto	0.02	74	1537	20.02	497	8.29	6.86	24.0	SR	1.80	5.7	0.35	0.25	0.40	8
2	Kaitabarago	0.02	70	1548	19.93	489	8.03	6.04	23.1	SRC	0.75	4.7	0.70	0.00	0.30	6
3	Kayihara	0.01	66	1537	20.02	498	8.07	6.60	23.2	S	1.60	1.8	0.70	0.00	0.30	9
4	Kyaninga (South)	0.24	58	1531	20.07	420	8.34	6.82	24.3	SR	5.85	2.2	0.40	0.00	0.60	14
5	Kyegere	0.12	53	1566	19.79	250	8.31	6.63	24.0	SRC	2.15	1.7	0.01	0.40	0.59	0
6	Nyabikora	0.07	7.7	1561	19.83	188	8.31	6.34	24.7	SRL	1.20	1.7	0.15	0.50	0.35	0
7	Saka (crater)	0.01	8.5	1566	19.79	612	7.59	6.27	25.5	SRL	0.45	15.9	0.45	0.40	0.15	3
	Kasenda															
8	Kanyabutetere	0.01	5	1188	22.85	401	8.62	7.82	25.6	SRC	0.78	19.3	0.00	0.80	0.20	6
9	Kanyamansira	0.02	30	1177	22.94	394	8.96	6.60	25.9	SRC	0.82	18.2	0.90	0.00	0.10	3
10	Kanyamukali	0.02	11	1150	23.16	920	8.60	7.81	26.2	SR	0.65	8.2	0.10	0.70	0.20	2
11	Kanyanchu	0.01	4.8	1233	22.48	568	8.26	7.90	26.6	SRCLW	0.93	4.5	1.00	0.00	0.00	11
12	Kanyango	0.12	58	1259	22.27	493	8.75	6.49	25.0	SRL	0.45	22.1	0.25	0.65	0.10	1
13	Kasenda	0.09	13.5	1244	22.39	312	7.63	6.85	24.6	SR	0.83	13.1	0.40	0.05	0.45	4
14	Katanda	0.37	152	1340	21.62	419	8.51	6.72	23.9	SR	2.00	1.9	0.35	0.50	0.15	6
15	Kerere	0.27	68	1184	22.88	263	8.04	6.62	24.8	RC	3.63	3	0.80	0.00	0.20	13
16	Kifuruka	0.13	3.7	1403	21.11	411	8.33	7.33	22.9	SRCLW	0.82	15.6	0.45	0.45	0.10	11
17	Kisibendi	0.04	4.5	1126	23.35	277	9.30	6.21	25.0	SR	0.03	215	0.80	0.00	0.20	2
18	Kitere	0.10	51	1160	23.07	711	8.97	7.06	26.7	SR	0.83	16.8	0.33	0.07	0.60	0
19	Kyanga	0.12	54	1146	23.19	1112	9.11	7.03	24.9	SRC	1.40	9	0.80	0.15	0.05	1
20	Kyerbwato	0.01	12.5	1233	22.48	411	8.47	7.67	26.7	SRCL	1.65	1.7	0.90	0.00	0.10	13
21	Lugembe	0.08	15	1281	22.09	407	8.30	7.40	23.6	SR	1.35	6.3	0.20	0.60	0.20	4
22	Mahuhura	0.19	154	1254	22.31	600	8.97	7.92	24.6	SRC	5.60	8.4	0.38	0.02	0.60	4
23	Mbajo	0.08	35	1234	22.47	504	8.64	6.85	24.5	SRL	1.30	5.6	0.30	0.10	0.60	9
24	Mubiro	0.16	70	1208	22.69	718	9.02	7.39	26.7	SRC	3.20	1.8	0.40	0.15	0.45	4
25	Murusi	0.21	57	1226	22.54	382	8.54	6.58	26.1	SR	1.40	1.3	0.35	0.25	0.40	2
26	Mwengenyi	0.29	140	1397	21.15	352	8.43	6.90	24.5	SRCLW	3.35	1.6	0.40	0.40	0.20	10
27	Njarayabana	0.12	38	1179	22.92	857	8.84	8.00	24.9	SR	1.20	9.2	0.35	0.15	0.50	6
28	Nkuruba	0.01	34.5	1480	20.48	370	8.31	6.52	23.5	S	1.01	27.8	0.80	0.00	0.20	4
29	Ntambi	0.32	111	1158	23.09	5820	9.75	9.34	24.8	SC	0.40		0.90	0.05	0.05	2
30	Nyabikere	0.39	47.3	1376	21.32	271	7.89	6.85	25.6	SRC	0.61	17.2	0.84	0.01	0.05	12
31	Nyahirya	0.01	79	1444	20.77	379	8.18	6.67	22.2	SL	0.97	13.6	0.60	0.10	0.30	5
32	Nyamswiga	0.03	43	1447	20.75	330	7.76	6.76	22.8	SRCL	1.10	9.9	0.35	0.20	0.45	3
33	Nyamugosani	0.11	37	1234	22.47	988	8.94	8.49	27.1	SR	1.52	3.5	0.10	0.35	0.55	1
34	Nyantonde	0.12	180	1387	21.24	501	8.76	6.94	23.4	SR	3.10	2.27	0.15	0.60	0.25	1
35	Rukwanzi	0.08	169	1332	21.68	425	8.33	7.10	24.1	S	5.02	5.5	0.92	0.02	0.06	8
36	Wandakara	0.03	10.5	1158	23.09	1125	8.76	7.68	26.1	SR	0.70	9.8	0.02	0.65	0.33	8
	Wandakara - swamp	0.01	0.4	1146	23.19	1452	8.21	8.20	25.2	W	0.10		0.10	0.80	0.10	1
37	Wankenzi	0.16	59	1158	23.09	496	8.65	6.27	24.3	SR	0.36	13.7	0.10	0.50	0.40	6
	Kikorongo															
38	Kikorongo	0.92	9.8	915	25.06	22400	9.58	9.64	30.7	S	1.20	4.5	1.00	0.00	0.00	0
39	Kitagata	0.62	8.9	914	25.07	135400	9.63		29.0	S	0.05		1.00	0.00	0.00	0
	Bunyaruguru															
40	Bagusa	0.33	0.9	905	25.14	61100	10.62	10.70	27.4	S	0.24	670.6	1.00	0.00	0.00	0
41	Bugwagi	0.60	85	1048	23.98	441	9.02	7.22	26.1	SR	2.45	3.8	0.45	0.40	0.15	7
42	Chibwera	0.76	10.5	971	24.60	457	8.91	8.01	26.8	SCW	1.35	6.7	1.00	0.00	0.00	4
43	Ibamba	0.01	1.2	1073	23.78	104	6.55	5.81	28.2	RLW	0.35	7.5	0.10	0.75	0.15	5
44	Karolero	0.51	35	1103	23.54	181	8.05	7.01	26.8	SL	3.80	3.3	1.00	0.00	0.00	5
45	Kako	0.17	29	1396	21.16	89	8.18	6.53	25.0	S	2.30	1.2	0.08	0.85	0.07	1
46	Kamweru	0.20	43	1232	22.49	170	9.59	6.38	25.3	S	0.55	34.5	0.05	0.65	0.30	5
47	Kacuba	0.05	14.5	1102	23.54	148	8.75	7.00	26.9	SRCL	1.49	11.5	1.00	0.00	0.00	8
48	Kasirya	0.09	43	1251	22.34	302	8.72	6.63	26.3	SR	2.35		0.15	0.50	0.35	7
49	Katinda	0.44	17	1024	24.18	743	9.48	7.60	26.0	SR	0.53	42.6	0.01	0.70	0.29	2
50	Kibengo	0.88	4.8	914	25.07	264	9.92	7.41	29.3	SR	0.20	103	1.00	0.00	0.00	6
51	Kigezi	0.39	29	1302	21.92	265	8.49	6.55	26.4	SRC	0.99	13.7	0.11	0.47	0.41	2
52	Kyasunduka	0.50	2.1	1004	24.34	269	8.69	7.92	25.6	SR	0.30	288	0.60	0.20	0.20	1
53	Kyogo	0.02	3.4	1113	23.45	56	6.87	6.77	26.6	RCLW	3.00	2	1.00	0.00	0.00	3
54	Mafura	0.16	29	1255	22.30	259	9.29	6.26	22.7	SR	0.65		0.00	0.80	0.20	2
55	Maseche	0.32	0.2	908	25.12	68200	10.19	10.19	32.3	S	0.02	7.4	1.00	0.00	0.00	0
56	Mbugo	0.36	2.6	978	24.55	214	9.63	9.54	27.3	SR	0.51	76	0.20	0.70	0.05	4
57	Mirambi	0.53	22	1077	23.75	642	9.83	7.30	25.4	SR	0.90	24.2	0.00	0.70	0.30	3
58	Murabio	0.27	15	1098	23.58	141	8.42	6.91	27.5	SRCL	2.03	5.9	1.00	0.00	0.00	2
59	Nkugute	0.89	58	1409	21.06	121	8.72	6.91	24.5	SRL	0.90	15.9	0.21	0.64	0.15	5
60	Nshenyi	0.44	0.05	966	24.65	11230	10.05	10.20	29.3	S	0.02	26.3	1.00	0.00	0.00	0
61	Nyamusingere	3.84	4.3	978	24.55	681	9.40	9.14	26.6	SR	0.36	14.8	0.99	0.00	0.00	1
62	Nyungu	0.14	25	1172	22.98	430	9.40	7.64	24.7	SR	0.08	47.1	0.02	0.85	0.13	2

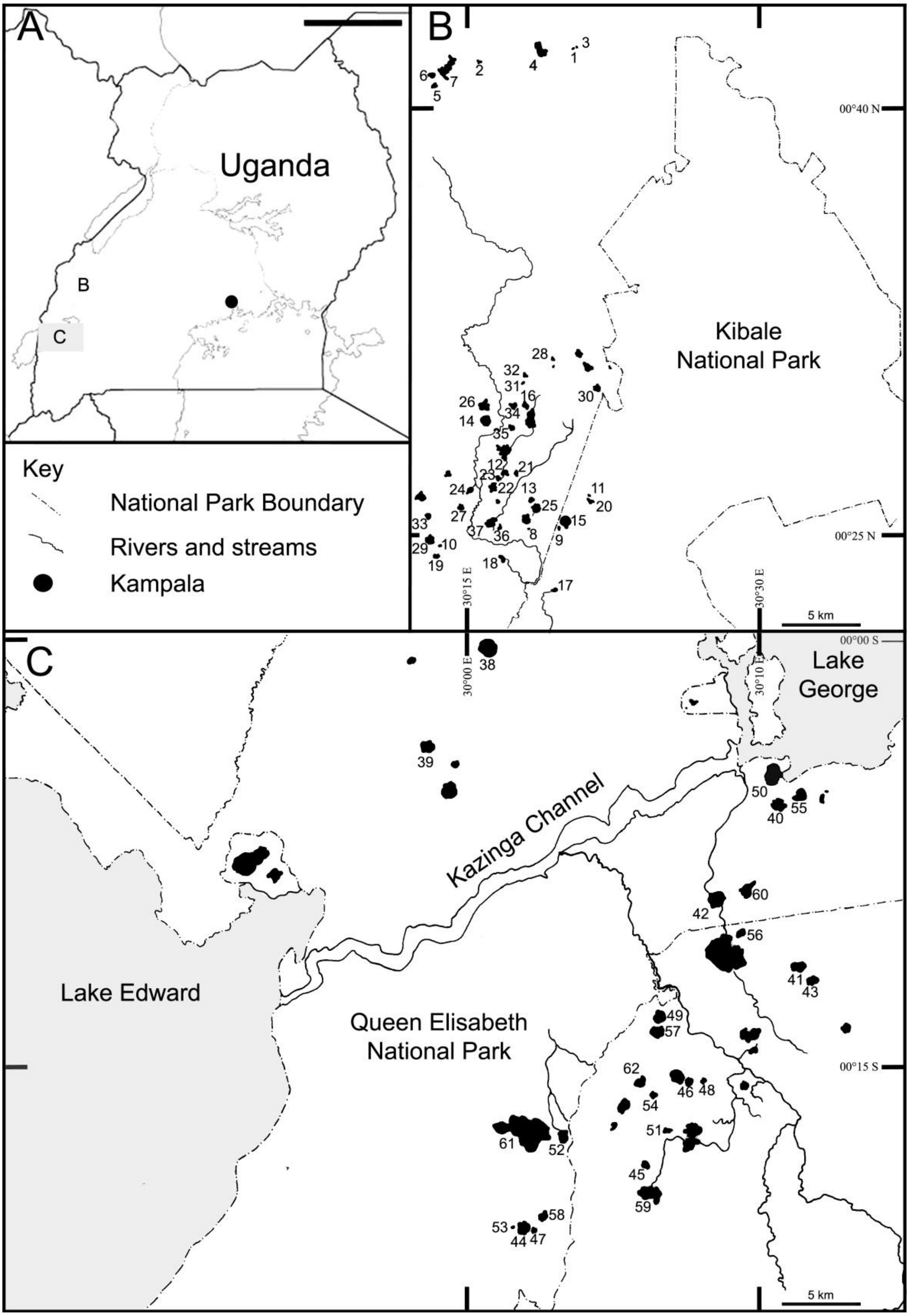

Figure 1: Map of the study region in western Uganda showing the locations of (A) the crater lake districts in the Edward-George branch of the Rift Valley, (B) the Fort Portal (lakes 1 to7) and Kasenda (lakes 8 to 37) districts, and (C) the Kikorongo (lakes 38 to 39) and Bunyaruguru (lakes 40 to 62) districts.

2.2.2 Field sampling and laboratory analyses

In 2007-2008 we conducted four dry-season (January-February or August-September) field campaigns in southwestern Uganda, surveying a total of 62 crater lakes. Latitude, longitude and elevation (in meter above sea level) were recorded by GPS (Garmin Csx 60), elevation to be used as a proxy for local mean annual air temperature (MAT). MAT data were estimated using region-specific linear relationships between elevation and temperature ($p<0.001$ in all cases). We derived MAT data from the Global Historical Climatology Network (GHCN-Monthly) data base (time series from the 1930s to 2006; four stations) and Global Summary of the Day (GSOD) data base (time series from 1957 to 2006; 10 stations). Lake bathymetry and maximum lake depth (Z_{max}) were determined by GPS-guided echo-sounding. Lake surface area (SA) was calculated using either field-measured diameter and/or circumference (small, circular crater lakes) or by analysis of topographical maps (larger lakes, often irregular in shape). Types of vegetation and land use within the crater catchment were quantified by mapping them from a viewpoint in the centre of the lake. We distinguished the following types of land use: stable ground cover (which included natural or secondary forest, savannah, and tree plantations), fallow land, habitation, and (subsistence and commercial crop) agriculture. Habitation constituted a significant fraction of total land cover in two crater basins only (Kasenda and Nyabikere) and was therefore not included in statistical analyses. The other three represent broad categories in runoff and soil erosion rates, ranging from low (stable) to intermediate (fallow land) and high (agriculture).

Surface-water temperature (SWTemp), pH, dissolved oxygen (DO) and specific conductance at 25°C (SCond) were measured at the time of sampling with a Hydrolab Quanta multiprobe. Transparency (Secchi) was measured using a 22-cm diameter Secchi disk. Collection and analysis of water samples for water chemistry followed the procedures described in Eggermont *et al.* (2007). Lakes were classified according to their primary production using a trophic level index (TLi) calculated using Secchi-disk depth and surface-water chlorophyll a (Chl a), Total Nitrogen (TN) and Total Phosphorous (TP) concentrations (Plisnier *et al.*, in prep).

The presence of fish was recorded in all 56 study lakes with SCond values < 1500µS/cm. Many lakes contain indigenous fish populations (Sato *et al.*, 2003), but non-indigenous fish were additionally introduced to increase available protein resources (Kizito et al., 1993; Crisman, 2001; Bwanika *et al.*, 2004). We did not include the effect of fishing per se in this study, as even inside national parks fish poaching is a common practice and no trustworthy information on fishing pressure is available.

Aquatic invertebrates including ostracods were sampled by repeatedly sweeping a 50-µm mesh net across planktonic and epibenthic habitat in near-shore (littoral) environments, and in the off-shore planktonic (pelagic) environment. The offshore benthic environment was not sampled as this was (near-)permanently anoxic (except in a few shallow lakes: Kifuruka, Kyogo and Nyamusingere). If habitats contained aquatic macrophytes, these were removed from the water and rinsed above the net to adequately sample the attached macro-invertebrates. Samples were instantly fixed in either formalin (5% formaldehyde) neutralized with powdered calcite, or in 40% ethanol. Concurrent sampling and identification of aquatic macrophytes was carried out along transects from the lake shore to the depth limit of aquatic plant growth. Submerged macrophytes in deeper water were sampled using a 4-m long rake. We used a set of categorical variables to represent the various types of littoral habitat. For this study (compare with Lebrun *et al*., in prep) we differentiated between five main types of littoral habitat (HA): sandy or rocky shores including those with submerged parts of terrestrial vegetation (HA-sand); emergent reed-like vegetation such as *Phragmites*, *Cladium* and *Typha* (HA-emer); submerged vegetation with few or no floating parts, such as *Ceratophyllum*, *Potamogeton* and *Chara* (HA-subm); submerged vegetation with considerable floating parts, mostly *Nymphea nouchali* (HA-float); and a swampy vegetation occurring at the edge of some lakes with *Cyperus papyrus* and *Miscanthidium violaceum* (HA-swamp). The total number of aquatic macrophyte habitat types present in a lake (#Macrophytes) was used as a macrophyte habitat diversity measure.

In the laboratory, samples were rinsed using a 50-µm mesh sieve. Ostracod specimens were sorted, identified and enumerated under a stereo-microscope at high magnification (up to 120x). When sufficient material was available, soft parts of several specimens were prepared and mounted on microscopic slides, and valves were mounted on metal stubs and imaged using Scanning Electron Microscopy (Philips XL30 SEM) at the Royal Belgian institute for Natural Sciences (Brussels, Belgium). All other specimens were stored in 70% ethanol in small glass vials. Identification was based on primary literature for tropical Africa (e.g., Vavra, 1897; Lowndes, 1931), recent taxonomic reviews (e.g. Martens, 2001; Savatenalinton & Martens, 2009) and aided by a reference collection from Lake Naivasha, Kenya (Verschuren 1996). Here, we focus on description of the valve morphology, and relate ecological information to morphospecies distinguishable on the basis of valve morphology, to aid application of ostracods in palaeoecological reconstruction and water-quality assessments.

2.2.3 Statistical data analysis

Environmental data were screened for use in statistical analysis to explore ostracod-environment relationships. Among the chemical constituents of the lake waters, Br^-, NO_3^- and SO_4^{2-} were eliminated from the analysis because concentrations were undetectable at >50% of the sites. All retained variables were tested for normality using the Shapiro-Wilks test (Shapiro *et al.*, 1968). The variables lake surface area (SA), Conductivity (SCond), TP, TN, Chl a, TOC, Na^+, Mn^{2+}, dissolved phosphorus (P), $S^{+/-}$ and Cl^- were normalized using a log transformation. K^+, Sr^{2+}, F^- and #Macrophytes were square-root transformed to approximate normal distributions. Z_{max}, MAT, Secchi depth, the three remaining land-cover categories (Stable, Agriculture, Fallow land), pH, SWT, DO, Ca^{2+}, Mg^{2+}, Mg^{2+}/Ca^{2+}, dissolved silica

(Si), and DIC were left untransformed. Relationships among the environmental variables were assessed using a Pearson's correlation matrix. Correlation matrices and normality tests were generated using the software package STATISTICA 5.5 (Statsoft, 2000).

A Pearson's correlation matrix was used to determine possible relationships between species richness and environmental variables. To allow a meaningful comparison, we used species richness per lake rather than a more sophisticated diversity index, because even with comparable sampling effort among sites, the number of individuals recovered varied by two orders of magnitude. We estimated total species richness using Chao's formula and two re-sampling estimators (Colwell & Coddington, 1994). Exploratory analysis of habitat preference was based on absolute counts of species in the samples. Evaluation of species distribution among the studied lakes is based on a presence-absence dataset of 275 planktonic and epibenthic samples. For multivariate statistical analysis, these samples were pooled per lake, across habitat types in order to obtain a representative presence-absence dataset for each lake. Species of which live specimens were found in only one lake were excluded from correspondence analyses. Presence of juvenile stages was recorded, but these were not included with the adult records as identification of juveniles to species level was only possible for a few of the species encountered.

Further analyses were conducted only on those freshwater lakes (SCond < 1500µS/cm) where ostracods were found. Two data sets were constructed for correspondence analysis: (i) presence of a species in a lake was recorded if multiple (>1) live specimens were found; (ii) this was augmented with records of single specimens and empty ostracod valves of sub-recently deceased individuals. We used Detrended Correspondence Analysis (DCA; Hill & Gauch, 1980) and Canonical Correspondence Analysis (CCA; CANOCO v. 4.5; ter Braak & Šmilauer, 2002) to explore presence-absence relationships among species, and between ostracod species and environmental variables in the different lakes. Lacking Chl a-data for lakes Kasirya and Mafura were substituted by the average value for all other freshwater lakes. The same principle was applied for missing water chemistry data from Kerere. For the multivariate analyses we further excluded Lake Kisibendi, whose peculiar ostracod community (see Results) caused it to be treated as an outlier. The final data set of 34 environmental variables and 52 lakes was centred and standardized to allow comparison of disparate variables (ter Braak & Šmilauer, 1998). DCA indicated gradient lengths of 2.57 and 1.85 for dataset (i) and (ii) respectively. As the range of 1.5 to 3 represents a window over which both unimodal or linear analysis can be applied, both exploratory CCA and RDA analyses were performed. DCA and exploratory CCA resulted in similar ordination plots, indicating that here CCA was justified (ter Braak & Šmilauer, 1998). Consequently CCA was used for further analysis. Rare species were down-weighted, and forward selection of environmental variables was used to identify which variables explained the greatest amount of variance in the species assemblages. In case of similar contributions, priority was given to variables with known ecological relevance. We used a Monte Carlo permutation test with 499 permutations to test whether the first axis and the trace, the sum of all eigenvalues, significantly explained part of the variation in the species data (ter Braak & Verdonschot, 1995).

2.3 Results

A total of 33 species from 26 genera were found in 57 of the 62 studied lakes (Table 2) and illustrated in figures 2-6. Three taxa could not be illustrated due to either scarcity of specimens or poor conservation of the valves. For those taxa we refer to the primary taxonomic literature or recent reviews (Table 2). Chao's formula suggests a total regional species richness of 37 (± 4) species, while the first- and second-order jackknife estimates are 38 and 40 species respectively. This indicates that this survey may have missed between four and seven ostracod species, or 11-17% of the regional species pool.

Table 2: Ostracod taxa (species and subspecies) encountered in 63 surface waters of western Uganda, with reference to the original taxonomic descriptions, valve illustrations in Fig.2-6 or published references, and the number of lakes where taxon presence was recorded with two or more live specimens (#P; corresponds to the "living" dataset), at least one live specimen (#S) or with either live specimen(s) or sub-recent empty valves (#F; corresponds to the Full data set), Total number of live specimens found (#T). Abbreviation used in figure 2-6: LV, left valve; RV, right valve; Cp, carapax. * Species previously reported from Uganda.

Species	Illustration	#P	#S	#F	#T
Superfamilia Darwinuloidea					
Alicenula inversa Martens & Rossetti, 1997	Figure 2: A-C	11	14	19	43
Darwinula stevensoni Brady & Robertson, 1870	Figure 2: G-H	14	16	26	90
Vestalenula cuneata Klie, 1939	Figure 2: D-F	8	8	14	29
Superfamilia Cytheroidae					
Limnocythere notodonta Vavra, 1906	Figure 2: I-K	3	3	4	20
Cytheridella chariessa Rome, 1977	Figure 3: A-E	29	29	32	129
Gomphocythere sp. type Wandakara	Figure 3: F-J	12	16	21	57
Gomphocythere expansa Sars, 1924	Figure 3: K-M	4	4	8	10
Superfamilia Cypridoidea					
Candonopsis africana Klie, 1944	Figure 3: N-Q	39	41	47	327
Physocypria capensis (Sars, 1985) Klie, 1933	Figure 2: L-N	7	9	13	81
Neozonocypris mirabilis Klie, 1944	Figure 3: S-V	10	10	10	80
Cypris decaryi Gauthier, 1933	Figure 3: R	1	1	1	3
**Hemicypris fossulata* (Vavra) McKenzie, 1966	Figure 4: A-B	3	3	4	7
**Heterocypris obliqua* Lowndes, 1936	Figure 4: C	8	9	10	51
Cypricercus inermis Brady, 1904	Savatenalinton & Martens, 2009	3	3	3	10
Neocypridella fossulata Daday, 1910	Rome, 1962 (as *Eucypris palustris*)	1	1	1	3
Strandesia minuta Klie, 1936	Figure 4: D-G	3	4	5	10
Strandesia vinciguerrae Masi, 1905	Figure 4: H-J	2	2	3	5
Acocypris platybasis Lowndes, 1932	Figure 5: A-D	1	1	1	5
**Chrissia icosacanthus* Lowndes, 1931	Figure 5: E-H	3	3	5	29
Stenocypris major Baird, 1859	Figure 5: I-M	5	6	7	16
Bradycypris strigata Klie, 1939	Figure 6: L	1	1	1	4
Martenscypridopsis pygmaea Sars, 1924	Figure 5: O-Q	2	2	2	11
Potamocypris mastigophora Methuen, 1910	Figure 5: R-W	12	12	18	105
Potamocypris palludum Gauthier, 1939	Figure 5: N	4	4	7	10
Plesiocypridopsis cf. *albida* Vavra, 1897[a]	Figure 4: K-N	8	11	15	132
Sarscypridopsis elizabethae Sars, 1924	Figure 6: A-F	4	5	6	42
Cypridopsis vidua –complex Müller, 1776	Figure 6: G-I	20	21	29	783
Zonocypris costata Vavra, 1897	Figure 6: J-K	43	48	51	1367
**Oncocypris mulleri* Daday, 1910	Figure 6: M-Q	2	2	3	15
Oncocypris sp. type Katanda	Figure 6: R-T	6	8	9	251
Oncocypris sp. type Kyaninga	Figure 6: U-W	4	6	7	148
Cypridopsis type Kerere	Not available	1	1	1	3
Strandesia juvenile type Ekikoto	Figure 4: O-R	4	4	6	18

[a] Our specimens match the species described by Vavra, 1897, except that most Ugandan specimens had somewhat pointed posterior valves (see Figure 5: K, M-N).

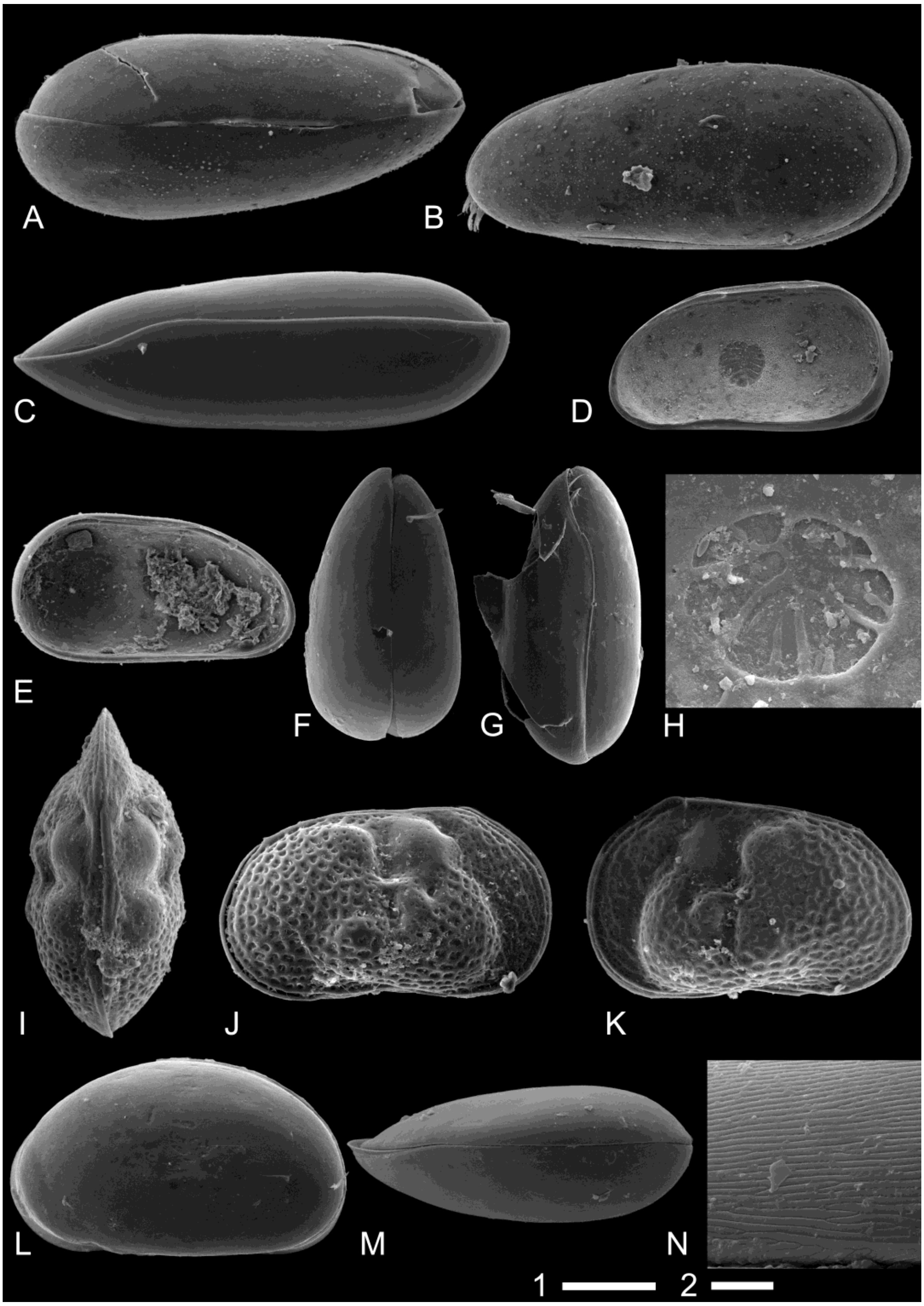

Figure 2: *Alicenula inversa* (A-C); *Vestalenula cuneata* (D-F); *Darwinula stevensoni* (G-H); *Limnocythere notodonta* (I-K); *Physocypria capensis* (L-N). ***A. inversa:*** A. female, Cp, dorsal view. B. female, Cp, left lateral view. C. female, Cp, ventral view. ***V. cuneata:*** D. female, RV, internal view. E. female, LV, internal view. F. female, Cp, dorsal view. ***D. stevensoni:*** G. female, Cp, ventral view. H. female, LV, internal view, detail of muscle scar. ***L. notodonta***: I. female, Cp, dorsal view. J. female, Cp, right lateral view. K. female, Cp, left lateral view. ***Physocypria capensis***: L. female, Cp, left lateral view. M. female, Cp, dorsal view. N. female, Cp, dorsal view, detail of surface. Scale 1 = 100 µm for A-B and I-K; 200µm for L-M; 20µm for N. Scale 2 = 100 µm for C-E and F-G; 20µm for H.

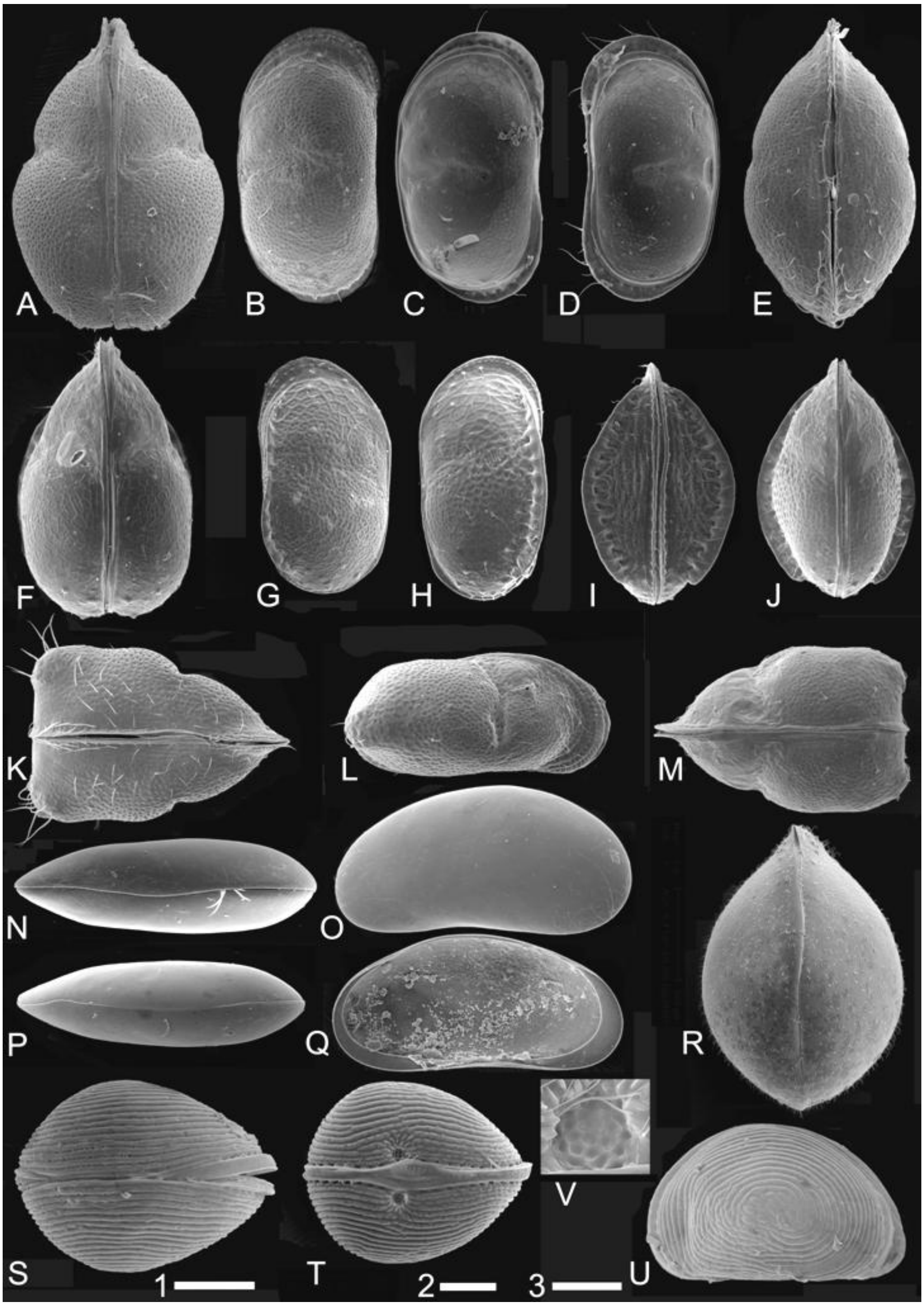

Figure 3: *Cytheridella chariessa* (A-E); *Gomphocythere* sp. type Wandakara (F-J); *Gomphocythere expansa* (K-M); *Candonopsis africana* (N-Q); *Cypris decaryi* (R); *Neozonocypris mirabilis* (S-V). ***C. chariessa:*** A. female, Cp, dorsal view. B. female, RV, external view. C. female, LV, internal view. D. female, RV, internal view. E. male, Cp, ventral view. ***G.*** sp. type Wandakara: F. female, Cp, dorsal view. G. female, LV, external view. H. male, RV, external view. I. male, Cp, ventral view. J male, Cp, dorsal view. ***G. expansa:*** K. female, Cp, ventral view. L. female, RV, external view. M. female, Cp, dorsal view. ***C. africana:*** N. female, Cp, ventral view. O. female, Cp, left lateral view. P. female, Cp, dorsal view. Q. female, LV, internal view. ***C. decaryi:*** R. female, Cp, dorsal view. ***N. mirabilis:*** S. female, Cp, dorsal view. T. female, Cp, ventral view. U. female, LV, external view. V. female, Cp, ventral view, detail of circular tubercle. Scale 1 = 200µm for A-J; 500µm for R. Scale 2 = 200µm for K-M; 10µm for V. Scale 3 = 200µm for N-Q; 100µm for S-U.

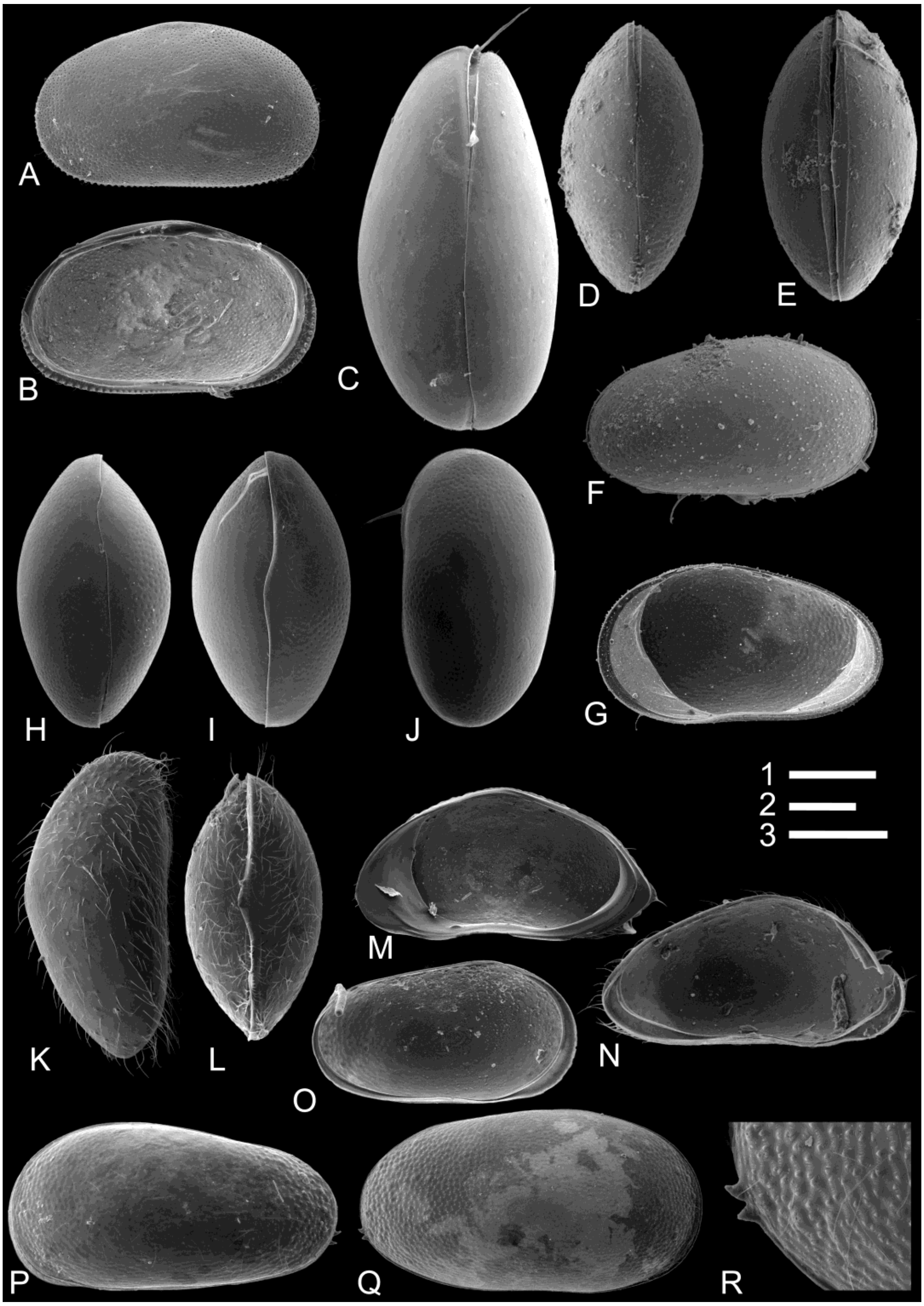

Figure 4: *Hemicypris fossulata* (A-B), *Heterocypris obliqua* (C), *Strandesia* cf. *minuta* (D-G), *Strandesia vinciguerrae* (H-J); *Plesiocypridopsis* cf. *albida* (K-N); *Strandesia* juvenile type Ekikoto (O-R). ***H. fossulata* :** A. female, LV, external view. B. female, LV, internal view. ***H. obliqua:*** C. female, Cp, dorsal view. ***S. minuta:*** D. female, Cp, dorsal view. E. female, Cp, ventral view. F. female, Cp, right lateral view. G. female, RV, internal view. ***S. vinciguerrae:*** H. female, Cp, dorsal view. I. female, Cp, ventral view. J. female, Cp, left lateral view. ***P.* cf. *albida*:** K. female, Cp, right lateral view. L. female, Cp, ventral view. M. female, RV, internal view. N. female, LV, internal view. ***Strandesia* juvenile type Ekikoto:** O. juvenile, RV, internal view. P. juvenile, LV, external view. Q. juvenile, RV, external view. R. *Idem*, detail of caudal spines. Scale 1 = 300µm for A-B and O-Q; 200µm for D-G; 75µm for R. Scale 2 = 250µm for C; 200µm =H-J. Scale 3 = 200µm for K-N.

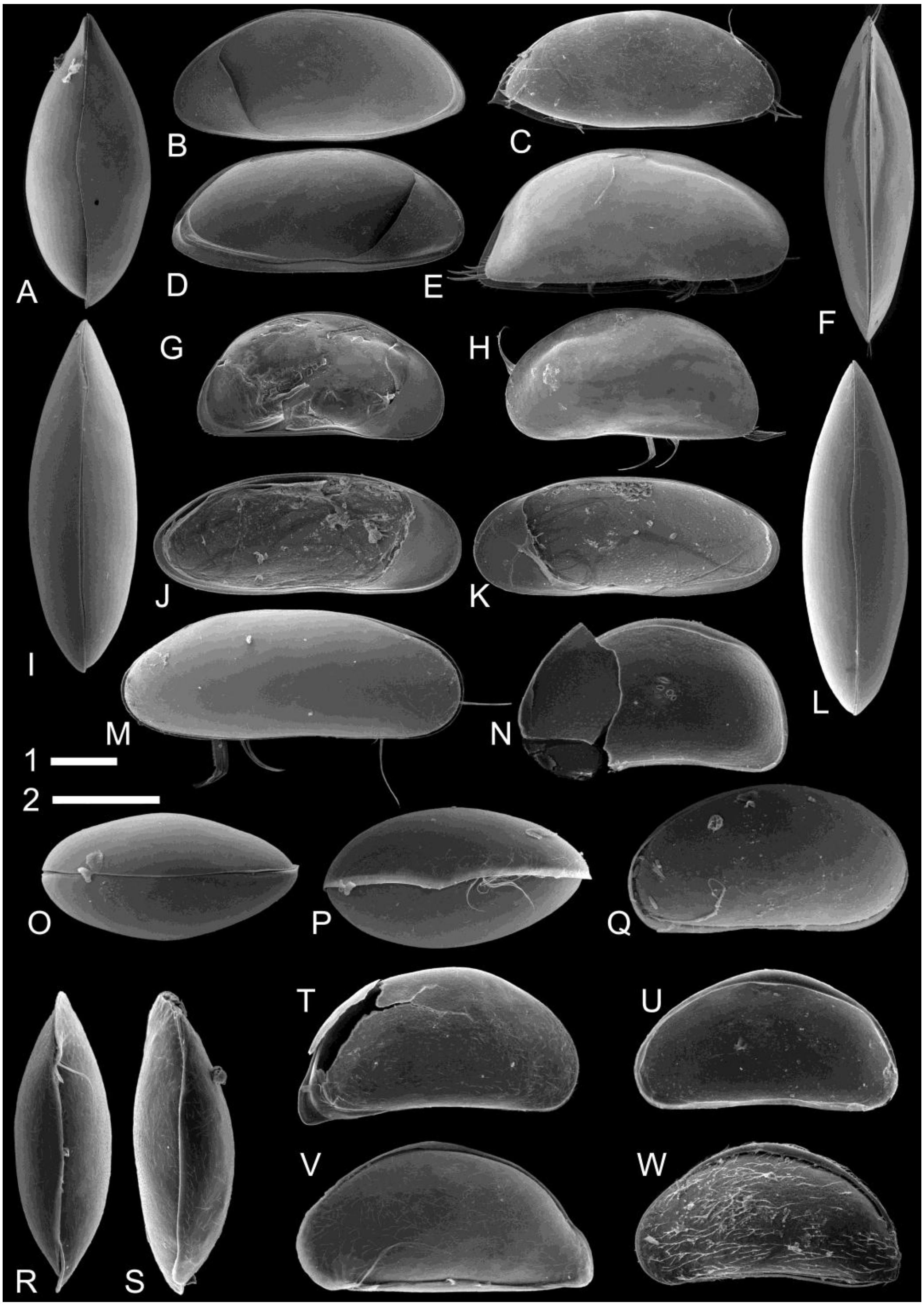

Figure 5: *Acocypris platybasis* (A-D), *Chrissia icosacanthus* (E-H), *Stenocypris major* (I-M), *Potamocypris palludum* (N), *Martenscypridopsis pygmaea* (O-Q), *Potamocypris mastigophora* (R-W). ***A. platybasis:*** A. female, Cp, ventral view. B. female, RV, internal view. C. female, Cp, right lateral view. D. female, LV, internal view. ***C. icosacanthus:*** E. female, Cp, right lateral view. F. female, Cp, dorsal view. G. Juvenile female, LV, internal view. H.juvenile female, Cp, left lateral view. ***S. major major:*** I. female, Cp, dorsal view. J. female, LV, internal view. K. female, RV, internal view. L. female, Cp, ventral view. M. female, Cp, right lateral view. ***P. palludum:***N. female, RV, internal view (damaged). ***M. pygmaea:*** O. female, Cp, dorsal view. P. female, Cp, ventral view. Q. female, Cp, left lateral view. ***P. mastigophora:*** R. female, Cp, ventral view. S. female, Cp, dorsal view. T. female, Cp, right lateral view. U. female, RV, internal view.V. female, Cp, left lateral view. W. female, Cp, left lateral view. Scale 1= 500µm for A-D. Scale 2 = 1mm for E-H, 500µm for I-M,200µm for N and R-W, 150µm for O-Q.

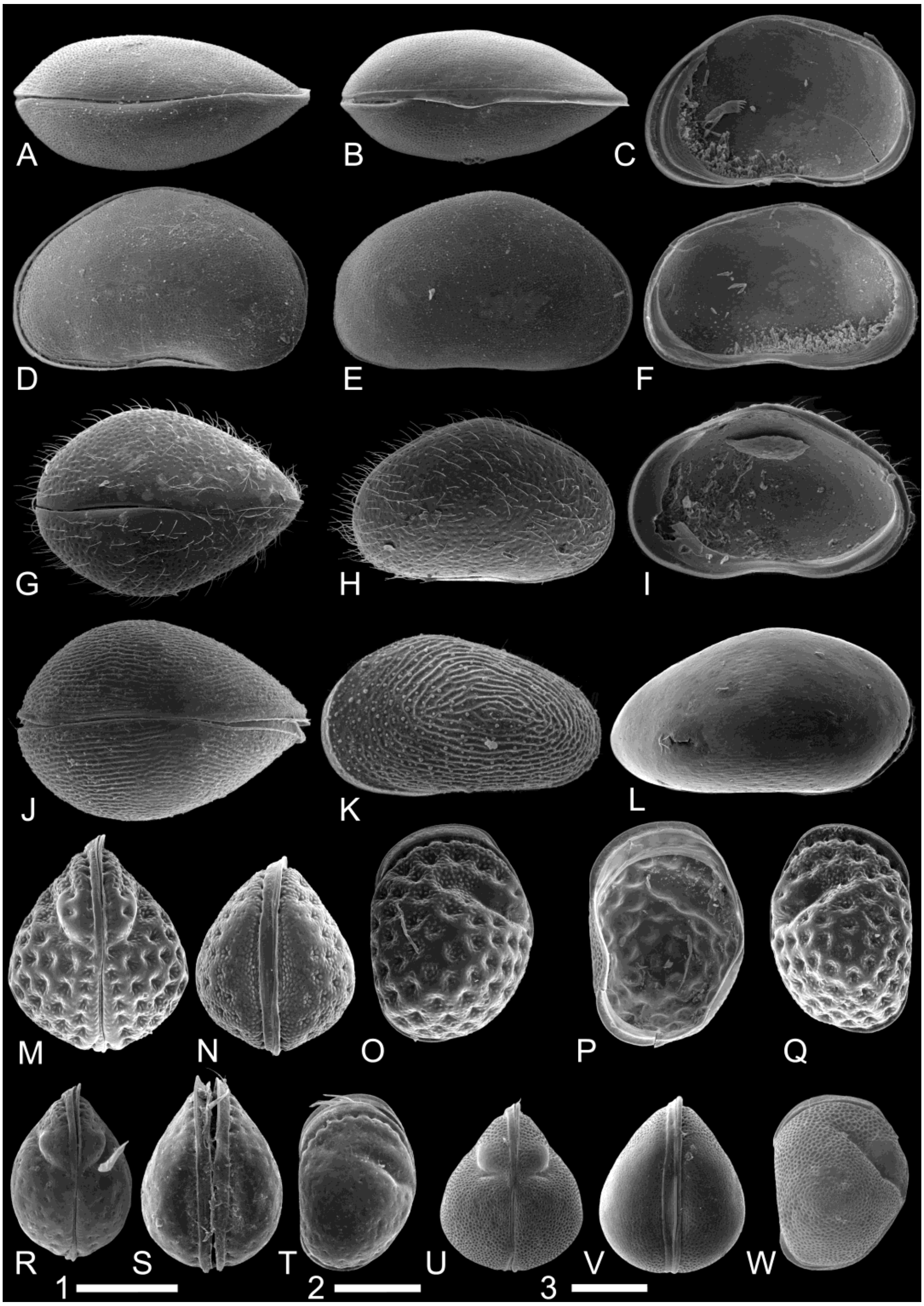

Figure 6: *Sarscypridopsis elizabethae* (A-F), *Cypridopsis vidua*-complex (G-I), *Zonocypris costata* (J-K), *Bradycypris strigata* (L), *Oncocypris mulleri* (M-Q), *Oncocypris sp.* type Katanda (R-T), *Oncocypris* sp. type Kyaninga (U-W). ***S. elizabethae:*** A. female, Cp, dorsal view. B. female, Cp, ventral view. C. female, RV, internal view. D. female, Cp, left lateral view. E. female, Cp, right lateral view. F. female, LV, internal view. **C. *vidua*-complex*:*** G. female, Cp, dorsal view. H. female, Cp, right lateral view. I. female, RV, internal view. ***Z. costata:***J. female, Cp, dorsal view. K. female, LV, external view. ***B. strigata:*** L. female, RV, external view. ***O. mulleri:*** M. female, Cp, dorsal view. N. female, Cp, ventral view. O. female, LV, external view. P. female, RV, internal view. Q. female, RV, external view. ***O.* sp. type Katanda*:*** R . female, Cp, dorsal view. S. female, Cp, ventral view. T. female, Cp, left lateral view. ***O.* sp. type Kyaninga:** U. female, Cp, dorsal view. V. female, Cp, ventral view. W. female, Cp, left lateral view. Scale 1= 200µm for A-F. Scale 2 = 200µm for G-I, 250µm for M-W. Scale 3 = 200µm for J-L.

The four most widely distributed ostracod species in the western Uganda crater lakes are *Zonocypris costata*, *Candonopsis africana*, *Cytheridella chariessa* and the *Cypridopsis vidua* species-complex: these four species were each encountered in about half or more of the sampled lakes, either as living populations or as recently deposited empty valves (Table 2: Full data set). *Zonocypris costata* and *C. africana* were found in virtually all investigated freshwater lakes. Juveniles of *Z. costata* were also encountered in four of the six freshwater lakes where no adults or full-grown valves were found. *Zonocypris costata* was frequently recorded from all types of habitats, whereas live *C. africana* was limited to samples from littoral habitats with sandy or muddy bottoms, reed or submerged macrophytes; and was lacking in samples from swampy habitats, floating vegetation and the pelagic zone (Fig. 7). On the other hand, empty *C. africana* valves were found in all habitat types.

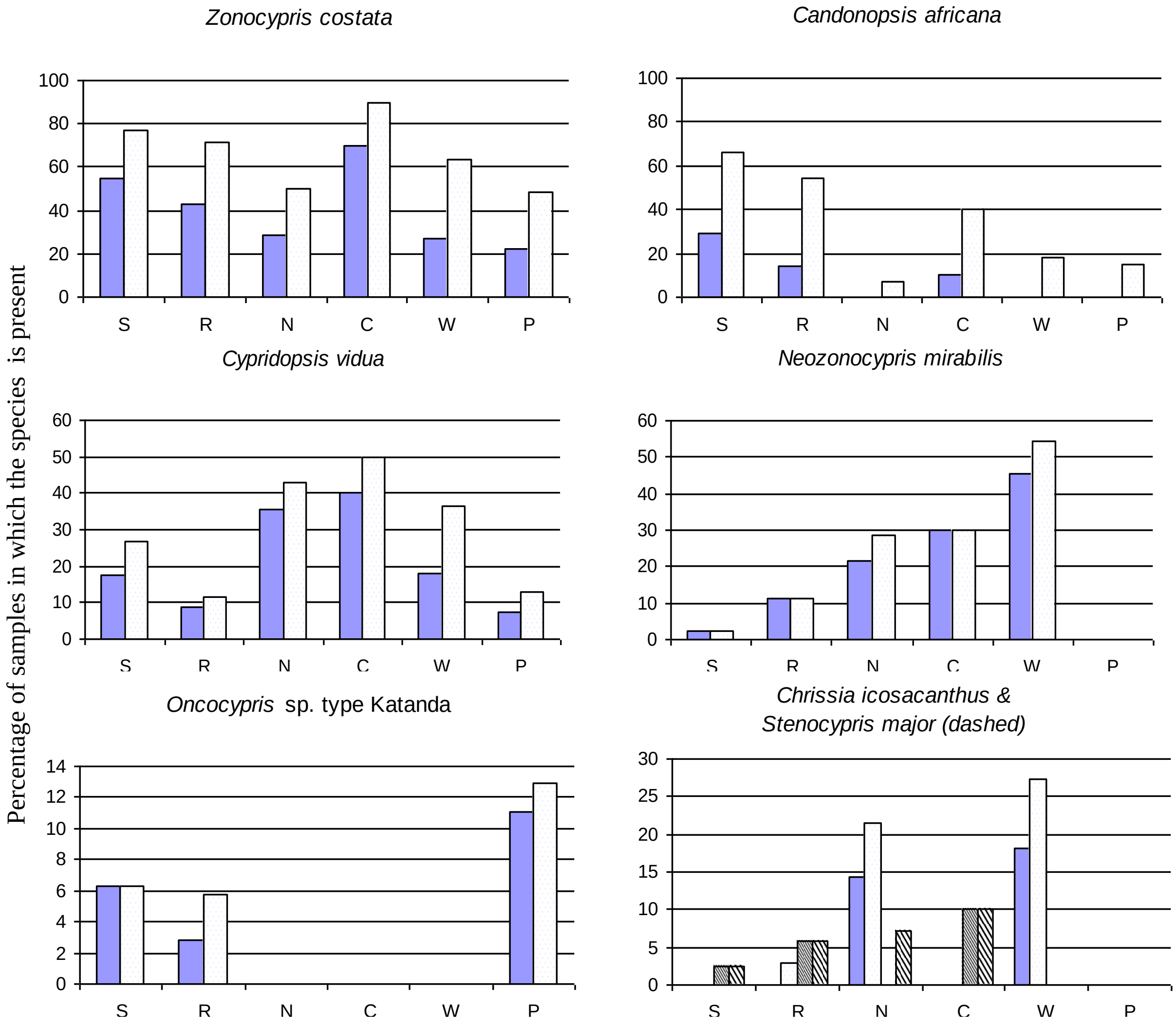

Figure 7: Percentage of samples collected from each habitat type in which an ostracod species was found, for the four most common species (*Zonocypris costata*, *Cypridopsis vidua*, *Candonopsis africana* and *Oncocypris* sp. type Katanda) and three selected other species (*Neozonocypris mirabilis, Chrissia icosacanthus* and *Stenocypris major*) and for the "living" (grey) and Full (white) presence-absence data sets as defined in Table 2. The habitat types are sandy or rocky shores, including those with submerged parts of terrestrial vegetation (S), emergent reed-like vegetation (R), submerged aquatic macrophytes with considerable floating parts (N), submerged aquatic macrophytes with little or no floating parts (C), swampy littoral vegetation (W), and the open-water pelagic zone (P).

Across all sampled sites, the four most common species were *Z. costata*, *C. vidua*, *C. africana* and *Oncocypris* sp. type Katanda, comprising respectively 35, 20, 8, and 6% of all live ostracods collected. *Oncocypris* sp. type Katanda was found in only 9 lakes, but abundantly in lakes Ekikoto, Kyaninga and Katanda. All *Oncocypris* species (*mülleri* and two unidentified species recorded first from Lake Katanda and Lake Kyaninga, respectively) were found most frequently in pelagic samples. *Chrissia icosacanthus* and, to a lesser extent, *Stenocypris major* are characteristic for habitats with abundant aquatic macrophytes (Fig. 7). Species richness was highly variable between lakes, ranging from 0 at all of the five lakes with conductivity higher than 10,000 µS/cm (Kikorongo, Kitagatta, Bagusa, Maseche and Nshenyi) to 14 in Lake Kyaninga. In Lake Ntambi *C. africana* and *Z. costata* were found at conductivities up to 5800µS/cm. Given this overall poor representation of salinity-tolerant ostracod fauna in this collection, we eliminated the saline lakes from statistical analyses. Also in three freshwater lakes (Kyegere, Nyabikora and Kitere) no live ostracods were found, but fresh ostracod valves testify to their modern-day presence there. Both *Z. costata* and *C. africana* were lacking from the hypertrophic Lake Kisibendi; only two species, *O.* sp. type Katanda and *Potamocypris mastigophora*, were encountered.

In the freshwater lakes (SCond < 1500µS/cm), species richness (Ntaxa) was positively correlated with water transparency (Secchi: r= 0.361, P= 0.006) and the diversity of aquatic macrophyte habitat (#Macrophytes: r= 0.292, P= 0.027). Species richness was negatively correlated with the fraction of land in the crater basin under agriculture (r=-0.292, P= 0.029).

Five species were found in only one lake: *Cypris decaryi* (Lake Kyerbwato), *Neocypridella fossulata* (Lake Ibamba), *Acocypris platybasis* (Lake Kyaninga), *Bradycypris strigata* (Lake Kanyanchu), and *Cypridopsis* sp. (Lake Kerere). In Lake Kyaninga, *A. platybasis* was encountered almost exclusively in a shallow, swampy zone that is only intermittently connected to the main water body of the lake. *Acocypris platybasis* was also found in Wandakara swamp, a shallow temporary pool near Lake Wandakara. For several rare and uncommon species, including empty valves in species occurrence records doubles the number of lakes in which they are encountered (Table 2). For some species, this increased the percentage of samples from a specific habitat in which it was encountered, but it did not alter the selective occurrence of species in certain habitats (Fig.7).

DCA indicated a gradient length of 2.57 for the “living” dataset. The resultant CCA shows that the diversity of aquatic macrophyte habitat, the presence of sandy or muddy substrates and Chl a (indicating trophic status) were the most important predictors of ostracod community composition on CCA axis I (Fig. 8). In our dataset, *Neozonocypris mirabilis*, *Strandesia* sp. and the *Cypridopsis vidua* species-complex were associated with aquatic macrophytes, low conductivity and low aquatic productivity (Fig. 8). *Zonocypris costata and C. africana* are encountered in even the most productive lakes, but only *Physocypria capensis* was specifically associated with more productive lakes. Conductivity (~salinity), the presence of sandy or muddy substrates and climate (MAT) were the most important variables on axis II. This axis reflects some of the differences between the northern (Fort Portal and Kasenda) lakes typically situated on the wet shoulder of the Rift Valley and the southern (Bunyaruguru) lakes, the shallower of which are situated on the relatively dry floor of the Rift Valley (Fig. 8). The selected variables explain 21% of the total variance (Table 3). The Monte Carlo permutation test on both the first CCA axis and for all axes was highly significant (Axis I: F=3.67, P= 0.002; all axes: F= 2.38, P=0.002).

For the Full dataset, DCA indicated a gradient length of 1.85. The resultant CCA is similar to that for the "living" dataset, but does show some distinct differences. Aquatic macrophyte diversity, surface pH and the presence of sandy or muddy substrates were the most important predictors of ostracod community composition on CCA axis I (Fig 9). *Candonopsis africana* and the pelagic species *Oncocypris* sp. type Katanda were more abundant in lakes with somewhat higher pH and a sandy or muddy littoral zone lacking submerged aquatic macrophytes (Fig. 7 and 9). Conductivity, SWT, aquatic macrophyte diversity and Chlorophyll a were found to be the most important variables on axis II, whereas MAT was most important on axis III. The selected variables together explain 26% of the total variance (Table 3). The Monte Carlo permutation test on both the first CCA axis and for all axes together was also highly significant (Axis I: F=3.74, P= 0.002; all axes: F= 2.36, P=0.001).

Table 3: Summary statistics and canonical correspondence analysis (CCA) for the "living" (at least two live specimens found per site) and Full (live specimens or empty valves) ostracod data sets from western Uganda. Species richness is the raw ostracod taxon richness per site; numbers between brackets are standard deviations (+/- SD). Only environmental parameters selected by forward selection are indicated.

	"living" dataset	Full dataset
# lakes	52	55
# species per lake	5.3 (3.5)	7.0 (4.0)
DCA		
Gradient length (SD)	2.57	1.85
CCA % variance explained		
#Macrophytes	5.9**	6.2***
Conductivity	4.8**	5.4***
MAT	3.6**	3.7*
Chlorophyll a	4.3**	2.9*
HA-sand	5.2**	4.4**
pH		4.6**
SWT		4.2***
all canonical axes	20.5**	26.2**

* Significant at the $P < 0.05$ level

** Significant at the $P < 0.01$ level

*** Significant at the $P < 0.001$ level

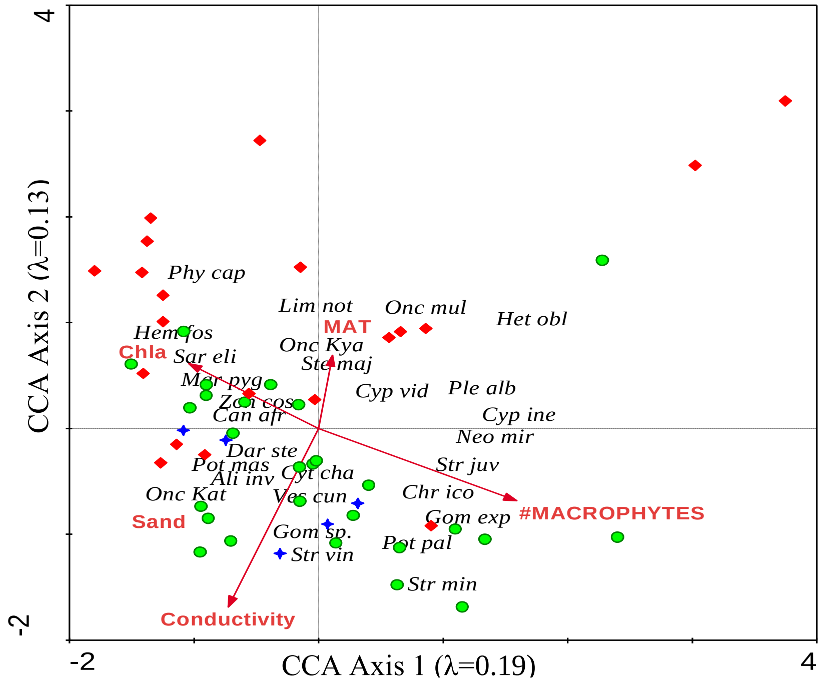

Figure 8: Canonical Correspondence Analysis (CCA) ordination of 28 ostracod taxa and the five most influential environmental variables from 52 Uganda crater lakes for the “living” dataset. Different symbols indicate lakes of the Fort Portal (cross), Kasenda (dot) and Bunyaruguru (diamond) districts. Species abbreviations are based on the first three letters of genus and species name, which are recorded in Table 2.

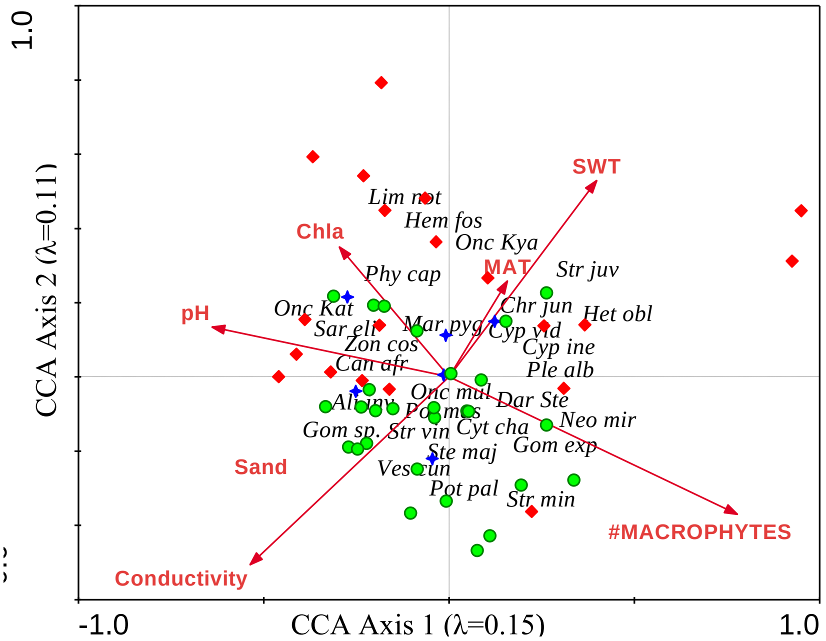

Figure 9: Canonical Correspondence Analysis (CCA) ordination of 28 ostracod taxa and the seven most influential environmental variables from 55 Uganda lakes for the Full dataset. Different symbols indicate lakes of the Fort Portal (cross), Kasenda (dot) and Bunyaruguru (diamond) districts. Species abbreviations are based on the first three letters of genus and species name, which are recorded in Table 2.

2.4 Discussion

Thus far, biodiversity assessments of East African freshwater ecosystems (Mutune *et al.*, 1996, Mwebaza-Ndawula, 2005) have rarely included ostracods, contributing to skewing of biodiversity estimates in favour of better-studied groups. Our illustrations and the above-mentioned primary taxonomic literature should provide some assistance in identifying ostracods from the study region. We recorded a total of 33 ostracod species in the western Uganda crater lakes; between four and seven additional species might be present in the regional species pool. In a study on the micro-crustacea of larger East African Rift lakes, Lowndes (1936) found seven ostracod species in Lake George, a shallow Rift lake situated close to the Bunyaruguru lake district. Four of these seven were not encountered in the present study: *Cypris latissima* (Müller), *Plesiocypridopsis newtoni* (Brady & Robertson) Rome, *Cypretta tenuicauda* Vavra and *Centrocypris horrida* (Vavra) Daday. That the present study missed some regional ostracod species is also suggested by the recovery of several juvenile specimens with characteristic morphology, which could not be assigned to any of the listed taxa. One of these, a *Strandesia* juvenile (type Ekikoto) was encountered in four lakes and was included in the analyses.

Ostracod species diversity was highest in freshwater lakes in the northern lake districts, where often various types of littoral habitat occur, including submerged and emergent aquatic macrophytes. Species diversity was low in most eutrophic lakes (e.g., one species in lakes Nyamusingere and Kyasunduka and two species in lakes Nyungu or Kisibendi), and only *Physocypria capensis* tended to occur specifically in more productive lakes. In Kenya, this species is mainly known from the naturally eutrophic Lake Naivasha. Elsewhere it is mainly known from lakes with sizable open-water habitat but has even been found in rivers, (Martens, 1984). *Candonopsis africana* and *Z. costata* were found in a wide range of conductivities ranging from around 100µS/cm up to 5800µS/cm. In the present study, no ostracods were found in the salt lakes with conductivities >10000µS/cm, despite the fact that several African species exist which are known to occur in saline and even hypersaline conditions (Martens *et al.* 1996). In his review on ostracods of athalassic saline lakes De Deckker (1981) noted the absence of ostracods from the inland saline waters of East Africa. In Spanish saline lakes it was shown that mainly ion composition, accounted for the observed distribution pattern of ostracods (Balatanás *et al.*, 1990). Several ostracod species have been identified from saline lakes and pans in southern Africa (Martens *et al.* 1996; McCulloch *et al.*, 2008) which are mostly of the Cl^- and SO_4^{2-}type (Seaman *et al.*, 1991). In contrast, most saline lakes in our study area are more or less concentrated soda lakes of the Na^+–K^+–$HCO3^{2-}$ type (Talling and Talling, 1965; Kilham, 1971). We suspect that this difference in ionic composition may be responsible for the absence of ostracods in our studied saline lakes.

A comparison of species richness with other studies on African lakes is difficult, due to strong dependence of species richness data on the number of sites included, sampling strategy, and habitat variation in and among sampling sites. In general, however, we can state that the regional species richness reported here is higher than that reported in earlier studies covering a range of small and larger African lakes (Lowndes, 1936; Lindroth, 1953; Rome, 1965), but lower than the species richness of Lake Tanganyika, where a large number of endemic species is present (Martens, 1994; Wouters & Martens, 2007).

Zonocypris costata was the most ubiquitous and widespread species, occurring in virtually all studied freshwater lakes and in all types of sampled habitats. This ability to tolerate a wide range of environmental conditions may appear to limit the immediate indicator value of the presence of this species. However, in a paleoecological study on a Kenyan lake, Verschuren *et al.* (2000) found that the presence of papyrus swamp and associated aquatic macrophyte habitat increased the abundance of *Z. costata* valves in the sediment record, demonstrating that for this species the availability of suitable habitat does effectuate abundance changes.

The *Cypridopsis vidua* species-complex is most likely comprised of a large number of (sometimes geographically) distinct crypic species that can not (always) be distinguished by the morphology of the valves (K. Martens, pers. comm.). The situation may be similar to the *Eucypris virens* species-complex, which is characterised by high levels of variability, both at the morphological (Martens, 1998; Baltanas et al., 2002) and genetic level (Rossi et al., 1998; ; Schön, 2007) and was recently proven to consist of over 40 cryptic taxa (Bode *et al.*, 2009). It is therefore not advisable to apply ecological information from one location to a population of another area. Here, we found representatives of the *C. vidua*-complex in all habitat types, but most often in littoral samples taken amongst floating and submerged aquatic macrophytes.

Neozonocypris mirabilis was originally described from a pond at the mouth of the Kibumba River near Lake Tanganyika (Rome, 1962). The site description lacks information on aquatic macrophytes. The only other documented record of this species is from Lake Keilak in Sudan, where it was found in an aquatic grass mat near the edge of the lake (Green et al. 1984). In this study it was found most often amongst abundant aquatic macrophytes.

The two largest-sized species, *A. platybasis* and *S. icosacantus,* were found almost exclusively in shallow, vegetated areas (partially) disconnected from the main waterbody of lakes containing fish, indicating that only in these areas they can avoid vertebrate predation. A more thorough study of these swampy areas surrounding some Ugandan crater lakes, as well as temporary pools distributed across the region, would probably yield more large-bodied species and a wider distribution of the two large species reported here.

Collecting empty *C. africana* valves in those habitats where no live specimens were found can be due to either temporal or spatial integration. In the first case, the species' seasonal occurrence in conjunction with specific environmental conditions would argue against including these empty valves in the analysis, as it will weaken its ecological indicator value.

In the latter case, species habitat preference would be obscured by passive transport of dead specimens between habitat types. It may be that *C. africana* did in fact occur in these habitats, but was not encountered alive due to lower population densities or has meanwhile disappeared, because of changing environmental conditions.

Oncocypris, which is morphologically adapted to swim and feed at the water surface (hyponeustic - Fryer, 1956) was the only genus found more often in the pelagic zone than in littoral habitat. Representatives of this genus are known from a wide range of freshwater habitats. *Oncocypris mulleri* has been found in temporary pools (Fryer, 1956), semi-permanent pools (Gauthier, 1939), crater lakes (Green et al., 1974 – as *O. debunshae*; this study) and the large Rift Lake Malawi (Fryer, 1957). In the present study, representatives of the genus do not exhibit a clear response to particular environmental parameters, but were generally found in low densities, except in Kyaninga, Ekikoto and Katanda. This local scarcity may have resulted in an underestimation of their actual distribution in the crater lake region. Excluding *Oncocypris*, empty valves of thirteen ostracod species were encountered in pelagic samples, albeit in low densities. This suggests a certain amount of passive post-mortem transport, and illustrates that caution should be applied when determining ostracod habitat preference from the distribution of empty valves. Although zooplankton nets were thoroughly rinsed after each sampling some of these records may reflect contamination with specimens or valves from prior sampling locations.

The difference in distribution of species based on either the Living or Full dataset is especially considerable for species which are typically encountered in low numbers. An argument can be made for the use of both resulting datasets. The first will certainly reflect only those ostracods alive at the time of sampling, and thus the population adapted to measured environmental conditions. The second dataset may include species that have recently disappeared due to changing environmental conditions or seasonal habitat variability. It may, on the other hand, provide a more complete view of the total fauna of the lake, as even intensive sampling can miss certain extant species (Frey, 1964; Davidson *et al*., 2007). It should be noted that in the case of ostracods, the use of valves can cause some underestimation of species richness if species are present that can not be distinguished on the basis of valve morphology alone (as in some species of *Potamocypris, Ilyocypris* and others).

In studies from temperate regions, Ca, Mg, and the Mg/Ca ratio are often found to be the ecological variables that determine ostracod species composition (Bunbury & Gajewski, 2005; Viehberg, 2006; Van der Meeren *et al*, in press). In our study area the presence and diversity of aquatic macrophyte habitats and sandy or muddy shores were found to be more important. While ionic composition is one of the factors determining the composition of aquatic macrophyte communities in these lakes (Lebrun et al., in prep.), in general the chemistry of these lakes is rather uniform, strongly reflecting the similarly uniform mineralogy of the volcanic rocks of this region (Killham, 1971). Also, despite differences between the Living and Full datasets as revealed by the correspondence analyses, the main explanatory variables remain the same: the presence and diversity of aquatic macrophytes, salinity (and/or pH), the presence of sandy or muddy habitat, lake trophic status (as Chl a) and mean annual air temperature (as a proxy for mean annual surface-water temperature). With the exception of chlorophyll a and surface-water temperature, most of these variables do not undergo pronounced seasonal changes in the studied lakes. The main difference between both data sets is that in the Full dataset, pH and surface-water temperature are selected as additional explanatory variables. One factor that may limit their use for palaeo-environmental reconstructions in Ugandan crater lakes is the low bottom pH in many of the deeper lakes, which will tend to etch and dissolve their shells before they are permanently buried (Holmes, 2001).

In Conclusion, our study significantly expands knowledge of the Ostracod fauna of western Uganda with 29 new species for the region and knowledge of their distribution along major environmental gradients. There is a large potential in the investigated region for applications of ostracods in water-quality monitoring and palaeolimnological studies, as they were encountered in all fresh and slightly saline lakes surveyed, and to a large extent their distribution is found to be determined by a limited number of known environmental variables.

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3

Ostracod (Ostracoda, Crustacea) communities in shallow Kenyan lakes and ponds

Abstract

The ostracod fauna of East Africa, and more specifically Kenya, is taxonomically well documented, however accurate information on the habitat requirements of individual species is often lacking and limits their use in ecological and management applications. We analyzed the species composition of ostracod communities in 37 shallow lakes and ponds in southern Kenya along with an assessment of abiotic and biotic habitat characteristics. Our study sites comprise a wide variety of lentic aquatic habitats, ranging from small, mostly dilute ephemeral pools to large permanent lakes, both fresh and saline, situated at altitudes between 700 and 2800 m a.s.l.. We found a total of 32 species of Ostracoda, amongst which *Physocypria capensis*, *Sarscypridopsis elizabethae* and *Oncocypris mulleri* were both the most widely distributed and often locally most abundant species. Species richness indices and comparison with previous studies indicates that often only part of the ostracod communities were sampled, which can be explained in part by both the seasonally and inter-annually dynamic nature of the sampled ecosystems. Canonical correspondence analysis of species-environment relationships indicates that littoral vegetation cover, elevation (a proxy for mean annual air temperature) and surface-water temperature best explain the observed variation in ostracod community composition. Fish presence and lake depth also strongly influence species composition, with large (>1.5 mm) species being more common in shallow, often ephemeral waters lacking fish. We provide scanning electron micrographs (SEM) of the valve morphology of all encountered ostracod taxa, in order to aid their identification in biodiversity, water-quality and palaeoecological applications.

Keywords: Ostracoda – Kenya - tropical limnology – palaeolimnology – Lake Naivasha

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Rumes, B., K. Martens & D. Verschuren. Ostracod (Ostracoda, Crustacea) communities in shallow Kenyan lakes and ponds. In preparation.

3.1 Introduction

There have been a fair number of studies on ostracods in Kenya, with Daday (1910) being one of the first and Verschuren *et al.* (2000) one of the most recent. Early works by Daday (1910), Klie (1933, 1939), Lindroth (1953), and Lowndes (1936) focused mainly on taxonomy and provided little in the way of ecological information. Interest in local ostracod ecology increased when their potential for palaeolimnological applications was illustrated by Dussinger (1973). Subsequently, ostracods from sediment records of Kenyan rift lakes were used in lake-based climate reconstructions (Peypouquet *et al*., 1979; Cohen *et al.*, 1983; Richardson & Dussinger, 1986). In a study on the substrate preference of zoobenthos associations in Lake Turkana, Cohen (1986) described the distribution of individual ostracod taxa across different benthic habitats within a single large lake. Verschuren *et al.* (2000) applied paleoecological methods to the sediment record of Lake Naivasha to determine the response of ostracod taxa to changes in salinity, depth and macrophyte cover. Studies in regions outside of Africa have shown the distribution of ostracod species to be determined by temperature (Viehberg, 2006; Horne 2007), lake depth (Mourguiart & Carbonel 1994), hydrochemical variables (Bunbury & Gajewski, 2005), and macrophyte habitat structure (Kiss, 2007).

We analyzed the composition of ostracod communities in 37 shallow lakes and ponds situated along important ecological gradients in southern and southeastern Kenya in order to determine which environmental parameters best explain the composition of local ostracod communities. This survey covers a sizable fraction of all standing freshwater habitats in the region, ranging from small ephemeral pools to large permanent lakes, in the highlands and at lower altitudes. This study is expected to contribute significantly to the knowledge of ostracod faunas in small and semi-permanent or ephemeral waters in Kenya, especially as these have rarely been included in previous surveys.

3.2 Methods

3.2.1 Study area

Two field surveys were conducted in August 2001 and January 2003, yielding zooplankton and epibenthos samples from 37 standing waters (Table 1; Figure 1) situated at surface altitude from 700 to 1150 m above sea level (m a.s.l.) in the southeastern lowlands (10 sites) and between 950 and 2800 m a.s.l. in the central Rift Valley and adjacent highlands (27 sites). The study sites include small dilute ponds, large lakes, man-made reservoirs, warm turbid temporary waters without aquatic vegetation and macrophyte-rich permanent lakes. In this equatorial region seasonal variation in local air temperature is limited and mean annual air temperature is closely linked with altitude (Kiai *et* al, 2002). Rainfall seasonality is strong throughout the study region, being predominantly bimodal east of the Rift Valley but trimodal in Western Kenya. Total annual rainfall ranges from 350 mm in the arid south to 1100-1500 mm over the highlands flanking the Rift Valley. Natural vegetation near the study sites ranges from dry *Acacia* bush land and wooded savannah to mountain forest at higher altitudes, but much of the latter has been replaced by a cultural landscape (Mergeay *et al.*, 2006).

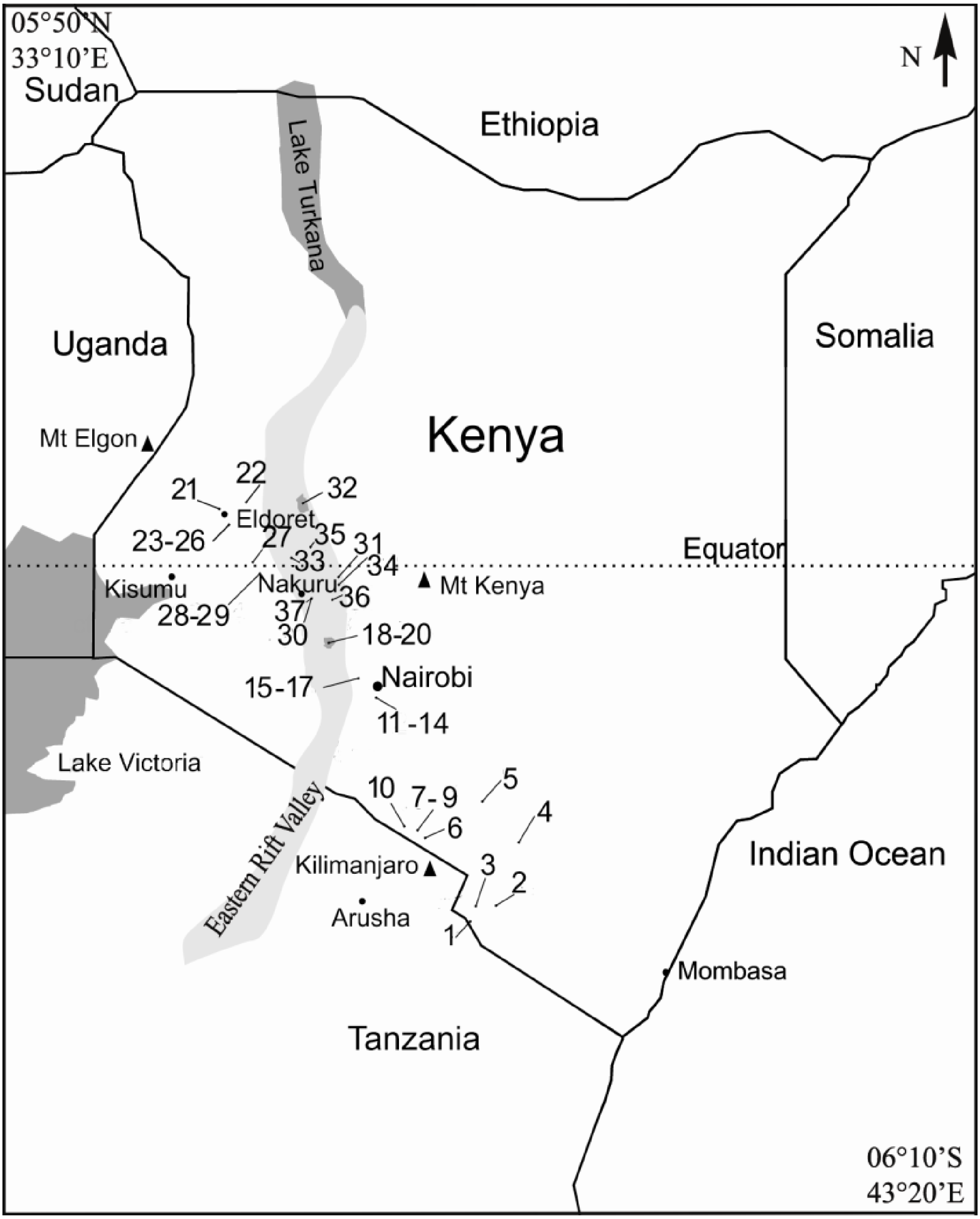

Figure 1: Schematic map of Kenya with location of the study sites. Site numbers refer to table 1.

Table 1: Studied waterbodies in Kenya, with data on geographical position, date of visit (Visit), Altitude (Alt) in m asl, maximum depth in m (Z_{max}), lake surface area (SA) in ha, surface-water conductivity (SCond) in µS/cm at 25°C, Surface water pH (pH), surface water temperature (SWT) in °C, Secchi-depth in m (Secchi), littoral vegetation cover (Litt. – see Methods for definition of the four classes), macrophytes over (Macr. – see Methods for classes), Chlorophyl a (Chl a) measurements in µg/l, fish presence (1) or absence (0) (Fish PA), Ostracod species richness (Ntaxa). Reservoirs situated along the road are referred to by the names of the cities connected by the adjacent road (i.e. Voi-Nairobi 1 is situated along the road from Voi to Nairobi).

N°	Name	Code	Geographical position	Visit	Alt	Z_{max}	SA	SCond	pH	SWT	Secchi	Litt. 0-4	Macr. 0-4	Chl*a*	fish PA	N taxa
1	Lake Jipe	Jipe	03°34.60'S, 37°46.05'E	01/2003	735	1.8	2500	1140	8.5	28.5	0.30	4	0	45.4	1	7
2	temp.pond Taveta-Taita 1	TaiTa1	03°24.52'S, 38°03.54'E	01/2003	1115	0.5	0.015	100	8.8	32.3	0.10	0	0	15.6	0	3
3	temp.pond Taveta-Taita 3	TaiTa3	03°24.68'S, 37°49.74'E	01/2003	1102	0.5	0.02	235	7.7	28.2	0.10	0	0		0	2
4	perm.pond Voi-Nairobi 1	VoNB1	02°45.41'S, 38°15.27'E	01/2003	695	0.5	0.04	53	7.6	32.6	0.10	0	0		0	4
5	perm.pond Voi-Nairobi 2	VoNB2	02°21.05'S, 37°53.33'E	01/2003	1031	0.6	0.04	236	7.7	31.5	0.10	0	0		0	5
6	Amboseli Olokenya swamp	Amb1	02°42.11'S, 37°18.68'E	01/2003	1155	1.0	1.2	179	7.1	19.8	0.80	3	3	56.9	1	0
7	Amboseli Serena Lodge	Amb2	02°42.00'S, 37°15.42'E	01/2003	1159	1.0	15	172	7.2	21.4	0.80	3	3	32.6	1	0
8	Amboseli Enamishera	Amb3	02°40.21'S, 37°14.63'E	01/2003	1150	1.5	30	255	7.8	24.7	0.80	4	3	128.9	1	0
9	Amboseli Lake Kioko	Amb4	02°38.50'S, 37°13.55'E	01/2003	1153	1.2	50	539	7.8	25.0	0.50	4	4		1	3
10	Amboseli Lake Amboseli	Amb5	02°36.07'S, 37°12.52'E	01/2003	1150	0.1	10000	4690	9.5	29.1	0.01	0	0	397.6	0	3
11	Nairobi Nat. Park Narogomon dam	NBNP1	01°21.00'S, 36°47.92'E	01/2003	1707	3.8	1.5	188	7.0	21.3	0.40	4	0	80.7	0	3
12	Nairobi Nat. Park Hyena Dam	NBNP2	01°20.30'S, 36°48.64'E	01/2003	1709	1.5	1	260	7.1	21.7	0.30	3	0	128.9	1	3
13	Nairobi Nat. Park 3	NBNP3	01°21.86'S, 36°50.58'E	01/2003	1709	1.0	0.015	141	6.8	23.0	0.60	2	0	72.6	1	0
14	Nairobi Nat. Park Hyrax valley	NBNP5	01°22.86'S, 36°46.98'E	01/2003	1716	1.0	1	250	7.6	23.5	0.40	3	1		1	0
15	Semiperm. pond Limuru 1b	Lim1b	01°06.99'S, 36°37.89'E	01/2003	2306	0.8	0.15	201	7.3	21.5	0.15	0	0		0	2
16	Perm. lake Limuru 2	Lim2	01°06.34'S, 36°37.82'E	01/2003	2294	2.5	25	155	7.5	23.1	0.70	2	4	22.3	1	12
17	Perm. Lake Limuru 3	Lim3	01°08.35'S, 36°40.73'E	01/2003	2135	4.5	1.5	414	7.8	24.6	0.50	0	0	72.2	1	0
18	Lake Naivasha main	LN	00°46.34'S, 36°21.66'E	01/2003	1897	4.5	15000	292	9.2	22.9	0.20	4	1		1	2
19	Lake Naivasha Crater	CIC	00°45.80'S, 36°24.55'E	08/2001 & 01/2003	1897	14.0	195	375	8.7	22.5	1.20	0	0	87.4	1	4
20	Lake Oloidien	Oloid	00°48.89'S ,36°15.85'E	01/2003	1897	3.0	600	2590	10.0	23.3	0.30	0	0	374.5	1	7
21	Eldoret Sigawet Dam	Sigaw	00°35.08'N, 35°13.06'E	01/2003	2014	1.5	5	214	8.5	22.5	0.20	2	0	121.7	1	0
22	Lake Katalin	Katal	00°38.42'N, 35°28.91'E	01/2003	2337	4.5	15	78	6.6	19.5	0.37	2	2	28.9	0	3
23	Perm. pond Eldoret Nakuru 1a	ElNa1a	00°26.41'N, 35°18.32'E	01/2003	2185	0.5	0.1	196	6.9	14.1	0.50	1	4	26.5	0	9
24	Perm. pond Eldoret Nakuru 1b	ElNa1b	00°26.41'N, 35°18.32'E	01/2003	2185	0.4	0.03	381	7.6	16.2	0.30	0	1		0	7
25	Perm. pond Eldoret Nakuru 2	ElNa2	00°21.66'N, 35°21.08'E	01/2003	2217	1.5	0.05	171	6.9	14.5	0.50	1	3		1	3
26	Perm. pond Eldoret Nakuru 3	ElNa3	00°19.99'N, 35°21.92'E	01/2003	2214	0.8	0.03	221	7.0	16.3	0.40	4	1		0	1
27	Lake Narasha	ElNa4	00°02.65'N, 35°32.47'E	01/2003	2764	7.2	200	34	5.6	16.0	2.20	3	3	13.8	0	4
28	Perm. pond Eldoret Nakuru 5	ElNa5	00°03.60'S, 35°38.38'E	01/2003	2471	0.8	0.01	204	6.6	20.8	0.25	4	2		0	2
29	Perm. pond Eldoret Nakuru 6	ElNa6	00°04.92'S, 35°39.49'E	01/2003	2536	0.5	0.2	117	6.6	24.9	0.10	4	0	33.1	0	3
30	Perm. pond Nakuru Naivasha 2	NaNa2	00°20.50'S, 36°10.14'E	01/2003	1920	1.0	0.05	178	7.8	20.4	0.20	2	0		0	5
31	Lake Ol Bolossat	OlBol	00°09.91'S, 36°25.98'E	01/2003	2358	2.0	2000	1960	9.0	20.6	0.20	1	0	86.6	1	4
32	Lake Baringo	Barin	00°39.12'N, 36°03.64'E	08/2001 & 01/2003	967	4.0	10800	1600	8.5	26.0	0.05	3	0	311.9	1	4
33	Mogotio Kapchelukung Dam	Mogot	00°05.00'N, 36°05.00'E	01/2003	1200	1.5	0.9	90	7.1	22.2	0.20	1	2	33.2	1	7
34	Kanga Reservoir	Kan1	00°11.85'S, 36°23.64'E	08/2001	2350	2.0	1	1000	7.7	20.5		0	0		1	3
35	Bogoria	Bog	N 00°13.43' E 36° 05.80'	08/2001	993	9.0	3000	67200	10.0	29.6	0.12	0	0		0	0
36	Elementea	Ele	S 00°26.55' E 36° 14.56'	08/2001 & 01/2003	1775	0.6	3333	29100	10.7	26.0	0.10	0	0		0	0
37	Nakuru	Nak	S 00°21.54' E 36° 03.91'	08/2001	1827	0.8	5000	37700	10.0	28.2	0.22	0	0		0	0

3.2.2 Field sampling and laboratory analyses

Surface-water temperature (SWT), pH and specific electric conductivity at 25°C (SCond) at the time of sampling were measured with a Hydrolab Quanta® multi-probe. Water transparency (Secchi) was measured using a 20-cm diameter Secchi disk. Water transparency exceeded maximum lake depth only at permanent pond Eldoret Nakuru 1a. Latitude, longitude and altitude (Alt, in m a.s.l.) were recorded using a hand-held GPS unit (Garmin International Inc.). Maximum lake depth (Zmax) was determined by GPS-guided echosounding. Open-water surface area (SA) was taken from the literature or calculated using GPS data. The abundance of aquatic macrophytes (Macr, vertical projection of floating and submerged aquatic plants) and emergent littoral vegetation (Litt) was estimated on a scale from 0 to 4 (0: no aquatic or littoral vegetation; 1: 1-5% cover of the water surface or shoreline contour; 2: 5-10%; 3: 10-25%; 4 > 25%). Free-floating water plants (e.g. *Pistia stratioides*) were also included in this estimate. Fish presence was primarily assessed from fish scales and bones in surface sediments, validated by field observations of fish and/or piscivorous birds, or fishery information from local people. Phytoplankton standing stock, as an estimate of lake trophic status, was deduced by measuring the chlorophyll a (Chl *a*) content of surface water, from methanol extracts using the spectrophotometric method (Talling & Driver 1963). Chl *a* data were available for only 21 of the 37 study lakes.

The zooplankton and epibenthos communities were sampled qualitatively using a conical tow-net of 25 cm diameter and 150 µm mesh, always combining several vertical and horizontal hauls, and taking care to include zones with submerged macrophytes and littoral vegetation. Samples were washed in the net and preserved in 100% ethanol. In the laboratory, samples were rinsed using a 50-µm mesh sieve. Live ostracod specimens and empty valves were sorted, identified and enumerated under a stereo-microscope at up to 120x magnification. When sufficient material was available, soft parts of several specimens were prepared and mounted on microscopic slides, and valves were measured and mounted on metal stubs for imaging with Scanning Electron Microscopy (Philips XL30 SEM). All other specimens were stored in 70% ethanol in glass vials. Identification was based on primary taxonomic literature for tropical Africa (e.g., Daday, 1910; Klie 1933; Lindroth, 1953), recent taxonomic reviews (e.g., Martens, 1990a, b; Savatenalinton & Martens, 2009) and aided by a 22-species reference collection from Lake Naivasha, Kenya (Verschuren 1996). Soft-part diagnostic features were used to confirm species identifications, but here we illustrate valve morphology only, and relate ecological information to morphospecies distinguishable on the basis of valve morphology. All but four of the encountered species are illustrated in this paper or in Rumes *et al*. (previous chapter). The remaining four taxa (*Globocypris trisetosa, Hemicypris intermedia, Cypricercus inermis* and *Paracypretta* sp.) could not be illustrated due either to the scarcity of specimens or poor conservation of valves. For help in the identification of these species we refer to the primary taxonomic literature or recent reviews.

3.2.3 Data analyses

Variables were tested for normality using Shapiro-Wilks tests (Shapiro *et al.*, 1968). SCond, Zmax, SA and Secchi were log-transformed as their distribution among study sites was positively skewed around the mean. Pearson's correlation and principal component analyses (PCA, based on a correlation matrix) were used to explore patterns of co-variation between the environmental variables (Alt, Zmax, SA, SCond, pH, SWT, Secchi, Litt, Macr, Chl *a* and fish P/A). We used independent two sample *t*-tests to determine whether environmental variables significantly differed between sites where fish were present or absent. Correlation matrices and normality tests were generated using the software package STATISTICA 5.5 (Statsoft, 2000). A Spearman rank correlation matrix was used to determine possible relationships between local species richness and environmental variables. For a meaningful comparison we used simple species richness rather than a more sophisticated diversity index because even with similar sampling effort between sites, the number of individuals recovered in samples was highly variable. We estimated total species richness for the study area using Chao's formula and two re-sampling estimators (Colwell & Coddington, 1994). This formula estimates the total number of species present in the area based on the observed number of species, the number of species present in only single sample, and the number of species present in exactly two samples.

A species presence-absence dataset was constructed for all sampling sites. Presence of a species in a lake was recorded if multiple (>1) specimens were found. Only species encountered in at least two sites were included in correspondence analyses, resulting in a reduced dataset of 10 environmental variables and 26 sites. for multivariate statistical analyses. We used Canonical Correspondence Analysis (CCA; ter Braak & Šmilauer, 1998) to explore relationships between ostracod species composition and local environmental variables using the software program Canoco 4.5. The long principal gradient in Detrended correspondence analysis (DCA axis 1 length = 4.01 SD) favoured application of an ordination technique based on unimodal species responses (Hill & Gauch, 1980, Lepš & Šmilauer, 2003). Rare species were down-weighted, and forward selection of environmental variables was used to identify which variables significantly ($p<0.05$, Monte Carlo Permutation test with 999 permutations) explained the greatest amount of variance in ostracod community composition. In case of similar contributions, priority was given to variables with known ecological relevance. The independent contribution of each environmental variable to explained variance in the species data was evaluated using variation partitioning. To evaluate whether environmental variables influence ostracod species composition through size-selective processes (such as predation by fish) we determined an average length of ostracods living at each site, using the average of the mean adult lengths ($n = 6$, when available) of all ostracod species present at that site. The association between fish presence/absence and average ostracod length was evaluated through an independent two sample *t*-test on the difference of average ostracod length in the group of sites with and without fish. Lacking a normal distribution, the association between lake depth, as rough proxy for lake seasonal permanence, and average ostracod length was evaluated by applying a Mann-Whitney U-test on the difference of average ostracod length in the group of temporary, shallow (Zmax $\leq$ 1m) and more stable, deeper (Zmax $\geq$ 1,5 m) sites. Independent two sample *t*-tests were also used to analyze the distribution of the most abundant taxa in relation to the main environmental variables.

3.3 Results

3.3.1 Environmental gradients

Surface-water temperature was negatively correlated with altitude (Table 2), reflecting the relation between altitude and mean annual air temperature. Transparency is positively correlated with lake depth and the abundance of submerged and floating vegetation, and negatively correlated with surface-water conductivity, pH and surface-water temperature. Lake surface area is positively correlated with both SCond and pH, reflecting the differences between the dilute, small rain-fed ponds and the larger lakes, where accumulation or evaporation has increased ionic concentration (Talling & Talling, 1965). SCond is also positively correlated with pH and chlorophyll *a*. Fish tended to be present in deeper sites which also have higher transparency (*P*-values of Mann-Whitney *U*-tests: 0.002 and 0.01, respectively).

Table 2: Correlation matrix of environmental parameters from shallow Kenyan lakes and ponds.

	Alt	Zmax	SA	SCond	pH	SWT	Secchi	Litt	macr
Zmax	0.1921								
SA	-0.150	* 0.362							
SCond	-0.187	0.010	*** 0.647						
pH	-0.318	-0.001	*** 0.650	*** 0.833					
SWT	***-0.697	-0.198	0.217	* 0.341	** 0.532				
Secchi	* 0.358	** 0.539	-0.133	*-0.394	**-0.474	***-0.586			
Litt	0.049	0.164	0.040	*-0.345	*-0.427	-0.271	* 0.348		
Macr	0.133	0.049	-0.075	*-0.361	**-0.466	**-0.488	*** 0.568	* 0.374	
Chl a	-0.282	-0.229	* 0.583	*** 0.796	** 0.674	0.335	**-0.599	-0.271	-0.411

*P < 0.05, ** P < 0.005, *** P <0.001

A PCA ordination was made of all 37 sampled waters and 10 measured environmental parameters. In addition, Chl a was included as a supplementary or passive variable, as this data was lacking from a number of sites, and as such did not influence the ordination (Lepš & Šmilauer, 2003).

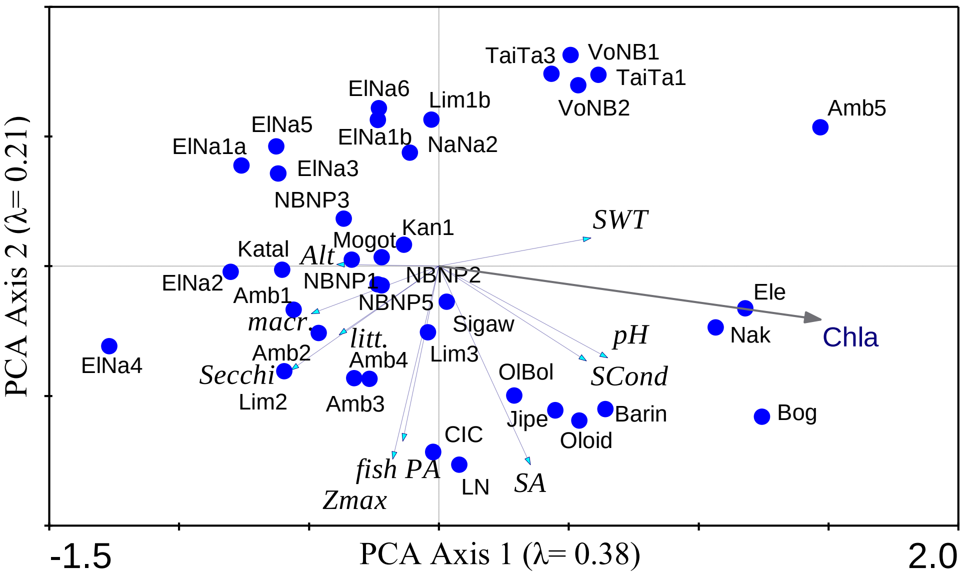

Figure 2: Principal components analysis (PCA) of 37 study sites in Kenya and 11 selected environmental variables (vectors); Chl a is included as a neutral variable.

The first two PCA axes together account for 59% of the environmental variance in the dataset ($\lambda_1 = 0.376$ and $\lambda_2 = 0.211$; Fig. 2). PCA axis 1, which explains 38% of the total variation is positively related to Chl a, SWT, pH and SCond, and negatively related to altitude, Secchi and macro. PCA axis 2, which explains 21% of the environmental variation is negatively related to fish P/A, Zmax and SA. Sites from the same region tend to be clustered together as they were similar with respect to most of the measured environmental variables. Waters in the upper right PCA quadrant are mainly warm, shallow, turbid, devoid of fish and aquatic macrophytes and have minimal littoral vegetation. In the upper left quadrant there are a number of relatively cold and shallow highland lakes with low conductivity and a pH of mostly less than 7. Highland lakes with fish, aquatic macrophytes and littoral vegetation are situated in the lower left quadrant, and large saline lakes are situated in the lower right quadrant.

3.3.2 Ostracod distribution

We found 32 ostracod species in 22 genera in 27 of the 37 study sites; the other 10 sites contained no live ostracods at the time of either field survey. Chao’s formula suggests a total species richness of 44 (± 8) species for all standing waters in the surveyed region, with first- and second-order jackknife estimates of 43 and 48 species, respectively. This suggests that our survey may have missed between 11 and 16 ostracod species (26-33%) of the regional species pool. No significant correlation was found between ostracod species richness (Ntaxa) and the measured environmental parameters.

Sarscypridopsis elizabethae (14 sites), *Physocypria capensis* (13 sites) and *Oncocypris mulleri* (8 sites) were the most widely distributed species, and with respectively 22, 23 and 17% of all live ostracods specimens often also constitute the most abundant species locally.

Only three other species were recovered from more than four sites: *Potamocypris palludum*, *Oncocypris* sp. type Kyaninga and *Sclerocypris jenkinae.* Species richness per site was highly variable, ranging from 0 (10 sites) to 12 (permanent lake #2 near Limuru)(Table 1). No ostracods were found in the hypersaline rift lakes Bogoria, Elementeita and Nakuru, in the Sigawet reservoir in Eldoret, in several smaller lakes and ponds in Amboseli and Nairobi national parks, and permanent lake #3 near Limuru. Fish presence was recorded in all fresh waters lacking ostracods, and their transparency (Secchi) was significantly higher than in the freshwater sites containing ostracods (Mann-Whitney *U*-test: $P = 0.02$). Nearly one third of all encountered ostracod species were found in only a single site (Table 3). Ostracods were most abundant in the fishless permanent ponds Nakuru-Naivasha 2, Eldoret-Nakuru 1a and1b, Voi-Nairobi 2 and Lake Oloidien. Several large ostracod species were exclusively (*Cypris latissima, Heterocypris giesbrechtii*) or mostly (*Chrissia junodi* and *Stenocypris curvirami*) found in (temporary) waters lacking fish.

Table 3: Overview of the species encountered in Kenya, with indication of the SEM illustrations, the number of lakes where species presence was recorded (#P), total number of live specimens encountered (#S). Abbreviation used in figure 3-5: LV, left valve; RV, right valve; Cp, carapax.* Species previously encountered in Kenya.

Species	Illustration	#P	#S
Superfamilia Darwinuloidea			
Vestalenula cuneata Klie, 1939*	Rumes, previous chapter	3	18
Superfamilia Cytheroidae			
Limnocythere notodonta Vavra, 1906	Rumes, previous chapter	3	22
Limnocythere michaelseni – group	Figure 3: A	2	25
Superfamilia Cypridoidea			
Physocypria capensis (Sars, 1895) Klie, 1933*	Rumes, previous chapter	16	579
Neozonocypris mirabilis Klie, 1944	Rumes, previous chapter	1	40
Cypris latissima (G.W. Müller, 1898)*	Figure 4: A	4	44
Globocypris trisetosa Klie, 1939*	See Martens, 1990	1	6
Pseudocypris bouvieri Daday, 1910	Figure 4: B-F	1	13
Hemicypris intermedia (Lindroth, 1953) Bate, 1970*	See Martens, 1984	1	45
Hemicypris sp. type Baringo	Figure 3: B	1	3
Heterocypris giesbrechtti (Müller, 1898) Löffler, 1961	Figure 3: D-H	4	38
Heterocypris obliqua Lowndes, 1936	Figure 3: C	4	21
Cypricercus inermis Brady, 1904	See Savatenalinton & Martens, 2009	1	12
Strandesia minuta Klie, 1936*	Rumes, previous chapter	2	14
Strandesia vinciguerrae (Masi, 1905) Müller, 1912	Figure 3: I-L	1	4
Acocypris platybasis Lowndes, 1932*	Rumes, previous chapter	4	11
Chrissia junodi junodi (Delachaux, 1919) Martens, 2001*	Figure 4: G-J	4	31
Stenocypris curvirami Lowndes, 1932*	Figure 4: K-M	4	13
Stenocypris major Baird, 1859*	Rumes, previous chapter	2	7
Sclerocypris cf. *clavularis* Sars, 1924	Figure 4: N-R	1	6
Sclerocypris jenkinae Klie, 1933*	Figure 5: A-F	5	62
Sclerocypris venusta (Vavra, 1897) Martens, 1986*	Figure 4: S-W	2	158
Paracypretta sp.	See Martens, 1984	1	2
Cypridopsis vidua-complex (O.F. Müller, 1776)	Figure 3: M-Q	4	37
Martenscypridopsis pygmaea Sars, 1924	Rumes, previous chapter	1	2
Plesiocypridopsis aldabrae (Müller, 1898) McKenzie, 1971*	Figure 3: R	1	7
Potamocypris mastigophora Methuen, 1910*	Rumes, previous chapter	3	6
Potamocypris palludum Gauthier, 1939	Rumes, previous chapter	6	16
Sarscypridopsis elizabethae Sars, 1924	Rumes, previous chapter	14	558
Zonocypris costata Vavra, 1897*	Rumes, previous chapter	2	6
Oncocypris mulleri Daday, 1910*	Rumes, previous chapter	8	423
Oncocypris sp. type Kyaninga	Rumes, previous chapter	5	271

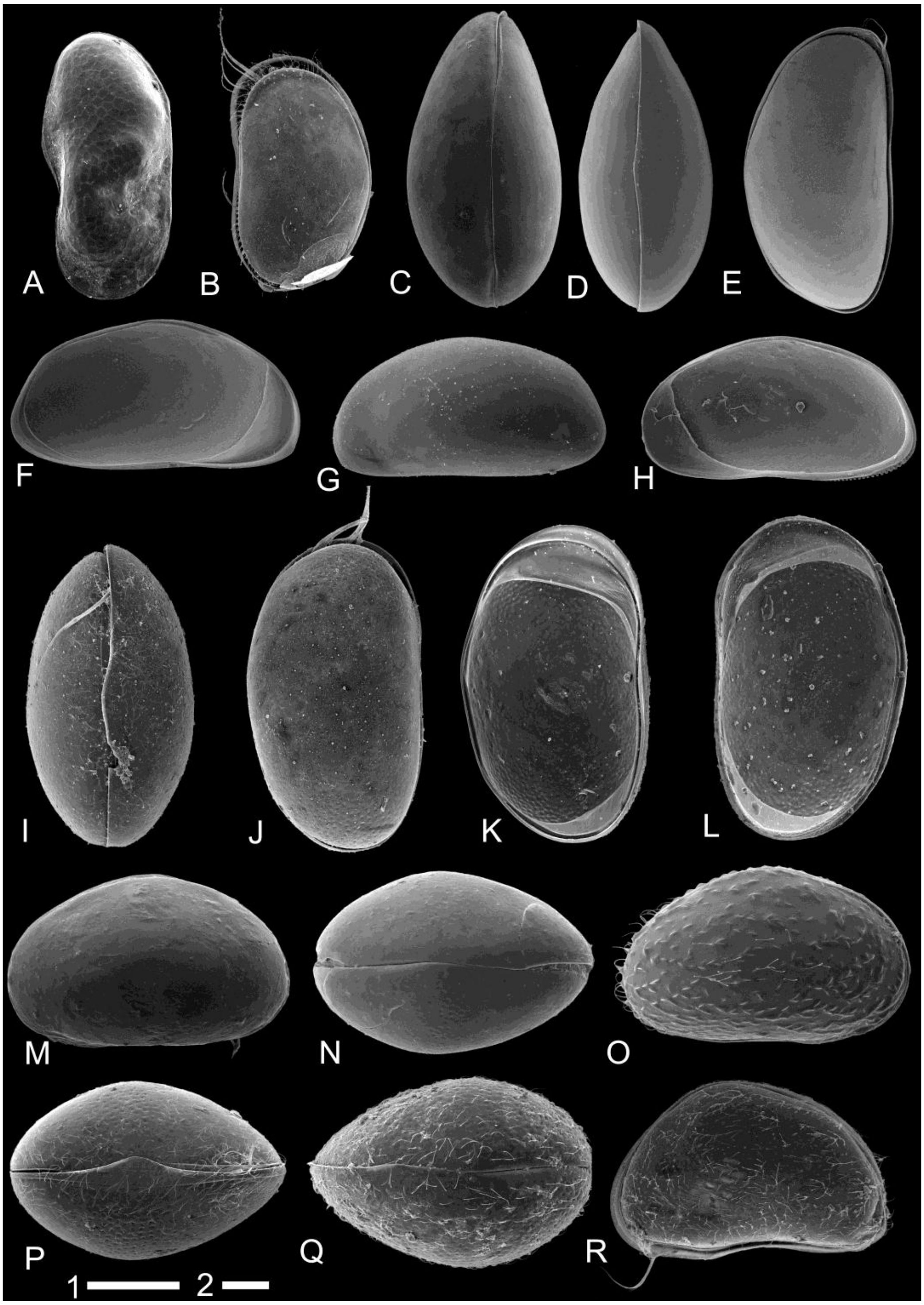

Figure 3: *Limnocythere michaelseni* - group (A); *Hemicypris* sp. type Baringo (B); *Heterocypris obliqua* (C); *Heterocypris giesbrechtti* (D-H); *Strandesia vinciguerrae* (I-L); *Cypridopsis vidua species* complex (M-Q); *Plesiocypridopsis aldabrae* (R). ***L. michaelseni* – group**: A. male, LV, external view. ***H.* sp. type Baringo**: B. female, Cp, left lateral view. ***H. obliqua***: C. female, Cp, dorsal view. ***H. giesbrechtti:*** D. female, Cp, ventral view. E. female, Cp, right lateral view. F. female, LV, internal view. G. female, Cp, left lateral view. H. female, RV, internal view. ***S. vinciguerrae***: I. female, Cp, ventral view. J. female, Cp, right lateral view. K. female, LV, internal view. L. female, RV, internal view. ***C. vidua* species complex**: M. female, Cp, left lateral view. N. female, Cp, dorsal view. O. female, Cp, right lateral view. ***C.* sp. type Narogomon**: P. female, Cp, ventral view. Q. female, Cp, dorsal view. R. ***P. aldabrae*** : R. female, Cp, left lateral view. Scale 1 = 200µm for A, M-R. Scale 2 = 300 µm for B-H; and 200µm for I-L.

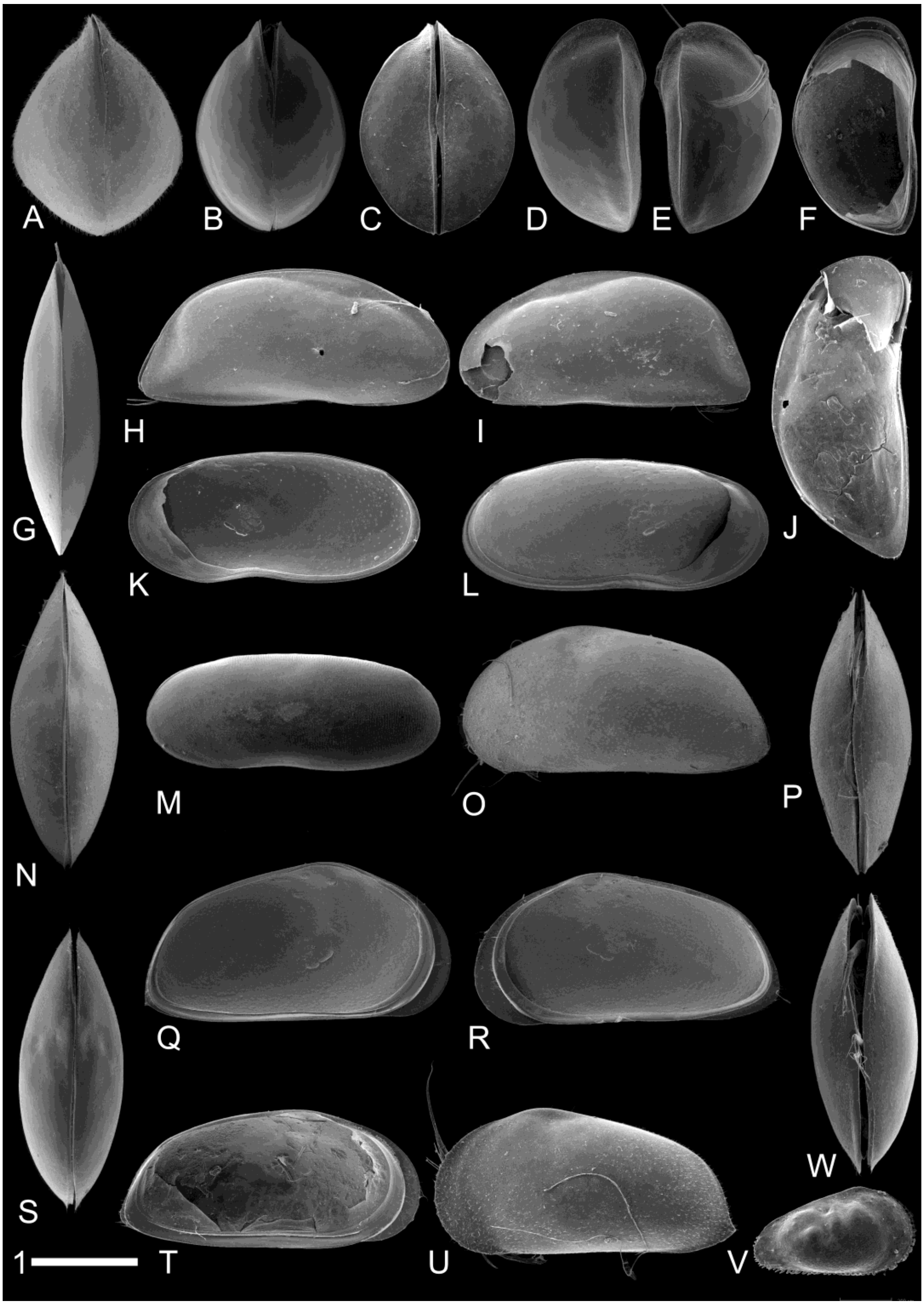

Figure 4: *Cypris latissima* (A); *Pseudocypris bouvieri* (B-F); *Chrissia junodi junodi* (G-J); *Stenocypris curvirami* (K-M); *Sclerocypris* cf. *clavularis* (N-R); *Sclerocypris venusta* (S-W). ***C. latissima***: A. female, Cp, dorsal view. ***Pseudocypris bouvieri***: B. female, Cp, dorsal view. C. female, Cp, ventral view. D. female, RV, external view. E. female, LV, external view. F. female, LV, internal view. ***Chrissia junodi junodi***: G. female, Cp, ventral view. H. female, Cp, right lateral view. I. female, Cp, left lateral view. J. female, LV, internal view. ***Stenocypris curvirami***: K. female, RV, internal view. L.. female, LV, internal view. M. juvenile, LV, external view. ***Sclerocypris* cf. *clavularis***: N. female, Cp, dorsal view. O. female, Cp, left lateral view. P. female, Cp, ventral view. Q. female, LV, internal view. R. female, RV, internal view. ***Sclerocypris venusta***: S. female, Cp, dorsal view. T. female, LV, internal view (specimen tilted backwards). U. female, LV, external view. V. juvenile, RV, external view. W. female, Cp, ventral view. Scale 1 = 1000µm for A-J, N-W and W; 750µm for K-M; 400µm for V.

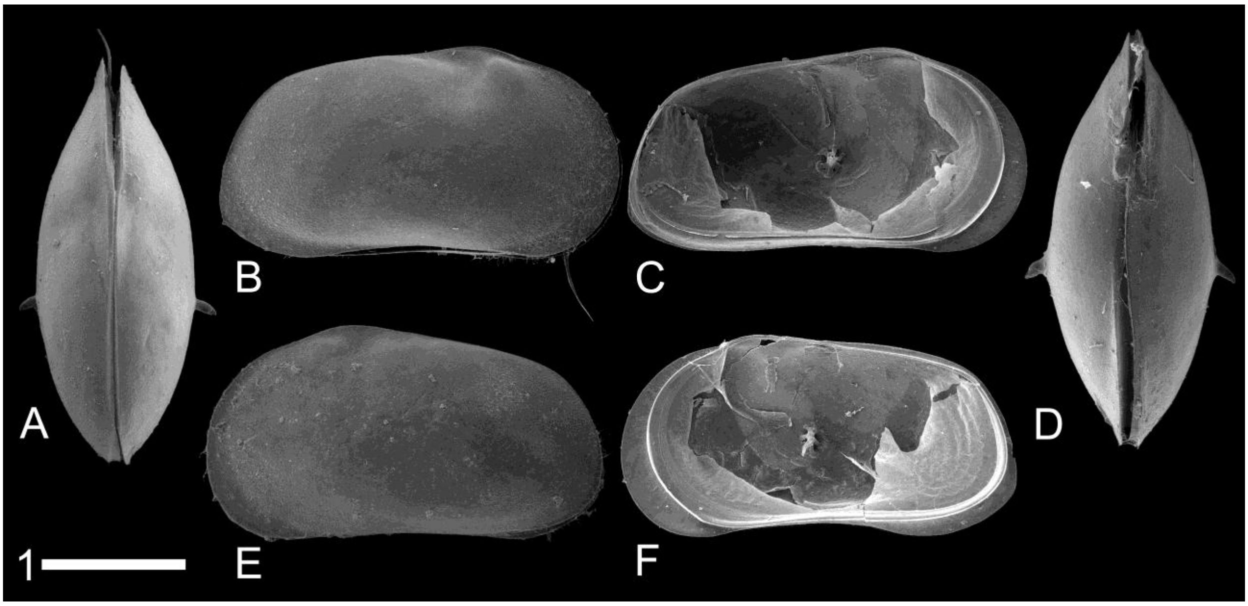

Figure 5: ***Sclerocypris jenkinae***: A. female, Cp, dorsal view, tuberculate. B. female, Cp, right lateral view, atuberculate. C. female, LV, internal view. D. female, Cp, ventral view, tuberculate. E. female, Cp, left lateral view, atuberculate. F. female, RV, internal view. Scale 1 = 1000µm for A-F.

3.3.3 Multivariate community analysis

DCA indicated a gradient length of 4.01 for the environmental dataset of the 27 sampling sites inhabited by ostracods. The resulting CCA with forward selection reduced the number of significant environmental variables to three, together explaining 22% of the total observed variance: emergent littoral vegetation, SWT and pH (F-value: 2.07; P= 0.001; see also Fig. 6 and Table 4). Variation partitioning between the different environmental variables in the CCA attributed 36% of the total explained variation to emergent littoral vegetation, 33% to SWT and 26% to pH ($P < 0.05$). CCA axis 1 reflects a gradient in littoral vegetation as well as in lake depth. Deeper, permanent lakes, with littoral emergent vegetation are situated to the left of axis 1, whereas shallow temporary ponds are situated to its right. CCA axis 2 reflects the environmental gradient from highland freshwater sites with pH below 7 in the bottom quadrants, to the alkaline lakes occupying the floor of the Rift Valley Floor in the upper quadrants. In our dataset, *Sclerocypris venusta*, *Cypris latissima* and *Heterocypris giesbrechtii* were specifically associated with warm and turbid ponds devoid of littoral or aquatic vegetation and fish. *H. giesbrechtii* is typical of temporary waterbodies and can be found in moderately saline waters (Holmes *et al.*, 1998). McKenzie (1971) reported that it can tolerate dessication. *Strandesia minuta* and *Chrissia junodi* were specifically found in relatively cool highland sites with low pH and SCond (Permanent pond Eldoret Nakuru 1a, Lake Narasha). *Potamocypris mastigophora* was found in larger lakes with abundant littoral emergent vegetation (Lakes Naivasha, Jipe and Kioko).

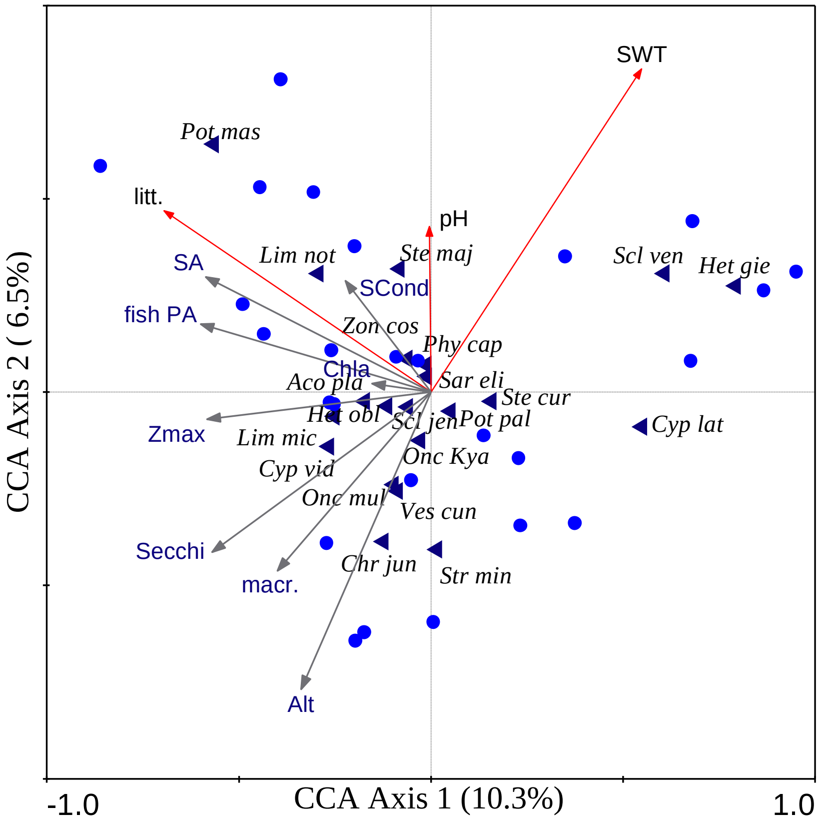

Figure 6: Canonical Correspondence analysis (CCA) of 21 ostracod species occurring in at least two sites (triangles), study sites with ostracods (circles), and the three selected environmental variables (red vectors); other environmental variables are included as neutral variables (grey vectors). Species abbreviations as in Table 2.

Table 4: Summary statistics and canonical correspondence analysis (CCA) for ostracod data sets from Kenya. Species richness is the raw ostracod taxon richness per site; numbers between brackets are standard deviations (+/- SD). Percentage variance explained by each environmental variable in constrained correspondence analysis (CCA) using a single environmental variable at a time. The significance is based on 999 unrestricted Monte Carlo Permutations (p<0.05*, p<0.01**, p<0.001***). Only bold displayed variables were selected for CCA (Fig. 6).

	Kenya dataset
# lakes	27
# species per lake	3.9 (2.1)
DCA	
Gradient length (SD)	4.01
CCA % variance explained	
Alt	6.9*
Z_{max}	6.5*
SA	6.1
SCond	4.2
Litt.	8.0**
Macr.	4.4
pH	5.5
SWT	7.6*
Secchi	6.8*
Fish PA	5.6
all canonical axes	22.0***

3.3.4 Univariate statistics

Ostracod communities in Kenyan lakes and ponds that are devoid of fish contain more large-bodied species than that of ponds with fish (*t*-test*: P = 0.003*; Fig. 7). Presence or absence of fish rather than the depth of the waterbodies determined ostracod species composition. This was illustrated by the fact that there was no significant correlation between lake depth and average ostracod length. Of the six species found in at least five sites, only *Sclerocypris jenkinae* was found exclusively in permanent ponds or lakes with Zmax > 2m (*t*-test: *P* = 0.01). *Oncocypris mulleri* was found at eight sites, most of which are situated on the shoulders of the Rift Valley; hence *O.mulleri* is positively associated with lower SWT (*t*-test: *P* = 0.02). No significant relationships were found for the other four frequently encountered species.

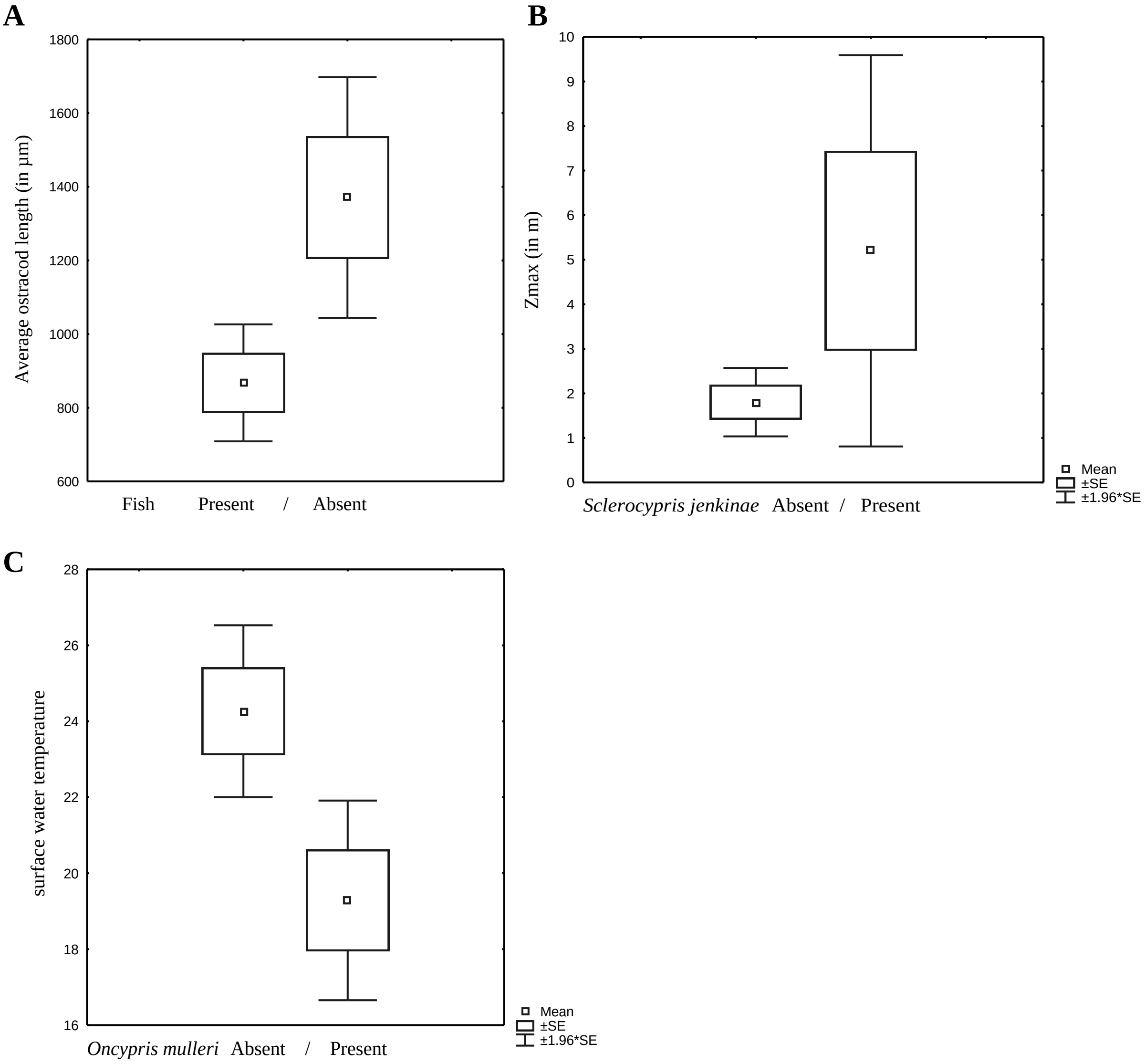

Figure 7: Box plots showing the association of A) average ostracod length with presence/absence of fish B) *Sclerocypris jenkinae* with maximal lake/pond depth C) *Oncocypris mulleri* with surface water temperature.

3.4 Discussion

3.4.1 Ostracod distribution

Ostracods were found in about 75% (27 out of 37) of our study sites. As in other studies in Central Africa (Lindroth, 1953; Rumes *et al.*, earlier chapter), no ostracods were found in saline inland lakes with conductivities >10,000µS/cm, despite the fact that several Ethiopian and South African species are known to occur in hypersaline conditions (Martens, 1990a; Martens *et al.* 1996) and the known affinity between the ostracod fauna of southern and eastern Africa (Martens, 2001).

There are some indications that the absence of large ostracod species in the freshwater ponds and lakes could be the result of a combination of sufficiently high water transparency (Secchi depth) and the presence of planktivorous and benthofagous fish. Firstly, the presence of fish in all the freshwater ponds and lakes lacking ostracods, indicates that these waters are not too ephemeral in nature to sustain ostracods. Secondly, large ostracods were abundant in both temporary pools as well as in permanent, fishless ponds. Thirdly, on average water transparency was higher in lakes and ponds lacking ostracods, although this difference was not significant. However, it remains doubtful whether fish predation would effectively suppress small, crawling benthic taxa such as *Limnocythere* or *Cypridopsis vidua*-species complex. North American representatives of *Cypridopsis vidua*-species complex can even avoid predation by resisting digestion (Vinyard, 1979).

Table 5: Additional ostracod species previously recorded living in the study area (based on Martens, 1984b and the primary literature mentioned therein)

Species	Location
Acocypris hyalina Lowndes, 1931	Lake Naivasha, swamp between Soy & Eldoret
Bradycypris strigata Klie, 1939	Lake Naivasha, swamp near Kinangop
Cypretta kenyensis Klie, 1939	Swamp near Nairobi
Hemicypris nonstriata Bate, 1972	Swamp North of Ngong Hills
Heterocypris humilis (Lindroth, 1953) Bate, 1970	Temporary pools North of Ngong Hills
Ilyocypris gibba (Ramdohr, 1808) Brady & Norman, 1889	Swamp on Ngong Hills
Heterocypris incongruens (Ramdohr, 1808) Claus, 1892	Pool in Machacos, South of Nairobi
Neocypridella fossulata (Daday, 1910) sensu Martens, 1984	Swamp near Nairobi
Chrissia cultrata (G.W. Müller, 1900) Martens, 2001	Swamp between Eldoret and Soy
Physocypria koenikei (Daday, 1910) Martens, 1982	Lake Jipe
Plesiocypridopsis humilior (Gauthier, 1934) Martens, 1984	Spring between Nairobi and Naivasha
Stenocypris acocyproides Klie, 1933	Lake Naivasha
Strandesia caudata Klie, 1939	Swamps near Nairobi, Lake Narasha, Kinangop

As in Lowndes (1936), Lindroth (1953) and Pieri *et al.* (2006), many species were recorded from only a single lake or pond. Due to the large number of species recorded from a single site, and concentration of high diversity ($\geq$ 7 species) over a handful of sites, the Chao regional species richness indicator suggests that 11 to 16 additional species may be present in the study area. We are aware of 13 species previously recorded from small to medium-sized waters in our study area that were not found in the present study (Table 5). Since our study did not include Lake Turkana and surrounding region nor cold, high-altitude lakes on Mt.Kenya, we also failed to encounter a substantial number of species listed by Lindroth (1953) and Löffler (1968). Certainly, the sizable number of missing species also reflects the fact that most sites were sampled just once. In a study of East African freshwater zooplankton, Green (1993) found that the long-term number of species found at any particular site could be two to three-and-a-half times the momentary number of species sampled. This result is consistent with a study of the *Daphnia* of Kenyan waters (Mergeay *et al.*, 2006), which found surficial bottom sediments to, on average, contain resting eggs of twice as many species as are present in the living community at the single moment of sampling. More frequent and extensive sampling would evidently yield a more integrated picture of ostracod distribution in Kenyan waters, both of potentially missing taxa and the currently recorded species. We expect some of those missing species to be found in the permanent lakes and swamps, where a combination of changing seasonal conditions and spatial habitat variation allows for a diverse ostracod fauna. A significant number of additional species may be recovered in the temporary pools. The temporary pool ostracod fauna of South West Africa has already been found to have high generic endemicity (Martens, 1998b).

On the other hand, this study also found eleven ostracod species that had not previously been reported from Kenya (Table 3), excluding the taxa which we did not identify to species level (e.g., *Hemicypris* sp. type Baringo, *L. michaelseni* group, *Oncocypris* type Kyaninga). Notwithstanding possibly incomplete sampling of the fauna, total species richness in this study is similar to that of a more extensive ostracod survey on 62 crater lakes in western Uganda (Rumes *et al.*, earlier chapter), with considerable overlap in taxa (See Table 2). The higher total expected species richness in Kenyan waters may reflect the larger environmental gradient represented by sampled sites, which in Kenya includes both permanent lakes and dilute temporary ponds. Species richness tended to be highest in small, dilute shallow ponds with abundant aquatic macrophytes. The large lakes Jipe (2500 ha) and Oloidien (600 ha) are notable exceptions, as they had no aquatic macrophytes at the time of sampling and a surface conductivity of 1140 µS/cm and 2590 µS/cm respectively, but still contained at least seven ostracod species. As in Eitam *et al.* (2004), ostracod species richness in temporary or semi-permanent ponds was rather low, indicating the importance of permanence of habitat in structuring ostracod community composition and diversity.

Considering their abundance in the present dataset, the low number of previously known locations (in Kenya) for the three most frequently encountered species (*Sarscypridopsis elisabethae*: no records; *Physocypria capensis*: 2 locations; *Oncocypris mulleri*: 2 locations) is notable although this is probably due to their relatively small size and our selection of previously unstudied waters. Some of the species found in (semi-) permanent ponds in this study had previously been recorded from similar temporary habitats from South Africa to the

Mediterranean (see for example Sars, 1924 and Pieri *et al.*, 2006). The absence or scarcity of the large-bodied (> 1.5 mm) species *C. latissima*, *H. giesbrechtti*, *C. junodi* and *S. curvirami* in lakes with fish is likely related to size-selective vertebrate predation. This phenomenon is known to be a major factor in determining zooplankton species in a lake (Brooks & Dodson, 1965), although selective predation on benthic crustaceans is less studied. There are several arguments indicating size-selective vertebrate predation in our study area. First, average ostracod length was found to be significantly larger in lakes without fish than in lakes with fish Secondly, several large-bodied species were found either exclusively or mostly in temporary ponds without fish, and thirdly there was no significant correlation between lake depth and average ostracod length. This effect of vertebrate predation could be reduced or even negated by the presence of abundant aquatic macrophytes (e.g. in permanent Lake Limuru 2) or low water transparency (e.g. in Lake Baringo). In fact, aquatic macrophytes have been shown to reduce the efficiency of both vertebrate and invertebrate predators (Diehl, 1992).

Sclerocypris jenkinae, one of the largest ostracods in our dataset, was found only in permanent lakes and ponds (Zmax > 2m) where fish were present. Historical records indicate that *S. jenkinae* has been found mostly in Lake Naivasha (as reviewed in Martens, 1986); the one record from a swamp between Eldoret and Soy (Klie, 1939) does not mention depth, nor whether it is temporary or not. Perhaps our *Sclerocypris jenkinae* is the *Sclerocypris* cf. *clavularis* (from Cohen, 1986) that was more abundant in samples taken from increasing depth (and with finer substrates) in Lake Turkana. The other *Sclerocypris* in our dataset all originated from shallow temporary or semi-permanent ponds, which seem to be the typical habitats for the majority of *Sclerocypris* species (Martens, 1986, 1988).

3.4.2 Ostracod community composition in Kenyan waters

Although Pieri *et al.* (2006) argue that the wide physical and chemical fluctuations typical of temporary and ephemeral habitats favour generalist, highly tolerant species, our CCA analysis reveals that ostracod community composition in Kenyan freshwater lakes and ponds is significantly influenced by the abundance of littoral vegetation, surface-water temperature, and pH. Variation partitioning indicates a substantial independent contribution of each of these three selected variables. All three variables are also known to directly or indirectly affect ostracod community composition in other geographic areas (Smith, 1993; Viehberg, 2006; Horne, 2007; Kiss, 2007). The abundance of littoral vegetation explained most of the variance in ostracod community composition. Several species were encountered typically only in shallow temporary to semi-permanent ponds lacking littoral vegetation, while others such as *Potamocypris mastigophora* were found only in the presence of abundant littoral vegetation. Emergent littoral vegetation and particularly the adhering detritus and micro-organisms form an important food source for various ostracod species (Benzie, 1989; Mbahinzireki *et al.*, 1991). It may also provide escape from predation. On the other hand, some species have been found to avoid the poorly oxygenated waters that can develop amongst dense littoral vegetation (Kiss, 2007). Surface-water temperature was negatively correlated with altitude and positively with pH and SCond. Here SWT is determined by a combination of altitude and the origin of the surface water, with some lakes receiving significant subsurface inflow of shallow, groundwater originating at higher altitude, while others are strictly rain-fed (see also Mergeay *et al.*, 2006). Groundwater-surface water interactions are important for ostracod species' distribution as they can cause changes in water chemistry, influencing species' ability to thrive (Ito & Forester, 2009). SWT also reflects the differences in ostracod community composition between relatively cold and dilute highland lakes (SWT: 15-23°C) and the large, saline and slightly alkaline lakes of the lowlands (SWT: 26-33°C). In our study *O. mulleri* was found almost exclusively in the colder and shallow highland lakes, although earlier records indicate that it is found in a wide range of conditions including temporary ponds (Fryer, 1956), semi-permanent ponds (Gauthier, 1939), crater lakes (Green *et al*., 1974 – as *O. debunshae*; Rumes previous chapter) and the large Rift Lake Malawi (Fryer, 1957). pH varies from slightly acidic (5.6 in Lake Narasha) to alkaline (10.0 in Lake Olodien). The most widely distributed species are encountered in a fairly broad range of pH (*O. mulleri*: 6.9-10; *Physocypria capensis*: 6.6-10.0), while other species were found to be limited to either slightly acidic (*Vestalenula cuneata*: 6.9-7.5; *Chrissia junodi*: 5.6-7.6) or mostly alkaline lakes (*P. mastigophora*: 7.8-9.2). *Potamocypris* spp. are known to dwell in areas of sub-aqueous groundwater discharge (Forester & Smith 1993, Verschuren *et al.*, 2000), and *P. mastigophora* specifically has been found to prefer silty and sandy substrates (Tudorancea *et al*., 1989). Its association with emergent macrophytes and occurrence in alkaline lakes in this study could be related to such seepage areas, where pH is lower than at the surface and, as a result, both *Potamocypris* and emergent macrophytes can thrive.

The effect of lake trophic status may be underestimated as incomplete data on phytoplankton standing stock (chlorophyll a) prevented adequate analysis. In a similar study on a rather more homogenous set of Ugandan crater lakes, lake productivity was found to be one of the most influential parameters determining ostracod community composition, in addition to the diversity of aquatic macrophytes, conductivity and mean annual air temperature (Rumes, previous chapter). Lacking information on the chemical composition of the studied waters has prevented us from analyzing the effect of various ionic concentrations and ratios on the distribution of ostracod species in shallow Kenyan lakes and ponds. In the study area, lakes are almost without exception sodium-bicarbonate waters and the concentration of most anions and cations is proportional to total conductivity (Talling & Talling, 1965). This is not the case for calcium and magnesium in more saline lakes due to selective precipitation in waters of increased conductivity (Talling & Talling, 1965). This magnesium/calcium ratio can be an important factor in determining ostracod species distribution (e.g. Bunbury & Gajewski, 2005), although it did not significantly influence ostracod communities in western Uganda (Rumes, previous chapter).

In conclusion, our study illustrates the large diversity in ostracod species present in Kenyan lakes and ponds. In general, the abundance of littoral vegetation, surface-water temperature, and pH significantly determined ostracod distribution in the study area. There are indications that presence/absence of fish in shallow permanent waters influences species composition by removal of large-bodied species due to size-selective predation.

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4

Ecological and taphonomic controls on the composition of fossil aquatic invertebrate assemblages across a wide environmental gradient of East African lakes

Abstract

Lake-sediment records of past climate and environmental change are often based on analyses of biological remains preserved in a single, mid-lake sediment core sequence which is assumed to represent a relatively stable integration, in space and in time, of the local aquatic community at the time of burial. In this study, the composition of aquatic invertebrate assemblages from recently deposited surface sediments of 61 crater lakes in western Uganda was compared with surveys of the living communities to determine i) the relative preservation potential of various taxa, and ii) the extent to which the surface-sediment assemblages from the centre of the lake reflect the corresponding living aquatic invertebrate community. Using indirect and direct ordination methods, we related the species composition of assemblages of Cladocera, Ostracoda and other aquatic biota to existing environmental gradients, and determined which environmental parameters influenced both fossil and live assemblages.

A total of 96 distinct types of invertebrate remains were encountered in the surface sediment samples, whereas 139 taxa were encountered in the live samples. Despite their relatively abundant occurrence in live samples, many pelagic cladoceran species left few recognizable remains, whereas chydorid (mostly epibenthic) cladocerans were nearly always more common in the fossil assemblages. For most ostracod species, fossil valves were encountered significantly less frequent than live specimens, with the exception of the free-swimming *Oncocypris* spp. and the numerically abundant *Zonocypris costata*. Remains of aquatic insects, Acari, Bryozoa, Turbellaria, and Thecamoeba were frequently encountered in the sediment.

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The composition of both living and fossil cladoceran assemblages in Ugandan crater lakes is mainly determined by surface-water conductivity, pH, and the extent and diversity of aquatic macrophyte habitat. Fossil cladocera assemblages are additionally influenced by lake depth and size, reflecting the impact of basin morphometry on pre-burial spatial integration. Living and fossil ostracod assemblages mainly reflect mean annual temperature, the presence of sandy or muddy near-shore habitat, and the distance from the sample site to the littoral zone (Dmin); the latter was particularly important in determining fossil ostracod distribution. In both live and fossil assemblages, Stratiomyidae, *Culex* sp. and *Ephydrella* type, were found to be indicative of elevated conductivities. *Plumatella* (Bryozoa) flottoblasts, mandibles from Baetidae (Ephemeroptera) and tests of *Arcella discoides* (Thecamoeba) were more frequent in lakes with abundant aquatic macrophytes. Linear and unimodal multivariate analyses indicated that surface-water conductivity, pH, and the diversity of aquatic macrophyte habitat best explained the observed distribution of various groups of aquatic biota among lakes.

For the fossil assemblages as a whole, transport-sedimentation processes dependent on both the distance from the littoral area to the core site and-lake depth were found to be the most important factors. As such, a good knowledge of basin morphometry and potential changes therein due to past lake-level fluctuation is essential to correctly infer past environmental changes from single, mid-lake cores.

Keywords: Cladocera - Ostracoda – palaeolimnology – preservation - taphonomy - tropical limnology – Uganda

4.1 Introduction

Biological remains in lake sediments can provide valuable information on environmental conditions during the lifetime of the organisms from which they originated. While detailed knowledge of contemporary species ecology is vital to an accurate interpretation of the fossil assemblages extracted from sediments, it is equally important to determine to what extent the fossil assemblage is representative for the different habitats present in the lake at the time of burial. Mid-lake surface-sediment samples are known to integrate biotic remains in space (i.e., from various lake habitats) and time (i.e. various seasons and years) (Frey, 1988). While the latter is undoubtedly true, an increasing number of studies cautions against a too general interpretation of the former (e.g., Eggermont *et al.*, 2007; Kattel *et al.*, 2007). For example, it has been shown that the composition of fossil surface-sediment assemblages is influenced by various factors such as basin morphometry, transport-sedimentation processes, dissolution and fragmentation of remains, bioturbation, and temporal and spatial variation in live assemblages (Korhola & Rautio, 2001; Moos *et al*, 2005; Zhao *et al*., 2006; Eggermont *et al.*, 2007).

In Africa, lake sediments constitute the most abundant continuous archives of past climate and environmental change (Verschuren & Russell, 2009). In the absence of instrumental and documentary records dating back more than 200 years, these natural archives are vital to document the magnitude and timing of historical fluctuations in climate (Verschuren, 2004), and to understand long-term ecological dynamics in response to these climatic fluctuations (Verschuren, 2003). A wide range of independent proxies preserved in lake sediments can now be used to create multi-disciplinary climate and palaeoecological reconstructions (Last & Smol, 2001a, b; Smol *et al.*, 2001 a, b). An important group of such proxies are based on the ecological indicator value of fossil remains of various aquatic biota (Cladocera, Ostracoda, aquatic insects, diatoms, aquatic plant macrofossils, etc.).

Cladocera (Crustacea: Branchiopoda) are an important component of the zooplankton and littoral zoobenthos of western Uganda crater lakes (Rumes, previous chapter). They are known to be good environmental indicators (Korhola & Rautio, 2001) and their remains can often be identified to the species level (Frey, 1986; Szeroczyńska & Sarmaja-Korjonen, 2007). As such, fossil cladocerans have been widely used successfully to infer environmental and community change over various temporal scales (e.g., Duigan & Birks, 2000; Mergeay *et al*., 2004; DeSellas *et al.*, 2008).

Ostracoda (Crustacea) constitute an important part of the littoral zoobenthos in the study region (Rumes, previous chapter 2), and possess a bivalved carapace of low-magnesium calcite which tends to preserve well. Due to the great ecological diversity of ostracod species, their fossil valves have been used frequently as palaeo-indicators of both natural and anthropogenic changes affecting lake environments (Holmes, 2001).

Many species of aquatic insects and various other groups of aquatic invertebrates also leave morphologically identifiable remains in lake sediments (Elias, 2006); and the Ugandan crater lakes are no exception (Rumes, 2005). Chironomids (Insecta: Diptera; non-biting midges) are among the best-studied groups (Walker, 2001), and in tropical Africa chironomids have been shown to be good indicators for past salinity (Eggermont *et al.*, 2006) and temperature change (Eggermont *et al*., 2009). Other less studied groups include larvae of aquatic insects (e.g. Culicidae, Ephydridae, Caenidae), Bryozoa, Acari (mites), Turbellaria, Thecamoeba (testate amoebae), and various others. In an exploratory study, Rumes *et al*. (2005) related their distribution in the sediments of Ugandan crater lakes to salinity, aquatic macrophyte distribution and lake trophic status. This study indicated that analysis of relatively large (>150 µm) invertebrate remains (rapid biological screening) would yield vital information on aquatic ecosystem conditions, but that a more thorough study was required to determine the indicator value of the various groups.

In this study, we analysed living communities and corresponding subfossil death assemblages of aquatic invertebrates in 61 maar-crater lakes in western Uganda, with the primary aim to assess the relative preservation potential of Cladocera, Ostracoda, aquatic insects and various other aquatic invertebrate taxa. In addition, we used ordination techniques to assess whether similar physical and chemical environmental parameters explain the distribution of the subfossil remains of these biota and the living communities from which they are derived.

4.2 Methods

4.2.1 Study area

The crater lakes (including a few small surface waters nearby) studied here are all located in one of the four main maar crater districts (Fort Portal, Kasenda, Katwe-Kikorongo, and Bunyaruguru; Melack, 1978) in southwestern Uganda (Figure 1). These lakes are small (surface area 0.01-0.92 km^2, except the 3.84 km^2 large compound lake of Nyamusingere), and are spread across the Edward-George branch of the East African Rift Valley along regional gradients between 914 and 1566 m elevation and semi-arid to subhumid climate regimes. The lakes range from fresh to hypersaline (56 to 135,400 µS/cm), from oligotrophic to hyper-eutrophic (Chl *a* 1 to 671 µg/l), and from shallow and unstratified to deep and permanently stratified (Table 1). Lakes on the moist shoulder of the Rift Valley are fed mainly by rain and surface runoff (and an occasional small stream input), and contribute to the regional groundwater through porous upper crater walls. Lakes on the dry Rift Valley floor are hydrologically closed, often saline, and maintained against a local moisture deficit by substantial inputs of shallow groundwater. Water levels of all lakes undergo modest to strong seasonal fluctuations, with some of the salt lakes known to dry up seasonally or intermittently. The lakes are mostly alkaline at the surface with an overall mean pH of 8.99 (range 6.55-9.92; SD = +/- 0.7). The freshwater lakes have been classified as sodium-potassium-magnesium-bicarbonate type lakes, strongly reflecting the mineralogy of regional volcanic rocks (Kilham, 1971). Over the full regional salinity range, ion concentrations are mostly determined by the evaporation of inflow water as predicted by simple evaporative concentration models (Kilham, 1971).

Natural vegetation surrounding the Ugandan crater lakes mainly reflects the local rainfall regime, and varies from dry grass savannah on the floor of the Rift Valley (Katwe-Kikorongo and northern part of Bunyaruguru) to semi-deciduous lowland forest on its shoulders (Fort Portal, Kasenda, and southern part of Bunyaruguru) (White, 1983). In most of the wetter, more densely populated areas, natural vegetation around the crater basins has now been replaced by an agricultural landscape. Routine burning of secondary vegetation and intense subsistence agriculture inside gently sloping crater basins has augmented their phosphorus loading, often causing eutrophication (Kizito *et al.*, 1993). Some lakes are situated within the boundaries of Kibale and Queen Elisabeth National Parks, where human activities are limited to fishing and low-intensity exploitation of the forest (Figure 1).

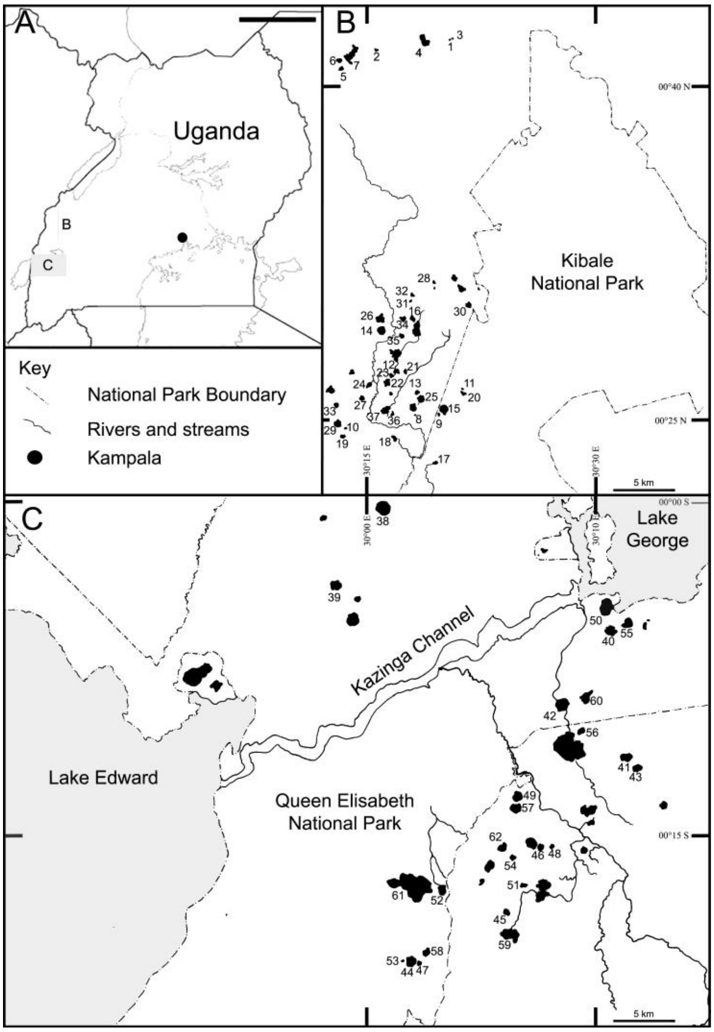

Figure 1: Map of the study region in western Uganda showing the locations of (A) the crater lake districts in the Edward-George branch of the Rift Valley, (B) the Fort Portal (lakes 1 to7) and Kasenda (lakes 8 to 37) districts, and (C) the Kikorongo (lakes 38 to 39) and Bunyaruguru (lakes 40 to 62) districts.

Table 1: Study lakes in western Uganda ordered by district, with data on lake surface area (SA), core site depth (Z_{core}), maximum depth (Z_{max}; indicated only when different from Z_{core}), Elevation (Elev), Mean Annual Temperature (MAT), surface-water conductivity (SCond) at 25°C, Surface water pH (pH), surface water temperature (SWT), littoral habitat types (Type), Secchi depth (Secchi), Chlorophyl a (Chl a), fractional area of land-cover types Stable (forest, savannah and plantation), Agriculture and Fallow, number of live taxa encountered (Nlive), number of fossil types (Nfossil), number of fossils recovered (#fossil) and the index of similarity (S).

Lake/District	SA	Z_{core}	Z_{max}	Elev	MAT	SCond	pH	SWT	Type					Secchi	Chl a	Stable	Agri	Fallow	Nlive	Nfossil	#fossil	S
	(km²)	(m)	(m)	(m asl)	(°C)	(µS/cm)		(°C)	sand	emer	Subm	float	swamp	(m)	(µg/l)							
Fort Portal																						
1 Ekikoto	0.02	72		1537	20.02	497	8.29	24.0	X	X				1.80	5.7	0.35	0.25	0.40	26	25	1423	0.57
2 Kaitabarago	0.02	35	70	1548	19.93	489	8.03	23.1	X	X	X			0.75	4.7	0.70	0.00	0.30	21	33	620	0.58
3 Kayihara	0.01	66		1537	20.02	498	8.07	24.5	X					1.60	1.8	0.70	0.00	0.30	30	19	2163	0.27
4 Kyaninga (South)	0.24	58		1531	20.07	420	8.34	24.3	X	X				5.85	2.2	0.40	0.00	0.60	39	41	492	0.59
5 Kyegere	0.12	53		1566	19.79	250	8.31	24.0	X	X	X			2.15	1.7	0.01	0.40	0.59	23	38	1314	0.49
6 Nyabikora	0.07	7.7		1561	19.83	188	8.31	24.7	X	X		X		1.20	1.7	0.15	0.50	0.35	19	25	946	0.56
7 Saka (crater)	0.01	8.5		1566	19.79	612	7.59	25.5	X	X		X		0.45	15.9	0.45	0.40	0.15	25	26	164	0.51
Kasenda																						
8 Kanyabutetere	0.01	5		1188	22.85	401	8.62	25.6	X	X	X			0.78	19.3	0.00	0.80	0.20	29	28	2337	0.56
9 Kanyamansira	0.02	30		1177	22.94	394	8.96	25.9	X	X	X			0.82	18.2	0.90	0.00	0.10	20	23	336	0.68
10 Kanyamukali	0.02	11		1150	23.16	920	8.60	26.2	X	X				0.65	8.2	0.10	0.70	0.20	18	22	226	0.26
11 Kanyanchu	0.01	4.8		1233	22.48	568	8.26	26.6	X	X	X	X	X	0.93	4.5	1.00	0.00	0.00	45	16	367	0.45
12 Kanyango	0.12	45	58	1259	22.27	493	8.75	25.0	X	X		X		0.45	22.1	0.25	0.65	0.10	16	25	198	0.33
13 Kasenda	0.09	13.5		1244	22.39	312	7.63	24.4	X	X				0.83	13.1	0.40	0.05	0.45	26	20	120	0.44
14 Katanda	0.37	42	152	1340	21.62	419	8.51	24.4	X	X				2.00	1.9	0.35	0.50	0.15	23	30	1529	0.60
15 Kerere	0.27	68		1184	22.88	263	8.04	25.8		X	X			3.63	3	0.80	0.00	0.20	45	35	478	0.45
16 Kifuruka	0.13	3.7		1403	21.11	411	8.33	22.9	X	X	X	X	X	0.82	15.6	0.45	0.45	0.10	45	24	273	0.47
17 Kisibendi	0.04	4.5		1126	23.35	277	9.30	25.0	X	X				0.03	215	0.80	0.00	0.20	8	15	67	0.45
18 Kitere	0.10	51		1160	23.07	711	8.97	26.7	X	X				0.83	16.8	0.33	0.07	0.60	5	23	247	0.23
19 Kyanga	0.12	54		1146	23.19	1112	9.11	25.7	X	X	X			1.40	9	0.80	0.15	0.05	16	12	346	0.40
20 Kyerbwato	0.01	12.5		1233	22.48	411	8.47	25.7	X	X	X	X		1.65	1.7	0.90	0.00	0.10	51	23	1605	0.50
21 Lugembe	0.08	15		1281	22.09	407	8.30	23.6	X	X				1.35	6.3	0.20	0.60	0.20	29	12	227	0.40
22 Mahuhura	0.19	54	154	1254	22.31	600	8.97	24.6	X	X	X			5.60	8.4	0.38	0.02	0.60	30	42	1882	0.52
23 Mbajo	0.08	35		1234	22.47	504	8.64	24.5	X	X		X		1.30	5.6	0.30	0.10	0.60	27	35	222	0.63
24 Mubiro	0.16	57	70	1208	22.69	718	9.02	26.7	X	X	X			3.20	1.8	0.40	0.15	0.45	22	40	1397	0.56
25 Murusi	0.21	57		1226	22.54	382	8.54	26.1	X	X				1.40	1.3	0.35	0.25	0.40	15	10	215	0.56
26 Mwengenyi	0.29	32	140	1397	21.15	352	8.43	23.6	X	X	X	X	X	3.35	1.6	0.40	0.40	0.20	57	40	628	0.55
27 Njarayabana	0.12	38		1179	22.92	857	8.84	24.9	X	X				1.20	9.2	0.35	0.15	0.50	17	11	312.5	0.38
28 Nkuruba	0.01	34.5		1480	20.48	370	8.31	23.5	X					1.01	27.8	0.80	0.00	0.20	20	25	280	0.42
29 Ntambi	0.32	111		1158	23.09	5820	9.75	24.8	X		X			0.40		0.90	0.05	0.05	5	12	400	0.47
30 Nyabikere	0.39	47.3		1376	21.32	271	7.89	24.9	X	X	X			0.61	17.2	0.84	0.01	0.05	61	23	184	0.38
31 Nyahirya	0.01	79		1444	20.77	379	8.18	23.2	X			X		0.97	13.6	0.60	0.10	0.30	21	30	742	0.52
32 Nyamswiga	0.03	43		1447	20.75	330	7.76	23.6	X	X	X	X		1.10	9.9	0.35	0.20	0.45	31	27	275	0.41
33 Nyamugosani	0.11	37		1234	22.47	988	8.94	27.1	X	X				1.52	3.5	0.10	0.35	0.55	7	18	1036	0.26
34 Nyantonde	0.12	38	180	1387	21.24	501	8.76	23.9	X	X				3.10	2.27	0.15	0.60	0.25	23	28	469	0.54
35 Rukwanzi	0.08	-	169	1332	21.68	425	8.33	24.4	X					5.02	5.5	0.92	0.02	0.06	30			
36 Wandakara	0.03	10.5		1158	23.09	1125	8.76	24.3	X	X				0.70	9.8	0.02	0.65	0.33	26	18	113	0.65
37 Wankenzi	0.16	59		1158	23.09	496	8.65	24.3	X	X				0.36	13.7	0.10	0.50	0.40	23	23	379	0.50
Kikorongo																						
38 Kikorongo	0.92	9.8		915	25.06	22400	9.58	30.7	X					1.20	4.5	1.00	0.00	0.00	5	7	343	0.62
39 Kitagata	0.62	8.9		914	25.07	135400	9.63	29.0	X					0.05		1.00	0.00	0.00	3	6	24	0.29
Bunyaruguru																						
40 Bagusa	0.33	0.9		905	25.14	61100	10.62	32.7	X					0.24	670.6	1.00	0.00	0.00	3	3	50.5	0.67
41 Bugwagi	0.60	71	85	1048	23.98	441	9.02	26.1	X	X				2.45	3.8	0.45	0.40	0.15	28	17	113	0.42
42 Chibwera	0.76	10.5		971	24.60	457	8.91	26.8	X		X		X	1.35	6.7	1.00	0.00	0.00	37	7	389	0.23
43 Ibamba	0.01	1.2		1073	23.78	104	6.55	25.7		X		X	X	0.35	7.5	0.10	0.75	0.15	61	34	459	0.55
44 Karolero	0.51	35		1103	23.54	181	8.05	27.0	X			X		3.80	3.3	1.00	0.00	0.00	39	13	302	0.44
45 Kako	0.17	29		1396	21.16	89	8.18	25.1	X					2.30	1.2	0.08	0.85	0.07	12	16	199	0.29
46 Kamweru	0.20	43		1232	22.49	170	9.59	25.3	X					0.55	34.5	0.05	0.65	0.30	23	18	103	0.32
47 Kacuba	0.05	14.5		1102	23.54	148	8.75	26.9	X	X	X	X		1.49	11.5	1.00	0.00	0.00	46	13	371	0.28
48 Kasirya	0.09	43		1251	22.34	302	8.72	26.3	X	X				2.35		0.15	0.50	0.35	22	16	126	0.32
49 Katinda	0.44	17		1024	24.18	743	9.48	26.0	X	X				0.53	42.6	0.01	0.70	0.29	20	8	375	0.44
50 Kibengo	0.88	4.8		914	25.07	264	9.92	29.3	X	X				0.20	103	1.00	0.00	0.00	26	14	228	0.32
51 Kigezi	0.39	29		1302	21.92	265	8.49	26.6	X	X	X			0.99	13.7	0.11	0.47	0.41	20	17	278	0.59
52 Kyasunduka	0.50	2.1		1004	24.34	269	8.69	25.6	X	X				0.30	288	0.60	0.20	0.20	13	8	97	0.38
53 Kyogo	0.02	3.4		1113	23.45	56	6.87	26.6		X	X	X	X	3.00	2	1.00	0.00	0.00	43	24	393	0.58
54 Mafura	0.16	29		1255	22.30	259	9.29	22.7	X	X				0.65		0.00	0.80	0.20	18	10	201	0.57
55 Maseche	0.32	0.2		908	25.12	68200	10.19	32.3	X					0.02	7.4	1.00	0.00	0.00	5	4	15	0.44
56 Mbugo	0.36	2.6		978	24.55	214	9.63	27.3	X	X				0.51	76	0.20	0.70	0.05	15	21	344	0.51
57 Mirambi	0.53	22		1077	23.75	642	9.83	26.8	X	X				0.90	24.2	0.00	0.70	0.30	29	6	341	0.25
58 Murabio	0.27	15		1098	23.58	141	8.42	27.5	X	X	X	X		2.03	5.9	1.00	0.00	0.00	25	14	211	0.47
59 Nkugute	0.89	58		1409	21.06	121	8.72	24.5	X	X		X		0.90	15.9	0.21	0.64	0.15	25	11	81.5	0.44
60 Nshenyi	0.44	0.05		966	24.65	11230	10.05	29.3	X					0.02	26.3	1.00	0.00	0.00	5	7	311.5	0.33
61 Nyamusingere	3.84	4.3		978	24.55	681	9.40	26.6	X	X				0.36	14.8	0.99	0.00	0.00	16	8	387	0.35
62 Nyungu	0.14	25		1172	22.98	430	9.40	24.7	X	X				0.08	47.1	0.02	0.85	0.13	19	11	128	0.55

4.2.2 Fieldwork

In the course of 2007 and 2008 we conducted four dry-season (January-February or August-September) field campaigns in southwestern Uganda, surveying a total of 62 crater lakes. Latitude, longitude and elevation (in meter above sea level; m asl) were recorded by GPS (Garmin Csx 60). Mean annual air temperature (MAT) data were estimated using region-specific linear relationships between elevation and temperature ($p<0.001$ in all cases; Eggermont *et al*. 2009). We derived MAT data from the Global Historical Climatology Network (GHCN-Monthly) data base (time series from the 1930s to 2006; four stations) and Global Summary of the Day (GSOD) data base (time series from 1957 to 2006; 10 stations). Lake bathymetry and maximum lake depth (Z_{max}) were determined by GPS-guided echo-sounding. Lake surface area (SA) was calculated using either field-measured diameter and/or circumference (small, circular crater lakes) or by analysis of topographical maps (larger lakes, often irregular in shape). Types of vegetation and land use within the crater catchment were quantified by mapping them from a viewpoint in the centre of the lake. We distinguished the following types of land cover: stable ground cover (which included natural or secondary forest, savannah, and tree plantations), (subsistence and commercial crop) agriculture, fallow land, and habitation. The latter constituted a significant fraction of total land cover in two crater basins only (Kasenda and Nyabikere) and was therefore not included in statistical analyses. Surface-water temperature (SWT), pH, dissolved oxygen (DO) and specific conductance at 25°C (SCond) were measured at the time of sampling with a Hydrolab Quanta multiprobe. SWT values used in analyses are from the January-February dry season, nine of these were derived from July-August dry season data (underscored values in table 1). Data from lakes visited both during the the January-February and July-August dry season suggests that seasonality in surface water temperature was relatively low (~1°C). Transparency (Secchi) was measured using a 22-cm diameter Secchi disk. Collection and analysis of water samples for water chemistry followed the procedures described in Eggermont *et al.* (2007). The presence or absence of fish was recorded in all study lakes with SCond values <1500µS/cm. Many lakes contain indigenous fish populations (Sato *et al.*, 2003), but non-indigenous fish were additionally introduced to increase available protein resources (Kizito *et al*., 1993; Crisman, 2001; Bwanika *et al.*, 2004). The presence of haplochromine fish in the freshwater lakes was confirmed either by field observations, information from local fishermen, or occurrence of juvenile specimens in the live littoral samples.

The present-day living aquatic invertebrate community was sampled qualitatively by repeatedly sweeping a 50-µm mesh net across planktonic and epibenthic habitat in near-shore (littoral) environments, and in the off-shore pelagic environment. If habitats contained aquatic macrophytes, these were removed from the water and rinsed above the net to adequately sample the attached macro-invertebrates. Samples were instantly fixed in either formalin (5% formaldehyde) neutralized with powdered calcite, or in 70% ethanol.

Concurrent sampling and identification of aquatic macrophytes was carried out along transects from the lake shore to the depth limit of aquatic plant growth (Lebrun *et al.*, in prep). Submerged macrophytes in deeper water were sampled using a 4-m long rake. For this study (compare with Lebrun *et al.*, in prep) we differentiated between five main types of littoral habitat (HA): sandy or rocky shores including those with submerged parts of terrestrial vegetation (HA-sand); emergent reed-like vegetation such as *Phragmites*, *Cladium* and *Typha* (HA-emer); submerged vegetation with few or no floating parts, such as *Ceratophyllum*, *Potamogeton* and *Chara* (HA-subm); submerged vegetation with considerable floating parts, mostly *Nymphea nouchali* (HA-float); and a swampy vegetation occurring at the edge of some lakes with *Cyperus papyrus* and *Miscanthidium violaceum* (HA-swamp). The total number of aquatic macrophyte habitat types present in a lake (#Macrophytes) was used as a macrophyte habitat diversity measure.

Depending on lake depth, bottom sediments were collected intact using either a piston corer operated with drive rods or a gravity corer. In deep meromictic lakes, sediment recovery by gravity corer was often poor due to expansion of methane gas in the sediment during ascent through the water column. In these lakes, unstratified samples of flocculent surface sediments were collected using a weighted Wildco Fieldmaster® horizontal water sampler, ensuring that only the topmost layer of unconsolidated surface mud was taken. Where lake depth did not exceed the capability of our gravity-coring equipment (~80 m), sediment samples were taken in the deepest part of the lake, which in these simple crater basins is almost always near their geographical centre. In Lake Kyaninga (135 m), surface sediments were sampled at 58 m depth from the floor of the shallower south basin. In Lake Rukwanzi, all attempts to sample surface mud failed, due to both the steep incline of the lake bottom at lesser depths (<100 m) and equipment failure at greater depth (~165 m). The minimum distance of the core site to shore (Dmin) was determined by analysis of topographical maps. Surface cores were extruded upright at the lake in 1-cm or 2-cm increments with a fixed-interval sectioning device (Verschuren, 1993), and sequential increments were transferred to watertight sampling bags for transport and storage.

4.2.3 Laboratory analyses

Preserved samples of the living community were rinsed on a 150-µm mesh sieve. Specimens were sorted, identified and enumerated under a stereo-microscope with up to 120× magnification. We disregarded all adult flying insects except aquatic Coleoptera and Hemiptera, fully terrestrial taxa such as Formicidae and Coccoidea, and groups that were inadequately or accidentally sampled (such as nematodes, rotifers and crayfish). We also excluded Copepoda and *Hydra* sp. from the study, as they rarely produce identifiable remains.

Surface-sediment samples were prepared for analysis of (sub-)recently deposited invertebrate remains by deflocculation in a 10% solution of potassium hydroxide (KOH) at 70°C (Walker

& Paterson, 1985). Between 1.2 and 49.3 ml of mud from the upper 5 cm of the sediment-water interface was processed to yield at least 100 individual specimens of identifiable fossils. The total varied between 15 and 2337, with a mean of 490 specimens. Very low fossil yields despite large volumes of sediment processed occurred in several of the saline (e.g., Lake Maseche) and hypertrophic lakes (e.g., Lake Kisibendi). Water content (WC) and basic sediment composition (% organic matter (OM), carbonate, and non-carbonate inorganic matter) of the sediment samples were determined by drying overnight at 105°C, burning at 500°C, and ashing at 1000°C (Bengtsson and Enell, 1986). Higher WC of lake sediments may be the result of bioturbation (Hall, 1994), and could reflect their potential to harbour a diverse interstitial and burrowing fauna (Martin *et al.*, 2005).

Deflocculated sediment samples were also rinsed on a 150-µm mesh sieve. The choice for a 150µm sieve, which strongly influenced the number and type of remains encountered, was made in order to allow relatively rapid sample processing. The retained organic residue was transferred to a transparent counting tray and scanned at up to 120× magnification under transmitted light. All distinctive invertebrate remains were either identified in situ or picked out with a fine needle, mounted in glycerine (50% glycerol and water) on microscope slides, and analysed at up to 400× magnification with an Olympus BH-2 compound microscope. Except for fish scales and remains of aquatic macrophytes, the minimum number of individuals of a given species tallied was based on the most abundant skeletal fragment in the samples (i.e., *Alona cambouei* valves rather than headshields) and on the minimum number of individuals from which the remains must have originated (i.e., two *Chaoborus* mandibles or two ostracod valves counted as one individual). For the identification of cladoceran remains, we used discriminatory characters on associated headshields and ephippia in addition to those on the carapaces, and direct comparison of those body parts with reference specimens in the live samples. As samples were rinsed on a 150-µm mesh sieve, unattached small cladoceran remains such as postabdomens (cf. Sarmaja-Korjonen ref.), postabdominal claws (cf. Kitchell & Kitchell, 1980) and mandibles (cf. Brugam, 1978) were not used for identification purposes. Identification benefited from primary taxonomic literature on various taxa documented from the region, recent taxonomic reviews, a previous exploratory study on the fossil remains of aquatic invertebrates in Ugandan crater lakes (Rumes, 2005), and a 22-species reference collection of Ostracoda from Lake Naivasha, Kenya (Verschuren 1996). Note that in Rumes *et al.* (2005) the subfossil mandibles of *Culex* sp. (as illustrated in figure 18) were erroneously identified as belonging to Leptoceridae. Beetle elytra were very rarely encountered and not included in the dataset of subfossil remains as no straightforward distinction could be made between terrestrial and aquatic species. Several types of Neorhabdocoela oocytes were recovered from the studied sediment samples (cf. Gelorini *et al,* in prep.); in this study, we only distinguished two major types based on the structure of the egg wall. Due to their small size (60-200µm), our study protocol likely underestimates the true abundance of these oocytes in the sediment; smaller representatives are a well-known non-pollen palynomorph often recovered from pollen preparations (Haas, 1996).

Chironomidae were not identified beyond family level as the ecological and taphonomic controls on the composition of fossil assemblages of this group have been the subject of various previous studies (Heiri, 2004; Eggermont *et al.*, 2007; Eggermont *et al.*, 2008).

4.2.4 Data analyses

Before exploring species-environment relationships, environmental data were screened for use in statistical analysis. Among the chemical constituents of the lake waters, [Br], [NO_3] and [SO_4] were excluded because their concentrations were below detection limit at >50% of the sites. All 39 retained variables were tested for normality using the Shapiro-Wilks test (Shapiro *et al.*, 1968). Some environmental variables were normalized using either log transformation (SA, Scond, TP, TN, Chl a, total organic carbon content (TOC), [Na], [K], [Ba], [Fe], [Mn], dissolved phosphorus [P], [S], [F], [Cl] and [DIC]) or square-root transformation ([Sr] and #Macrophytes). Z_{max}, Z_{core}, MAT, SWT, Secchi depth, the three remaining land-use variables (Stable ground cover: LU_st, Crop agriculture: LU_ag, Fallow land: LU_fa), pH, DO, [Ca], [Mg], dissolved silica [Si], WC, OM and Dmin exhibited normal distribution and were left untransformed. Relationships among the environmental variables were assessed using a Pearson's correlation matrix and principal component analyses (PCA) for both the full dataset of 61 study lakes (62 excluding Ntambi) and the dataset of the 56 freshwater lakes (Scond < 1500µS/cm). Lake Ntambi was excluded because of incomplete water-chemistry data. Based on these analyses we further reduced the environmental data to a set of biologically relevant variables to be used for our analysis of species distribution. Correlation matrices and normality tests were generated using the software package STATISTICA 5.5 (Statsoft, 2000).

Live sampling of the aquatic invertebrate communities in western Uganda crater lakes yielded a large number of aquatic insects and insect larvae, Acari, Mollusca, Thecamoeba and lesser numbers of Bryozoa (*Plumatella*), juvenile fish and frogs. Sampling methods did not collect all groups in such a way that the samples reflect their true abundances in the studied lakes, but were uniform across all lakes and as such allow comparison of faunal composition between lakes. For both the living communities and recent death assemblages, relative abundance and presence-absence datasets were constructed. For the living communities, data from different net samples were combined, and whole-lake relative abundances were based on equal proportions of total littoral and total pelagic abundances. The latter was done to compensate for the lower population densities in the pelagic zone. Per lake the number of living species (Nlive), the number of fossil taxa (Nfossil), the number of living specimens (#live) and the number of fossil remains (#fossil) were determined and tested for normality (#live and #fossil were log transformed). Margalef's index of species richness (*M*), which minimizes the effect of sample size bias (Dodd & Stanton, 1990), was calculated using the formula M = N-1/(ln#) where N is the number of species and # the number of living or fossil specimens recovered. To compare the species composition of living communities and recent death assemblages an index of similarity (*S*, ranging from 0 – 1) was calculated using the formula $S = 2C/(\text{Nfossil} + \text{Nlive})$ where Nfossil is the number of species in the recent death assemblage, Nlive the number of species in the living community, and C the number of species common to both (as in Cummins, 1994). In the same fashion, an index *S'* for the similarity in species' live and fossil distribution among lakes was calculated using the formula $S' = 2\text{B}/(\text{Lfossil} + \text{Llive})$ where Lfossil is the number of lakes where the species is encountered in the recent death assemblage, Llive is the number of lakes where the species is encountered in the living community, and B is the number of lakes where the species is encountered in both. Similarity indices were based only on taxa that were encountered in at least two sites. To ensure comparability, a similar taxonomic resolution was used for both living and fossil taxa. The relationships of diversity and similarity indices with environmental variables were assessed using a Pearson's correlation matrix.

We used ordination techniques to determine the main structuring variables in our data sets (ter Braak & Prentice, 1988). Missing Chl a-data for lakes Kasirya and Mafura were substituted by the average value of all other freshwater lakes. The same principle was applied for missing water chemistry data from lakes Kerere (fresh) and Kitagata (saline), using data respectively from the subset of fresh and saline lakes.

The percent species abundance data were square-root transformed prior to numerical analysis in order to stabilize their variances. Only species encountered in at least two sites were included in the ordinations. Ostracoda and Cladocera were absent from all lakes with surface-water conductivity higher than 6000 µS/cm (Lake Ntambi), with the exception of *Moina belli* in lakes Kikorongo and Nshenyi. Therefore, multivariate community analysis of Ostracoda and Cladocera was limited to the sets of freshwater lakes where both living specimens and fossil remains of these groups were encountered. For numerical comparison of the recent death assemblages with environmental variables and with the living communities we also excluded *Heterocypris obliqua* (Ostracoda) and *Macrothrix triserialis* (Cladocera) because their particular distribution in surface sediments (alternately absent or dominant) strongly influenced the total fossil dataset. Preservation of Macrothricidae valves is known to be irregular (Frey, 1988). To select between linear- or unimodal-based numerical techniques (ter Braak, 1986), we analysed each biological dataset by Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980), with non-linear rescaling, detrending-by-segments and down-weighing of rare taxa. When the datasets had compositional gradient lengths of more than three standard deviation units, we used species-response models based on unimodal distribution (Lepš & Šmilauer, 2003), i.e. Canonical Correspondence Analysis (CCA, ter Braak, 1986). When the compositional gradient length was smaller than three standard deviations, the linear method (i.e. Redundancy Analysis (RDA), Stewart & Love 1968) was deemed more appropriate. A series of partial CCAs (or RDAs) was carried out with each environmental variable as sole constraining variable to assess its explanatory power. The percent variance explained by each variable was calculated and the statistical significance assessed by Monte Carlo Permutation tests with unrestricted 999 permutations (ter Braak, 1990; Lotter *et al.*, 1997). Subsequently, the environmental data set was reduced to the most powerful variables, i.e. those explaining the highest amount of variance in the various data sets while excluding strongly correlated variables. Variables that did explain a significant part of the variance in the living communities, but were not significant in the fossil assemblages (or vice versa), were included in the analysis of the latter only as passive variables, and as such did not influence the ordination (Lepš & Šmilauer, 2003).

4.3 Results

4.3.1 Environmental gradients

In the full dataset of 61 lakes, correlations among environmental variables reflect the broad geographical gradient between the mostly small, fairly deep, and dilute lakes in the northern lake districts (Fort Portal, Kasenda) and the more often large, rather shallow, and saline lakes on the floor of the Rift Valley in the southern lake districts (Katwe-Kikorongo and Bunyaruguru; see Appendix 1 & 2). Saline lakes in our dataset were all relatively large (except Lake Kitagata) and shallow (Z_{max} <10 m). This trend is illustrated by the positive correlations between Scond and the variables SA, pH, SWT, Dmin, and MAT. However, when the saline lakes are excluded, the geographical gradient in environmental conditions is reversed from south to north, because freshwater lakes in the southernmost Bunyaruguru district are generally more dilute (299 ± 203µS/cm) than freshwater lakes in the Kasenda and Fort Portal districts (510 ± 235µS/cm). Transparency is positively correlated with lake depth and negatively correlated with Scond, pH and indicators of trophic level (such as Chl a, TN and TOC).

In the full, 61-lake dataset, the first two PCA axes together account for 45% of total environmental variance ($\lambda_1 = 0.316$ and $\lambda_2 = 0.133$; Fig. 2a). PCA axis 1, which explains 32% of the total variation, is positively related with indicators of salinity (Scond, [Na], [Cl], [K], and pH), temperature (SWT, MAT), productivity (TP, TN, Chl a, TOC) and, to a lesser extent, lake size (SA, Dmin). PCA axis 2, which explains 13% of the variation, is positively related with aquatic macrophytes (HA-float, HA-swamp, HA-subm, #Macrophytes), and with sediment composition (OM and WC); and negatively related with the concentration of certain ions ([Ca], [Mg], [Ba]) and with lake depth (Z_{max}, Z_{core}). All hypersaline lakes are situated at the utmost right of PCA axis 1 but close to it. Eutrophic lakes with little or no aquatic vegetation are also situated in the right quadrants of the ordination biplot (Fig. 2a), with shallow, naturally eutrophic lakes in the upper right quadrant and deeper lakes suffering human impact in the lower right quadrant. Lakes with abundant aquatic macrophytes are situated in the upper left quadrant. The lower left quadrant is typified by freshwater lakes from the northern lake districts which are mostly fairly deep, slightly concentrated (SCond typically between 500 and 1000µS/cm), with relatively high [Ca] and [Mg] concentrations and fringed with reed (*Phragmites*) or other emergent macrophytes.

In the dataset with only freshwater lakes, the first two PCA axes together account for 35% of total environmental variance ($\lambda_1 = 0.193$ and $\lambda_2 = 0.155$; Fig. 3). PCA axis 1, which explains 19% of the total variation, is positively correlated with aquatic macrophytes (Ha-float, HA-swamp, HA-subm, Macrophytes), and negatively correlated with indicators of salinity (Scond, [Na], [K], [Cl]). PCA axis 2, which explains 16% of the variation, is positively correlated with temperature (SWT, MAT), productivity (TP, TN, Chl *a*, TOC) and, to a lesser extent, lake size (SA, Dmin). PCA axis 2 is negatively correlated with transparency (Secchi) and lake depth (Z_{max} and Z_{core}). [Fe] and [Mn] showed strong positive correlation among them, and tended to be higher in shallow lakes, as has previously been found in a large sample of East African lakes (Talling & Talling, 1965).

Based on the above ordination of measured environmental variables, we exclude dissolved phosphorus (P) from further analyses because in both datasets it is strongly correlated with TP, and was often close to or below the detection limit. The conservative ions [Na], [Cl], [F], [K], and [S], as well as [DIC], are all positively correlated with salinity (Scond) and pH ($p < 0.001$) and as such provide little or no additional environmental information. The same can be said for [Mn] in relation to [Fe], and the biological trace elements [Sr] and [Ba] in relation to [Mg]. OM shows a highly significant correlation with WC, and only the latter will be used in further analyses. In most sampled lakes, surface sediments were sampled close to the greatest depth, therefore Z_{core} covaries strongly with Z_{max}. As invertebrate remains are unlikely to be transported upslope before burial, we consider only Z_{core} in further analyses.

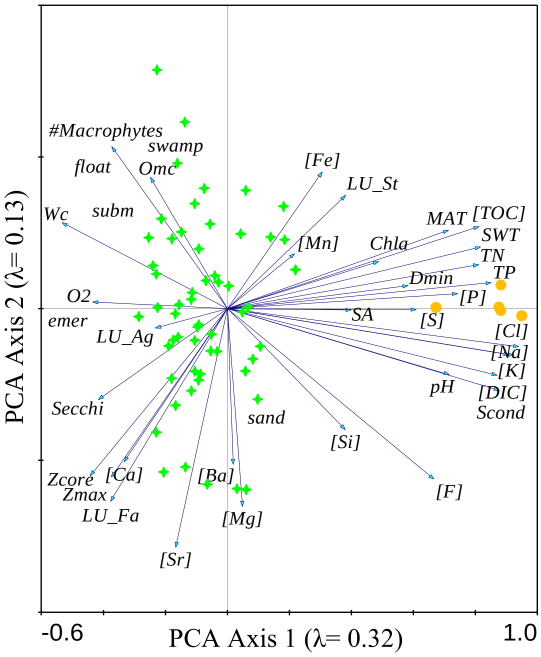

Figure 2: Principal components analysis (PCA) of 61 study sites (saline lake: full circle; freshwater lake: star) in Uganda and 39 environmental variables (vectors). Land-cover categories Stable, Agriculture and Fallow land plotted as LU_st, LU_ag and LU_fa, respectively.

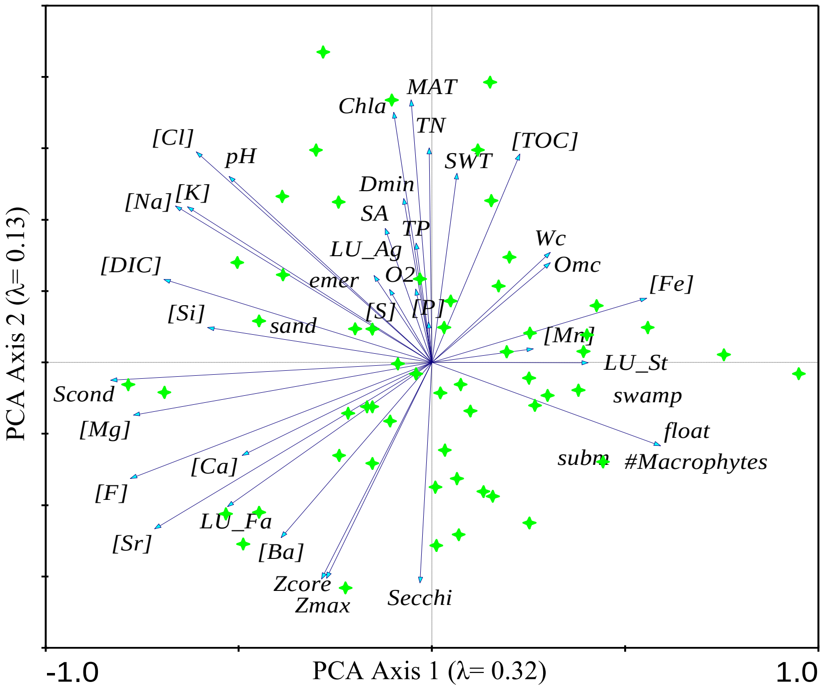

Figure 3: Principal components analysis (PCA) of 56 freshwater study sites (Scond < 1500µS/cm) in Uganda and 39 environmental variables (vectors). Land-cover categories Stable, Agriculture and Fallow land plotted as LU_st, LU_ag and LU_fa, respectively.

4.3.2 Faunistics and univariate analysis of species-environment relationships

We recorded a total of 139 living aquatic invertebrate taxa belonging to groups retained for analysis, and 96 types of fossil remains. The total fauna included 37 Cladocera, 35 Ostracoda, 51 aquatic insects and 29 other aquatic invertebrates. An overview of the 120 taxa encountered in at least two lakes (either living or fossil) is given in Table 2. In the truly saline lakes (Scond >10,000 µS/cm), living Ostracoda and Cladocera are either absent or limited to a single taxon (the cladoceran *Moina belli*). As a result, biodiversity was significantly higher in freshwater lakes than in saline lakes, with an average live taxon richness of 26.9 (SD: 12.8) versus 4.2 (SD: 1.1), and an average fossil taxon richness of 19.8 (SD: 8.3) versus 5.0 (SD:1.9). The diversity of cladoceran remains varied strongly among different freshwater lakes, ranging from zero to 15 species. Cladoceran fossils were absent in two eutrophic (Katinda and Mirambi) and one hypertrophic (Nyungu) freshwater lake, consistent with the similarly low number and abundance of living cladoceran species found in these lakes (respectively 2, 7 and 0). Analysis of the surface-sediment death assemblages revealed a wider distribution for most chydorid species than the one based on our samples of the living community (Table 2). As a result, chydorid diversity in freshwater lakes was higher in the surface-sediments than in the living community, with an average live taxon richness of 3.4 (SD: 3.3) versus an average fossil taxon richness of 4.1 (SD: 3.5). *Ceriodaphnia dubia*, *Moina micrura*, *Macrothrix triserialis* and most other pelagic Cladocera were rarely encountered in the sediment, despite their frequent occurrence in living samples. *Bosmina* *longirostris*, on the other hand, was found exclusively in the surface sediments, however also scarce and in just three lakes.

In the ostracods, fossil valves were found significantly less frequently than living specimens, with the exception of the free-swimming *Oncocypris* spp. and the numerically dominant *Zonocypris costata*, fossils of which were recovered from the surface sediments of 26 and 47 lakes respectively. Despite the often high number of fossil ostracod valves recovered (totaling nearly 7500 adult and 1600 juvenile specimens), only 20 of the 33 recorded species were found in more than one lake, and 5 species were encountered only once. No ostracod valves were recovered from the mid-lake surface sediments of Lake Murabio, and only a single juvenile valve in Lake Chibwera, although several species occurred in living samples from the littoral area of both these lakes. Lakes situated in the northern lake districts generally had a more diverse fossil ostracod fauna (5±2.8 species) than lakes in the southern lake districts (2±1.1 species). This difference in diversity was les pronounced in the living ostracod fauna of the northern (5±4.2 species) and southern (4±2.2 species) lake districts. Two ostracod species, *Zonocypris alveolata* and *Parastenocypris curvirami* were recorded only from the sediment, but like *Bosmina* in only very few lakes.

Several common insect taxa (such as *Chaoborus ceratopogenes*, Chironomidae, Baetidae), Acari, Bryozoa and Thecamoeba were also well-represented in the recent death assemblages. *Chaoborus anomalus* was present only in the shallow, turbid, hypertrophic Lake Kibengo. Aquatic beetle larvae and most aquatic Hemiptera were encountered in low numbers, and (excluding non-identifiable skeletal fragments in some sediment samples) were found only in samples of the living littoral community. Acari are well-represented in both the living community (60 lakes) and recent death assemblages (40 lakes). Remains of Oribatida in particular are found to preserve very well, confirming previous studies (Sølhoy & Sølhoy, 2000). Remains of other Acari were found in 26 lakes. They include both rare Hydracarina (which are soft-bodied and nearly always completely decompose shortly after death; Frey, 1964), and terrestrial taxa. In addition to the aquatic invertebrate remains, fish remains (scales, teeth and bones) were found in 29 lakes. The relative abundance of fish remains in the fossil assemblages increases with lake size and is positively correlated with Chl *a* ($r=0.431$, $p<0.01$; percent fish remains square-root transformed to approximate a normal distribution). Molluscs (snails and bivalves) were frequently present in living samples, but few remains were encountered in mid-lake surface mud. In the 6 hypersaline lakes, both the living community and fossil assemblages were characterized by a limited number of taxa, mostly larvae of Diptera (e.g., *Culex*, Stratiomyidae, *Ephydrella* type).

The similarity index between living and fossil samples of aquatic invertebrate communities in individual lakes ranges from 0.23 in Lake Kitere to 0.68 in Lake Kanyamansira (Table 1). Among freshwater lakes this similarity index is positively correlated with the total number of fossil taxa found ($r=0.47$, $p < 0.001$), and negatively correlated with Dmin ($r=-0.36$, $p <$

0.01). The average index of similarity between the living community and recent death assemblages was on average higher for chydorids (0.46; SD 0.17) than for ostracods (0.31; SD 0.30). In aquatic insects, the highest index of similarity was found for Chironomidae, Baetidae and *Chaoborus*. In the case of *Chaoborus* the index was lower than expected, probably because live *Chaoborus* actively migrated to the hypolimnion during daytime, which reduced the chance of *Chaoborus* being sampled.

Table 2: Summary information of live and subfossil death assemblages of aquatic invertebrate communities in 61 western Uganda crater lakes.

	Live	Relative abundance		Fossil	Relative abundance		Sites	
	Sites	Mean	Max	Sites	Mean	Max	in common	S’
Cladocera								
Pseudosida szalayi (1)	2	0.00	0.22	0	0.00	0.0	0	0.00
Diaphanosoma excisum (2)	2	0.01	0.29	0	0.00	0.0	0	0.00
Bosmina longirostris (3)	0	0.00	0.00	3	0.05	1.6	0	-
Alona cambouei (4)	18	0.28	5.05	29	2.61	71.7	15	0.64
Alona guttata (5)	8	0.11	5.21	4	0.49	20.0	3	0.50
Alona cf. *verrucosa* (6)	11	0.13	2.52	10	0.19	2.5	6	0.57
Alonella excisa (7)	6	0.03	1.45	8	0.19	4.1	2	0.29
Chydorus eurynotus (8)	7	0.02	0.76	16	1.38	26.4	6	0.52
Chydorus parvus (9)	30	0.80	8.90	37	2.56	43.9	25	0.75
Coronatella cf. *rectangula* (10)	1	0.03	2.13	6	0.21	6.6	1	0.29
Disparalona hamata (11)	11	0.13	4.56	10	0.18	3.5	6	0.57
Dunhevedia crassa (12)	12	0.18	6.25	27	1.58	23.9	10	0.51
Dunhevedia serrata (13)	4	0.07	4.17	4	0.09	2.6	2	0.50
Ephemeroporus barroisi (14)	4	0.09	5.07	20	0.35	8.2	2	0.17
Euryalona orientalis (15)	4	0.01	0.19	12	0.39	9.7	2	0.25
Graptoleberis testudinaria (16)	2	0.07	3.62	4	0.05	1.6	1	0.33
Karualona iberica (17)	15	0.17	3.33	24	2.66	30.2	11	0.56
Notoalona globulosa (18)	3	0.02	0.53	9	0.81	14.3	2	0.33
Oxyurella sengalensis (19)	6	0.18	10.42	6	0.51	13.5	2	0.33
Pleuroxus cf. *varidentatus* (20)	15	0.30	4.65	23	0.43	4.7	10	0.53
Pleuroxus toumodensis (21)	5	0.02	0.99	8	0.08	1.5	2	0.31
Pseudochydorus globosus (22)	27	0.15	1.39	40	2.68	33.3	24	0.73
Ceriodaphnia cornuta (23)	28	7.16	76.02	13	0.37	6.5	9	0.45
Ceriodaphnia dubia (24)	14	3.60	49.81	3	0.17	6.6	2	0.25
Daphnia laevis (25)	4	0.15	8.35	5	0.04	1.0	0	0.00
Simocephalus latirostris (26)	2	0.04	2.53	0	0.00	0.0	0	0.00
Simocephalus vetulus (27)	11	0.15	2.78	2	0.01	0.3	0	0.00
Iliocryptus spinifer (28)	1	0.00	0.18	2	0.02	1.0	1	0.67
Macrothrix triserialis (29)	29	1.66	33.33	6	0.42	7.0	6	0.35
Moina belli (30)	1	1.51	93.43	2	0.92	53.3	1	0.67
Moina micrura (31)	18	6.17	48.86	4	0.11	5.2	1	0.10
Moinodaphnia macleayi (32)	2	0.01	0.54	0	0.00	0.0	0	0.00
Chydoridae indet. (33)	-	-	-	18	0.36	6.7	-	-

	Live	Relative abundance		Fossil	Relative abundance		Sites	
	Sites	Mean	Max	Sites	Mean	Max	in common	S’
Ostracoda								
Alicenula inversa (34)	14	0.17	4.22	6	0.20	8.12	4	0.42
Darwinula stevensoni (35)	16	0.22	3.36	5	0.36	17.74	4	0.38
Vestalenula cuneata (36)	8	0.12	2.40	7	0.28	10.69	6	0.86
Limnocythere notodonta (37)	3	0.04	1.71	1	0.02	1.47	1	0.50
Cytheridella chariessa (38)	29	0.27	2.08	25	2.88	41.59	16	0.60
Gomphocythere sp. type Wandakara (39)	16	0.22	7.21	11	0.58	21.05	7	0.54
Gomphocythere expansa (40)	4	0.02	0.96	0	0.00	0.00	0	0.00
Candonopsis africana (41)	41	0.78	12.30	28	1.05	17.67	22	0.65
Physocypria capensis. (42)	9	0.22	5.72	1	0.33	19.95	0	0.00
Neozonocypris mirabilis (43)	10	0.04	0.70	1	0.01	0.89	1	0.18
Hemicypris fossulata (44)	3	0.02	0.46	0	0.00	0.00	0	0.00
Heterocypris obliqua (45)	9	0.04	1.15	3	0.03	1.04	2	0.31
Cypricercus inermis (46)	3	0.01	0.40	0	0.00	0.00	0	0.00
Strandesia minuta (47)	4	0.01	0.14	2	0.02	1.17	0	0.00
Strandesia vinciguerrae (48)	2	0.02	1.19	0	0.00	0.00	0	0.00
Plesiocypridopsis cf. *albida* (49)	11	0.04	0.57	3	0.02	0.59	2	0.29
Chrissia icosacanthus (50)	2	0.00	0.09	0	0.00	0.00	0	0.00
Stenocypris major (51)	6	0.03	0.97	1	0.01	0.52	0	0.00
Martenscypridopsis pygmaea (52)	2	0.01	0.53	2	0.04	1.84	2	1.00
Potamocypris mastigophora (53)	12	0.18	3.53	4	0.05	1.38	3	0.38
Potamocypris palludum (54)	4	0.01	0.43	2	0.02	0.82	0	0.00
Sarscypridopsis elizabethae (55)	5	0.04	1.12	3	0.12	5.70	2	0.50
Cypridopsis vidua-complex (56)	21	1.00	20.43	8	0.08	1.12	8	0.57
Zonocypris costata (57)	47	4.02	50.89	47	1.80	9.69	39	0.84
Oncocypris mulleri (58)	2	0.05	2.73	5	1.06	22.86	1	0.29
Oncocypris sp. type Katanda (59)	8	1.53	50.68	20	4.58	85.83	4	0.29
Oncocypris sp. type Kyaninga (60)	6	0.68	26.36	12	1.94	57.50	2	0.22
Strandesia juvenile type Ekikoto (61)	4	0.03	1.52	2	0.04	2.26	0	0.00
Stenocypris curvirami (62)	-	0.00	0.00	2	0.11	6.14	-	-
Insecta								
Chaoborus sp. (63)	39	5.34	50.00	55	18.79	73.33	37	0.80
Culex sp. (64)	13	1.74	55.77	6	2.00	53.33	3	0.32
Atrichopogon sp. (65)	2	0.00	0.07	0	0.00	0.00	0	0.00
Dashylea type (66)	8	0.08	3.33	0	0.00	0.00	0	0.00
Bezzia type (67)	19	0.10	3.40	1	0.00	0.29	0	0.00
Culicoides (68)	6	1.77	84.62	0	0.00	0.00	0	0.00
Stratiomyidae (69)	8	0.98	50.00	2	0.81	42.86	1	0.20
Ephydrella type (70)	4	0.81	50.00	4	2.49	61.39	1	0.25
Simulium sp. (71)	2	0.10	5.56	2	0.03	1.65	1	0.50
Chironomidae (72)	60	9.99	63.78	59	27.67	73.64	58	0.98
Trichoptera (73)	19	0.06	0.68	31	0.43	5.14	14	0.56
Hydrophilidae (74)	4	0.04	1.41	0	0.00	0.00	0	0.00
Gyrinidae (75)	3	0.05	2.56	0	0.00	0.00	0	0.00
Scirtidae (76)	7	0.03	0.90	0	0.00	0.00	0	0.00
Psephenidae (77)	2	0.00	0.25	0	0.00	0.00	0	0.00
Baetidae (78)	51	3.46	57.28	47	1.26	8.65	41	0.85
Caenidae (79)	22	0.12	1.37	43	0.66	3.97	18	0.56
Ephemeridae (80)	10	0.03	0.46	7	0.05	0.96	4	0.50
Odonata (81)	30	0.22	2.39	4	0.02	0.57	3	0.18
Corixidae (82)	4	0.01	0.34	2	1.33	80.17	0	0.00
Notonectidae (83)	47	3.44	53.16	12	0.14	1.99	9	0.31
Veliidae (84)	6	0.05	1.92	0	0.00	0.00	0	0.00
Mesoveliidae (85)	5	0.01	0.23	0	0.00	0.00	0	0.00
Gerridae (86)	15	0.08	1.52	0	0.00	0.00	0	0.00
Belastomatidae (87)	13	0.07	1.92	0	0.00	0.00	0	0.00
Pleidae (88)	12	0.03	0.51	0	0.00	0.00	0	0.00
Hydrometridae (89)	2	0.00	0.19	0	0.00	0.00	0	0.00
Neuroptera (90)	2	0.01	0.32	0	0.00	0.00	0	0.00

	Live	Relative abundance		Fossil	Relative abundance		Sites	
	Sites	Mean	Max	Sites	Mean	Max	in common	S'
Acari								
Macropylina type (91)	41	1.35	50.00	38	0.65	9.52	24	0.62
Pterogasterina (92)	7	0.03	0.49	2	0.02	0.64	1	0.22
Acari (93)	54	4.82	31.67	26	0.46	9.52	23	0.58
Neorhabdocoela								
Neorhabdocoela - Type 1 (94)	-	-	-	46	1.10	8.63	0	-
Neorhabdocoela - Type 2 (95)	-	-	-	3	0.02	0.72	0	-
Bryozoa								
Plumatella sp. (96)	6	0.45	16.14	41	2.13	25.08	6	0.26
Lophopodella cf. *carteri* (97)	0	0.00	0.00	2	0.02	0.88	-	-
Mollusca								
Gabbiela kichiwambae (98)	16	0.37	6.90	0	0.00	0.00	0	0.00
Melanoides tuberculata (99)	8	0.08	3.10	0	0.00	0.00	0	0.00
Pila wernei (100)	2	0.01	0.75	0	0.00	0.00	0	0.00
Biomphalaria sudanica (101)	27	0.26	2.88	2	0.00	0.21	2	0.13
Bulinus forkalis (102)	3	0.00	0.14	0	0.00	0.00	0	0.00
Bulinus tropicus (103)	8	0.07	0.96	0	0.00	0.00	0	0.00
Bulinus truncatus (104)	6	0.10	5.56	0	0.00	0.00	0	0.00
Bulinus ugandae (105)	6	0.02	0.43	0	0.00	0.00	0	0.00
Bulinus unident. juveniles (106)	8	0.01	0.37	0	0.00	0.00	0	0.00
Lymneae natalensis (107)	11	0.05	1.11	0	0.00	0.00	1	0.14
Segmentorbis angustus (108)	6	0.02	0.65	0	0.00	0.00	0	0.00
Sphaerium victoriae mohasicum (109)	3	0.00	0.15	0	0.00	0.00	0	0.00
Vertebrata								
Fish (110)	25	1.64	43.98	29	1.08	17.69	13	0.49
Anura (111)	18	0.24	8.33	0	0.00	0.00	0	0.00
Thecamoeba								
Centropyxis sp. (112)	53	13.67	69.71	22	1.03	26.62	21	0.57
Difflugia sp. (113)	34	2.61	44.30	2	0.15	7.55	2	0.11
Arcella discoides (114)	51	8.69	70.84	36	1.41	18.72	33	0.78
Arcella vulgaris (115)	33	2.14	50.47	12	0.55	24.46	10	0.47
Arcella costata (116)	6	0.05	1.04	0	0.00	0.00	0	0.00
Arcella gibbosa (117)	9	0.60	26.81	2	0.03	1.44	1	0.18
Arcella dentata (118)	9	0.03	0.88	0	0.00	0.00	0	0.00
Lesquereusia sp. (119)	15	0.13	2.53	1	0.01	0.36	0	0.00

The diversity of fossil assemblages is negatively correlated with Dmin, and Z_{core} (Table 3). In the freshwater lake dataset we found a negative correlation between Chl *a* and both living and fossil cladoceran species richness ($r = -0.41$ and $r = -0.37$ respectively, $p<0.01$), as well as the density of cladoceran remains ($r = -0.30$, $p<0.05$; #Clad per gram wet sediment was square root transformed). In our data set, fossil ostracod species richness was negatively correlated with TN ($r=-0.39$, $p <0.005$). The relative abundance of *Chaoborus* remains increases with increasing distance of the core site to the shore ($r=0.41$, $p<0.01$; or $r= 0.51$, $p<0.001$ when chironomids are excluded from the total assemblage), suggesting that *Chaoborus* is the principal fossil representative of the off-shore pelagic environment in our Uganda crater lakes dataset. In addition, the proportion of *Chaoborus* is, on average about two times higher in hypertrophic freshwater lakes than in oligotrophic lakes. This is further illustrated by a positive correlation between the trophic level index (Chl a/Secchi; Plisnier *et al*, in prep.) and the relative abundance of *Chaoborus* ($r= 0.32$, $p<0.05$; only when chironomids are excluded from the total assemblage). In freshwater lakes where both *Chaoborus* and chydorid remains are found, the ratio of *Chaoborus* to chydorids is positively correlated with Dmin (0.38,

$p<0.01$) and Z_{core} (0.38, $p<0.01$), and negatively correlated with #Macrophytes (-0.47, $p<0.001$). No significant correlation is found with any of the trophic level indicators.

Table 3: Pearson's correlation summary statistics for the diversity indices of the live and fossil data set with selected environmental parameters.

	Live dataset		Fossil dataset	
# lakes	56		55	
Average # species per lake (N)	28.9 (12.8)		19.8 (8.3)	
Average Margalef index (M)	4.1 (1.3)		3.4 (1.4)	
Pearson's correlation	Nlive	Mlive	Nfossil	Mfossil
Scond	-0.293*	-0.198	-0.014	-0.070
Secchi	0.280*	0.303*	0.422**	0.291*
Lu_st	0.322*	0.295*	-0.132	-0.146
pH	-0.500***	-0.458***	-0.439***	-0.447**
MAT	-0.058	-0.114	-0.561***	-0.519***
Chl a	-0.293*	-0.263	-0.392**	-0.239
#Macrophytes	0.661***	0.523***	0.260	0.211
Z_{core}	-0.130	-0.125	-0.368**	-0.336*
Dmin	0.158	-0.001	-0.517***	-0.512***

*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$

4.3.3 Multivariate community analysis

Cladocera

DCA of the living Cladocera communities and their fossil counterparts in 44 freshwater lakes produced gradient lengths of 4.9 and 3.5 SD units, respectively, indicating that numerical methods based on unimodal distributions are appropriate. For the living communities, partial CCAs using a single constraining variable indicate that Scond explains the largest amount of variation in this dataset (5.1%). Eight other variables explain a significant part of the total variation (Table 4), including MAT (4.5%), pH (4.4%) and #Macrophytes (4.3%). After exclusion of co-varying variables, we retained six environmental variables, together explaining 23% of the total observed variance in the living Cladocera communities: Scond, pH, MAT, #Macrophytes, Secchi and Z_{core} (F-value: 1.8; $p=0.001$; see also Fig. 4). CCA axis 1, capturing 8.6% of the total variation, represents a gradient in salinity (Scond) and the diversity of aquatic macrophyte habitat (#Macrophytes): dilute freshwater lakes with low pH and abundant aquatic macrophytes are situated in the right quadrants. CCA axis 2, capturing 5.5% of the total variation, represents a gradient from turbid, mostly shallow lakes situated near the bottom of the Rift Valley to deep, more transparent lakes. The pelagic species *Ceriodaphnia dubia* (taxon 24 in Table 2) and *Daphnia laevis* (25) become more important with increasing lake depth. Several taxa, including *Pseudosida szalayi* (1), *Moinodaphnia macleayi* (32), *Oxyurella sengalensis* (19) and *Dunhevedia serrata* (13) are associated with diverse aquatic macrophyte habitats.

For the fossil cladoceran assemblages, partial CCAs using a single constraining variable show #Macrophytes to be the strongest environmental variable. It explains 6.8% of the total variance (Table 4), followed by HA-subm (5.4%), HA-float (4.7%) and pH (4.6%).

Additional statistically significant variables are HA-swamp (4.3%), TN (4.0%) and Dmin (3.7%). Four environmental variables are retained for the CCA, which together explain 14% of the total variance in the fossil cladoceran assemblages: #Macrophytes, pH, TN and Dmin (F-value: 1.6, p=0.001; see also Fig. 4). CCA axis 1 explains 8.7% of the total variation and mostly represents a gradient in #Macrophytes. CCA axis 2, explaining 2.4% of the variance, represents a gradient from large, low-productivity (oligo- to mesotrophic) lakes to small, more acidic and productive (eutrophic) lakes. Cladoceran remains are less frequently recovered from surface sediments located further from the shore (high Dmin values), with the exception of *Moina micrura* (31). As in the living communities, several Chydoridae species such as *Alonella excisa* (7), *Oxyurella sengalensis* (19) and *Dunhevedia serrata* (13) are associated with aquatic macrophyte habitats. Remains of the pelagic *Ceriodaphnia dubia* (24) and *Daphnia laevis* (25) become more important with increasing TN and, to a lesser extent, lake depth (Z_{core}; Fig. 5).

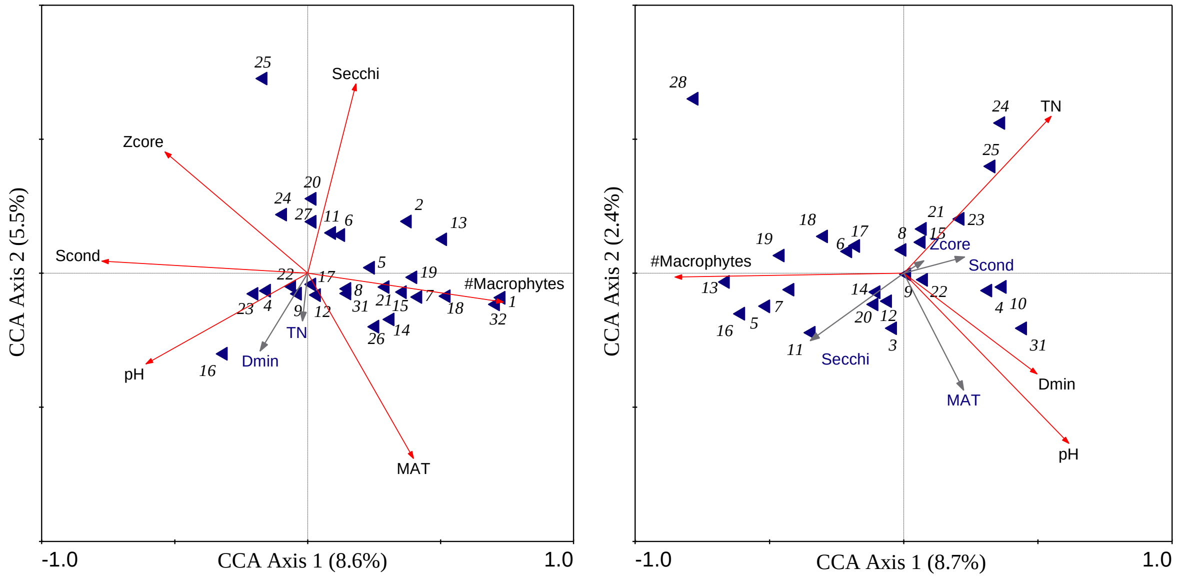

Figure 4: Canonical Correspondence Analysis (CCA) ordination biplot of 44 study sites in Uganda with species scores and major environmental variables A) live cladoceran assemblages B) fossil cladoceran assemblages (supplementary variables indicated in gray)

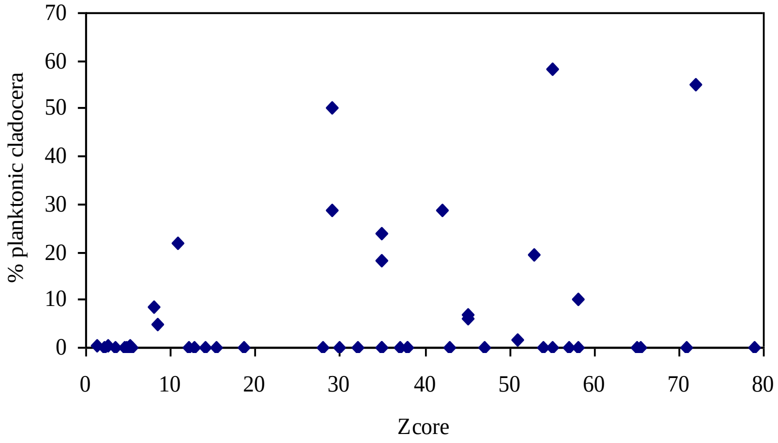

Figure 5: Percentage of planktonic cladocera in subfossil assemblages in the surface sediments of the studied freshwater lakes.

Table 4: Percentage variance explained by each environmental variable in constrained correspondence analyses (CCA) and redundancy analyses (RDA) using a single environmental variable at a time. The significance is based on 999 unrestricted Monte Carlo Permutations ($p<0.05$*, $p<0.01$**, $p<0.001$***). Bold displayed variables were used for CCA/RDA (Fig 7-8).

	Full dataset		Freshwater lakes dataset					
	Various groups		Various groups		Cladocera		Ostracoda	
	LIVE	FOSSIL	LIVE	FOSSIL	LIVE	FOSSIL	LIVE	FOSSIL
	CCA		RDA		CCA		CCA	
	Variance explained (%)							
SA	-	-	-	**5.2	-	-	**4.2	*4.4
MAT	-	*3.5	-	-	**4.5	-	*4.8	**6.2
Scond	***9.3	***18.2	***7.0	**5.9	*5.1	-	***6.7	-
Secchi	-	-	**5.0	-	*3.9	-	-	-
LU_St	-	-	-	-	-	-	-	-
LU_Ag	-	-	-	-	-	-	*3.6	-
LU_Fa	-	-	-	-	-	-	-	-
pH	**5.6	**6.4	***6.5	***7.8	*4.4	*4.6	***6.7	*4.1
SWT	***6.2	***9.8	-	-	-	-	**4.6	-
DO	*3.8	*3.6	-	-	-	-	-	-
TP	***6.2	***11.2	-	-	-	-	-	-
TN	***4.9	***8.1	-	-	-	*4.0	-	*4.7
Chl a	-	-	**6.7	-	-	-	-	*4.2
[TOC]	***5.9	***9.8	-	-	-	-	-	-
[Ca]	-	-	-	-	-	-	*4.5	-
[Mg]	-	-	*3.3	-	*4.2	-	**6.1	-
[Fe]	-	*4.7	-	*5.0	-	-	*4.8	-
[Si]	*3.0	-	**5.5	-	*3.9	-	-	-
#Macrophytes	**4.8	-	***11.9	**6.4	*4.3	***6.8	***7.5	-
HA-sand	-	-	-	-	-	-	***8.9	*5.1
HA-emer	*3.4	*4.5	-	-	-	-	-	-
HA-subm	*3.3	-	***7.5	-	-	***5.4	*4.0	-
HA-float	*3.8	-	***8.6	*4.5	*3.4	**4.7	**5.1	-
HA-swamp	-	-	*4.5	**6.2	-	*4.3	***7.7	-
Z_{core}	-	-	-	-	*3.6	-		*4.0
Wc	*3.7	**5.7	-	-	-	-	-	-
Dmin	-	*4.4	-	**6.4	-	*3.7	**4.9	**6.8

Ostracoda

DCA of the living ostracod communities and their fossil counterparts in the 43 freshwater lakes where both living and fossil ostracods were recovered produced gradient lengths of 3.4 and 3.9 SD units respectively, indicating that numerical methods based on unimodal distributions are appropriate. For the living ostracod communities, partial CCAs using single constraining variables indicate that environmental variables describing the general habitat type (HA-sand, HA-swamp, #Macrophytes, etc.) explain the largest amount of variation. An additional ten variables explain a significant part of the variation in this data set (Table 4). Exclusion of co-varying variables reduces the number of environmental variables to eight, together explaining 37% of the total variance: HA-sand, #Macrophytes, pH, Scond, Dmin, MAT, [Fe], and LU_Ag (F-value: 2.1; p=0.001; see also Fig. 6). CCA axis 1 captures 10.7% of the total variation, and represents a gradient of pH and #Macrophytes, as well as the presence of sandy (including rocky, but not vegetated) littoral habitat. CCA axis 2, which captures 6.9% of the total variation, represents a gradient from mostly shallow lakes with crater basins heavily impacted by human activity to deep, larger and more pristine sites (LU_ag and Z_{core}). *Neozonocypris mirabilis* (43) and *Heterocypris obliqua* (45) are associated with aquatic macrophyte habitat diversity. Few ostracod taxa are found in the more alkaline, often eutrophic or hypertrophic, freshwater lakes (lower left quadrant). Several free-swimming species (*Oncocypris* spp., 58-60 and *Physocypria capensis*, 42) are positively correlated with Dmin.

For the fossil ostracod assemblages, partial CCAs using single constraining variables indicate that Dmin is the most important environmental variable. It explains 6.8% of the total variance in the dataset (Table 4), followed by MAT (6.2%), HA-sand (5.1%), TN (4.7%), SA (4.4%), Chl *a* (4.2%), pH (4.1%) and Z_{core} (4.0%). Here six environmental parameters are retained, which together explain 24% of the total variance: Dmin, MAT, HA-sand, TN, pH and Z_{core} (F-value: 1.8, p=0.001; Fig. 6). CCA axis 1 explains 8.3% of the total variation and mostly represents a gradient in Dmin, MAT and TN. As seen in the PCA of freshwater lakes (Fig. 3), large and productive lakes crater lakes are often situated near the floor of the Rift Valley, while deeper, less productive lakes are situated in the colder, sub-humid shoulders. CCA axis 2 captures 5.8% of the variance. It is determined by the presence or absence of non-vegetated (sandy or rocky) littoral habitat, and also represents a gradient from deep, more alkaline lakes to small, more acidic lakes with diverse aquatic macrophyte habitat. Remains of most ostracod species are most common in the surface sediments of lakes in the northern district, and are more likely to be found in samples taken close to shore. With the exception of the rare *Stenocypris curvirami* (62; 2 lakes) and *Martenscypridopsis pygmaea* (52; 2 lakes), the distribution of most fossil ostracod taxa was negatively correlated with distance to shore (Dmin). However, a few taxa (e.g. *Oncocypris* sp. type Katanda (59*)*, *Strandesia* juvenile type Ekikoto (61) and *Sarscypridopsis elizabethae* (55) display a notable positive correlation with Z_{core}.

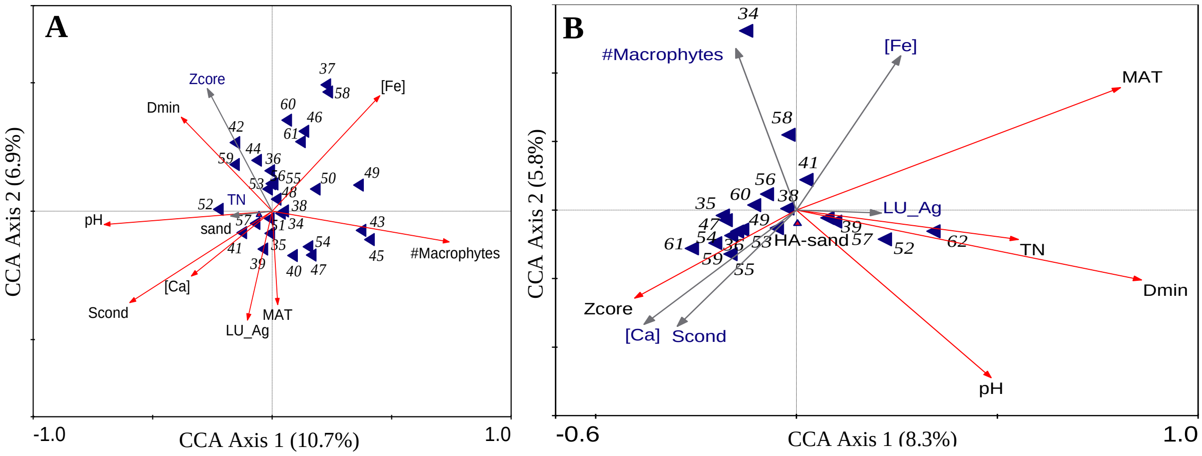

Figure 6: Canonical Correspondence Analysis (CCA) ordination biplot of 43 study sites in Uganda with species scores and major environmental variables A) live ostracod assemblages B) fossil ostracod assemblages (supplementary variables indicated in gray).

Aquatic insects and other invertebrate taxa

DCA of the living communities and corresponding fossil assemblages of aquatic insects and the various other groups of studied invertebrates in 60 lakes reveal gradient lengths of 4.0 and 3.0 SD units, respectively; hence we apply numerical methods based on unimodal distributions. For the living communities, partial CCAs with single constraining variables select 13 significant environmental variables. Excluding the strongly covarying variables reduces this number to five: Scond, #Macrophytes, HA-emer, DO, and [Si]. The resultant CCA explains 18.1% of the total variance (F-value: 2.4; p= 0.001; see also Fig. 7). CCA axis 1 captures 10.3% of the total variation and represents the salinity gradient. As in the PCA (Fig. 7), freshwater lakes are clustered together near the centre of the ordination biplot, whereas all six hypersaline lakes are situated near the far right end of axis 1. CCA axis 2, which explains 4.2% of the total variation, mainly represents a gradient in the diversity of aquatic macrophyte habitat. As already evident in univariate analysis, several aquatic Diptera such as *Culex* sp. (64), *Culicoides* sp. (68), *Dashylea* type (66), Stratiomyidae (69) and *Ephydrella*-type (70) are strongly associated with elevated salinity. Bryozoa, Mollusca and Thecamoeba are encountered only in the freshwater lakes.

Partial CCAs of the fossil assemblages, using single constraining variables, show that salinity (Scond) explains 18.2% of the total variance (Table 4). Eleven other variables also explain a significant part of the variation, among which are TP (11.2%), SWT (9.8%), HA-emer (4.5%) and Dmin (4.4%). Five environmental variables are retained for the CCA, together explaining 28.1% of the total variance: Scond, DO, [Fe], HA-emer and Dmin (F-value: 4.2, p=0.001; see also Fig. 7). CCA axis 1, which captures 21.5% of the total variation, mostly represents a gradient in Scond and HA-emer. CCA axis 2, which explains 4.5% of the variance, is mainly determined by [Fe] and Dmin. Similar to the living communities, several aquatic Diptera (*Culex* sp. (64), Stratiomyidae (69), *Ephydrella*-type (70)) are strongly associated with hypersaline lakes. Since in both data sets the majority of taxa are restricted to freshwater lakes, we also performed multivariate analysis on the freshwater lakes separately.

For the 55-lake freshwater dataset, DCA of the living communities and corresponding fossil assemblages revealed gradient lengths of 2.9 and 1.6 SD units respectively, indicating that in this case numerical methods based on linear distributions are most appropriate. For the living communities, partial RDAs using single constraining variables indicate that #Macrophytes, Scond, Chl a and pH explain most of the variation (respectively 11.9%, 7.0%, 6.7% and 6.5%). All four environmental parameters are retained for the RDA, and then together explain 23.3% of the total variance (F-value: 3.8, p=0.001; see also Fig. 8). CCA axis 1, capturing 17.2% of the total variation, represents a gradient in #Macrophytes and Chl a. CCA axis 2 captures a mere 3.1% of the variance, and is mainly determined by #Macrophytes, Scond and pH. The percent abundance of Chironomidae (72), *Chaoborus* (63) and fish remains (110) are all positively correlated with Chl a. Most Thecamoeba taxa (112-119) are positively correlated with #Macrophytes and negatively correlated with Scond.

Partial RDAs of the fossil assemblages using single constraining variables indicate that here pH explains the largest amount of variation (7.8%). Seven other variables explain a significant part of the variation, including Dmin (6.4%), #Macrophytes (6.4%) and Scond (5.9%) (Table 4). RDA with the five retained environmental variables (#Macrophytes, pH, Dmin, Scond, and [Fe]) explains 20.9% of the total observed variance (F-value: 2.6; p= 0.001; see also Fig. 8). RDA axis 1 captures 12.9% of the total variation, and represents a gradient of aquatic macrophytes, pH and Dmin. RDA axis 2 explains 4.7% of the total variation, and is mainly determined by Scond and [Fe]. Remains of several taxa (including Baetidae (78), Macropylina type (91), *Arcella discoides* (114) and *Plumatella* sp. (96)) are more abundant in the more dilute lakes where aquatic macrophyte diversity is high. Again, *Chaoborus* (63) and fish remains (110) but also Notonectidae (83) are positively correlated with Chl a, and with Dmin.

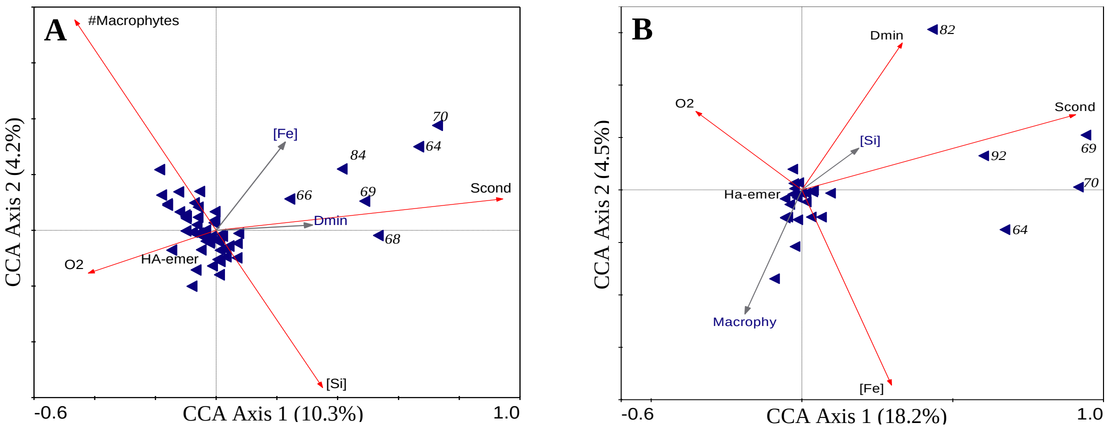

Figure 7: Canonical Correspondence Analysis (CCA) ordination biplot of 60 study sites in Uganda with species scores and major environmental variables A) live assemblages of aquatic insects and various other groups B) fossil assemblages (supplementary variables indicated in gray; freshwater taxa illustrated in detail below).

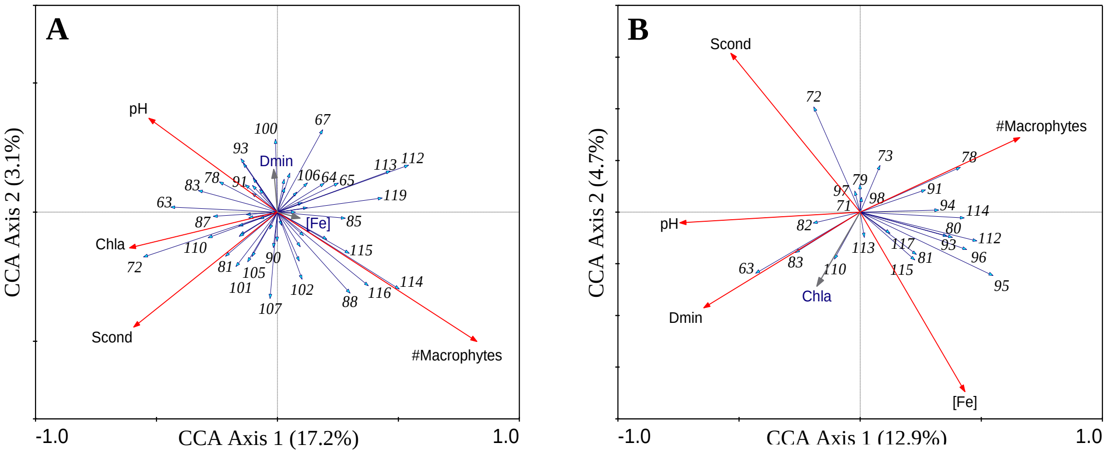

Figure 8: Redundancy Analysis (RDA) ordination biplot of 55 freshwater study sites in Uganda with species scores and major environmental variables A) live assemblages of aquatic insects and various other groups B) fossil assemblages (supplementary variables indicated in gray).

4.4 Discussion

4.4.1 *Taphonomy: the relationship between living communities and fossil assemblages*

Many taxa identified in our survey of the living aquatic communities of Ugandan crater lakes were not recovered from the recent death assemblages of those same lakes. In total 37 of the 111 taxa (33%) that were encountered in the living fauna of at least two lakes were not encountered in the sediments. This can be due to a number of different reasons, acting individually or in combination. Firstly, failure to find the remains of certain taxa in the fossil assemblages could be due to incomplete analysis of the aquatic invertebrate remains present in the sediment, as some remains are not sufficiently diagnostic to be identified, or are too small (e.g., postabdominal claws and mandibles of pelagic Cladocera) to be systematically recovered from the >150 µm residue. Secondly, successful recovery of a taxon from the fossil assemblage clearly depends upon its abundance in the living fauna. For example, aquatic beetle larvae and most aquatic Hemiptera were widely distributed among lakes (respectively 17 and 55 out of 60 lakes) but tended to occur in low numbers, and their remains were rare in fossil assemblages (14 lakes only). The combined abundance of all taxa that were not recovered from the surface sediments comprised less than 2% of the total living fauna. Thirdly, sediment-transportation processes (sediment focusing, erosion and redeposition) prior to permanent burial influence surface-sediment fossil assemblages by introducing taxa derived from terrestrial and nearshore aquatic environments to the offshore sediment record (Anderson, 1990, Hoffman 1998). Complete numerical integration of littoral and pelagic communities is rare (Frey, 1988), even in small and shallow lakes (Heiri, 2004; Eggermont et al., 2007b). Distance from shore and mean bottom slope of the lake basin were previously found to be critical in the contribution of littoral species to fossil assemblages (Kansanen, 1986). Also in our Ugandan dataset, the taxon similarity between the living communities and offshore fossil assemblages in individual lakes was significantly negatively correlated with the distance to shore ($r=-0.36$, $p < 0.01$). Also similar to results reported by Frey (1988) and Jeppesen *et al.* (2001), the proportion of planktonic to benthic taxa in fossil cladoceran assemblages increased with lake depth. Fourth, size and weight of the remains also plays a key role. For example, the shells of heavy, large-bodied littoral biota such as gastropods were very rarely encountered in the fossil assemblages of offshore surface sediment (only two juvenile shells and one operculum). However, additional screening of near-shore surface sediments in three study lakes (Kyaninga, Mbajo and Bugwagi) revealed numerous gastropod shell fragments (Rumes, unpublished data). Freshwater molluscan fossil assemblages can accurately reflect the local living community, but this requires selection of a near-shore sediment sequence and large sample volumes (up to 10,000cm^3; Cummins, 1994; Miller & Tevesz, 2001). These requirements are often incompatible with the need for a continuous palaeo-environmental record, and availability of only a single, small-diameter sediment core for analysis. On the other hand, ‘shell lag’ facies in the sediment record of climate-sensitive lakes are solid indicators of former lowstands (De Deckker, 1988). Finally, dissolution and fragmentation of remains during transport before burial causes bias towards preservation of taxa with skeletal elements more resistant to chemical or physical destruction. For example, preservation of thecamoeban tests differs among taxa, and in our dataset the fossil remains of larger, more robust taxa (e.g., *Arcella discoides, A. vulgaris* and *Centropyxis* sp.- S': 0.8, 0.5 and 0.6 respectively) better reflect their distribution in the living fauna than smaller (e.g., *Lesquereusia* sp., *Difflugia* sp.- S': 0.0 and 0.1 respectively) or possibly more fragile taxa (e.g., *A. dentata* – S':0.0) (Beyens & Meisterfeld, 2001; Table 2). Inversely, some taxa were far more common in the fossil assemblages than in our samples of the living community. These include the statoblasts (resting stages) of the sessile, colonial bryozoans *Plumatella* sp. and *Lophopedela* cf. *carteri,* the free-swimming ostracod *Oncocypris worthingtoni* and the phantom midge *Chaoborus* sp.. Sessile colonial bryozoans were not adequately sampled by repeatedly sweeping a 50-µm mesh net across planktonic and epibenthic habitat and were underrepresented in the dataset of the live community. The pelagic *Chaoborus* may have actively migrated to the hypolimnion during daytime, which reduced the chance of *Chaoborus* being sampled. In lakes with strong seasonal or interannual fluctuation of abiotic conditions, temporal integration of lake biota during burial in the sediments can result in mixed or 'incongruous' (Gasse *et al.,* 1997) fossil assemblages composed of species that normally do not occur together in the living community. This may explain why, in saline lakes, fossil assemblages in the surface sediment were on average more diverse than the living community sampled at the same time. The combination of temporal and spatial integration of lake biota in sediments is also the reason why in most lakes an analysis of fossil remains in surface sediments provides a more complete picture of local species richness in the chydorid Cladocera than extensive live sampling (Frey, 1960; Kattel *et al.*, 2007; Davidson *et al.*, 2007). Also in our Uganda cater lake dataset, fossil remains of chydorid Cladocera and *Bosmina* indicate a wider distribution of species than analysis of the living fauna would suggest. However, substituting field surveys with analyses of fossil assemblages in biodiversity studies is only appropriate for biota of which fossil remains can be identified to species.

Analysing larger sediment samples would probably increase the fraction of species encountered both in the living community and in the fossil assemblages. However, this would probably not greatly influence the overall relative abundance of major groups, as on average >400 fossil remains were identified per lake. Ostracoda, in particular, would probably have been better represented in the fossil assemblages if a larger sediment volume were screened: in our current analysis, only about half of lakes (31out of 56) yielded more than 20 ostracod valves (i.e. in 25 of the 56 lakes, 20 valves or less were recorded). Recovery of the minimum of 100 valves preferred for diversity analysis would often have required screening >50ml of sediment, a volume that is rarely available in multi-proxy analysis of lake-sediment cores. On the other hand, most low-yield lakes which we studied are large, stratified and have anoxic hypolimnia (18 out of 25 lakes with <20 fossil ostracods). In most cases low fossil ostracod abundance reflects incomplete spatial integration of biota derived from littoral habitat that is quite distant and dynamically separated from the mid-lake sediment sampling site. Indeed, fossils of the free-swimming ostracod *Oncocypris* are more widely distributed among the study lakes than live sampling suggested, whereas large-bodied species such as *Chrissia icosacanthus*, *Acocypris platybasis* and *Stenocypris major* that prefer sheltered shallow-water environments are mostly lacking in the mid-lake surface-sediment samples. Scarcity of non-free-swimming ostracod species in fossil samples is thus indicative of lake highstands, when mid-lake sediments are dominated by the fossils of biota living in the open-water environment.

It should be noted that two taxa, *Macrothrix triserialis* and *Heterocypris obliqua*, which were recovered both from the live fauna and the fossil assemblage, had to be excluded from the analyses as their particular distribution in the surface sediments (alternatively dominant or absent) precluded numerical analyses of the cladoceran and ostracod assemblages respectively. In the case of Macrothricidae, preservation of valves is known to be irregular (Frey, 1988). The absence of Macrothricidae valves in downcore analysis of African lake sediments (e.g. see Chapter 5 & 7) may indicate that Macrothricidae remains are limited to the most recently deposited surface sediments. In the case of *Heterocypris obliqua* the problem is caused by the fact that it is the only ostracod taxon recovered from the surface sediment of Lake Kako resulting in 100% relative abundance.

4.4.2 What fossil invertebrate assemblages reveal about the past lake environments

The two environmental variables most strongly structuring fossil cladoceran assemblages in our collection of 44 freshwater Ugandan crater lakes are the diversity of aquatic macrophyte habitat and pH. Surface-water conductivity, mean annual temperature, lake depth and [Mg] do not seem to significantly influence species distribution in fossil assemblages, although they were found to influence species distribution in the living communities. This reflects, first of all, the effect of differential preservation, since fossil remains of planktonic Cladocera (predominantly ephippia) were rare compared with remains of benthic chydorids (various diagnostic exoskeletal components besides ephippia; cf. Leavitt *et al.*, 1989; Davidson *et al.*, 2007). In these wind-sheltered tropical crater lakes, both seasonal and more permanent stratification rapidly lead to deoxygenation of the deeper water column, preventing development of a deepwater zoobenthos community. As a result, mid-lake fossil benthos assemblages will always be dominated by the near-shore community irrespective of lake size or depth (cf. Hofmann 1987), and thus reflect the habitat features that control species diversity and composition in that near-shore community. Consequently, the effect of lake size on the degree of spatial habitat integration is relatively modest.

Most ostracod species were encountered in fewer lakes as fossil than they were in the living fauna (Table 2). Bottom pH is lower than 7 in 31 of the lakes, raising the possibility that dissolution of the low Mg-calcite ostracod valves in corrosive bottom or interstitial waters prior to permanent burial may be responsible. No significant correlation was found between bottom pH and fossil ostracod yield or species richness. As discussed above our data suggests that transportation/sedimentation issues rather than dissolution are responsible, with their effects becoming increasingly significant in larger lakes. The environmental variables most strongly structuring fossil ostracod assemblages are the presence of sandy or muddy littoral habitat (HA-sand), mean annual temperature, pH, total nitrogen concentration, and the lake-size dependent variables depth and distance to shore (Fig 6). The same variables plus [Ca] and [Mg] structure the distribution of living ostracod species in our African lake data set. These latter are known to structure ostracod distribution in temperate regions (Bunbury & Gajewski, 2005; Viehberg, 2006). The effect of [Mg] is likely secondary since it is no longer significant when Scond is used as covariable. Scond, on the other hand, explains a significant, unique and independent part of the variation in this freshwater data set. That TN explains a significant part of the variation may be related to the fact that in our data set, fossil ostracod species richness is negatively correlated with TN. Lakes with high TN values are typically dominated by phytoplankton rather than aquatic macrophytes, resulting in an overall lower structural diversity in the more productive lakes. That both site depth and distance to shore significantly structure the fossil ostracod assemblage illustrates again the impact of pre-burial transportation dynamics. One would expect the relative abundance of the relatively common and free-swimming *Oncocypris* spp. to be positively related to lake size. However, due to the strong negative correlation of *Oncocypris* spp. with lake trophic state, no positive relationship with lake size was found (as lake size and trophic state are positively correlated in our dataset). Overabundance of *Z. costata* in both the living community and fossil assemblages from most sites is the result of this species' ability to tolerate a wide range of environmental conditions (Rumes, previous chapter). It is often the only ostracod species recovered from the sediment of eutrophic and hypertrophic lakes, although it is found in the highest densities in association with aquatic macrophytes (Rumes previous chapter; Verschuren *et al*, 2000b).

The environmental variables most strongly structuring the multi-group community of aquatic insects, Bryozoa, Thecamoeba, Mollusca and others (Table 4) are surface-water salinity, surface-water temperature, lake trophic state and the diversity of aquatic macrophyte habitat. The same variables also structure the fossil assemblages, with addition of the distance to shore. As noted in other studies, larvae of various groups of aquatic diptera dominate both the live and fossil fauna of the saline lakes (Hammer, 1986; Stephens, 1990; Rumes, 2005). Remains of *Culex* sp. (64), *Ephydrella* type (70), *S*tratiomyidae (69), as well as the hemipteran Corixidae (82) and the oribatid Pterogasterina (92) constitute a major part of the fossil assemblages in saline lakes while being much less abundant in freshwater lakes (Table 2). Freshwater lakes were inhabited by a much more diversified invertebrate fauna including Trichoptera (73), several Ephemeroptera (78-80), Neorhabdocoela (94-95), Gastropoda (98-108) and Thecamoeba (112-119). During the survey of the living fauna, many taxa, especially the gastropods, insects and *Plumatella* sp. (96), were found clinging to or living between submerged or emergent macrophytes. As in previous studies (e.g. Crisman *et al.*, 1986), fossil *Plumatella* abundance in the surface sediments appears to be determined by the relative local availability of such suitable substrates (Wiebach, 1980; Wood, 1991). Aquatic macrophytes provide an important food source and habitat for many species, and may also provide shelter or escape from predation (Merritt & Cummins, 1984). This explains why the raw diversity of aquatic macrophyte habitat (i.e., the number of different aquatic macrophyte associations; see Lebrun et al. (in prep.) explains a significant part of the variation in both the living communities and fossil assemblages of freshwater Ugandan crater lakes. Several Thecamoeba species, *Plumatella* sp (96), and the ephemeropteran family Baetidae (78) are distinctly more frequently encountered in lakes with diverse aquatic macrophyte habitat. In addition, living freshwater communities are significantly influenced by salinity, pH and also Chl *a*, suggesting direct or indirect influence of lake trophic status. In the overall fossil assemblages the effect of Chl *a* is no longer significant, however. We tentatively suggest that temporally integrated fossil assemblages perhaps lose the effect that seasonally increased Chl *a* has on the living community. Instead, as with the ostracods, distance to shore becomes an important additional explanatory variable.

Fossil *Chaoborus* mandibles, the only remains of pelagic insects identified in this study, were recorded in the fossil assemblages of all freshwater lakes (except Lake Kyogo, but there a single juvenile specimen was found in the living zooplankton). These predatory insect larvae benefit themselves from the presence and size of the hypolimnetic refugium to escape visual predation by fish (e.g. Borkent, 1981; Rine & Kesler, 2001; Rumes, 2005). The abundance ratio of *Chaoborus* to chydorid Cladocera in fossil assemblages is positively related to the site’s depth and distance to shore, since this determines the relative importance of pelagic versus littoral habitat (see Appendix 3). It is also negatively related to the diversity of aquatic macrophyte habitat, since this influences the diversity and abundance of littoral chydorid Cladocera. We therefore propose that in the sediment records of climate-sensitive African crater lakes, this ratio can be used to trace changes in lake depth through time. The relative abundance of *Chaoborus* in mid-lake fossil assemblages is higher in more productive freshwater lakes than in less productive lakes, which may indicate that their capacity to co-exist with zooplanktivorous fish is improved by the decrease in transparency associated with high algal biomass (Wissel et al., 2003). We therefore propose that in the sediment records of climatically stable African crater lakes, or over suitably short historical periods in climate-sensitive lakes, *Chaoborus* percent abundance can be used to trace through time the effect of cultural eutrophication on water quality.

In conclusion, the presence and relative abundance of individual aquatic invertebrate taxa in the fossil assemblages recovered from African crater lake sediments depends on their presence and relative abundance in the local living community (determined by habitat preference and tolerance to variation in abiotic conditions), on their potential to produce diagnostic, readily identifiable fossil remains (determined mostly by the nature of skeletal structures), and on local taphonomic processes (e.g. transportation, dissolution, sedimentation). Fossil remains of chydorid Cladocera, free-swimming ostracods, various dipteran larvae, Ephemeroptera, Bryozoa, Acari and the larger species of Thecamoeba recovered from mid-lake sediments reflect their distribution in the study area’s lake communities quite accurately. Fossil assemblages of non-free-swimming ostracods; various littoral aquatic insects, and molluscs in mid-lake sediments are less representative, mostly due to more limited pre-burial transport away from the littoral habitat they live in. A strong salinity gradient clearly influences the studied groups, as there are only a limited number of characteristic taxa that are encountered at conductivities higher than 5000µS/cm. In freshwater Ugandan crater lakes, the species composition of both living and fossil assemblages is strongly determined by pH and the presence and diversity of aquatic macrophyte habitat. The effect of lake trophic status on chydorid Cladocera (both living and fossil assemblages) may be an indirect effect of high algal biomass causing low transparency and die-off of submerged aquatic macrophytes. For all studied groups, the composition of fossil assemblages is influenced by lake depth at the core site and/or the distance of the core site to shore, which reflect how much post-mortem transport is needed to deliver dead invertebrate remains at the mid-lake core site (Table 4). As such, a good knowledge of basin morphometry and potential changes therein due to past lake-level fluctuation will be essential to correctly infer past environmental changes from mid-lake fossil assemblages.

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Appendix 1

Correlation table

	SA	Zmax	MAT	Scond	Secchi	LU_St	LU_Ag	LU_Fa	pH	SWT	DO	TP	TN	Chl a	[TOC]	[Na]	[K]	[Ca]	[Mg]	[Sr]	[Ba]	[Fe]	[Mn]	[P]	[S]	[Si]	[F]	[Cl]	[DIC]	Macrophytes	sand	emer	subm	float	swamp	Zcore	Wc	Omc
Zmax	0.029																																					
MAT	***0.480	**-0.4291																																				
Scond	0.241	-0.152	***0.438																																			
Secchi	0.040	***0.642	*-0.312	*-0.259																																		
LU_St	0.097	-0.151	**0.348	*0.321	0.038																																	
LU_Ag	-0.016	0.004	-0.136	*-0.276	-0.205	***-0.8588																																
LU_Fa	-0.176	*0.297	***-0.463	-0.181	*0.262	***-0.603	0.112																															
pH	***0.547	-0.142	***0.579	***0.612	*-0.298	0.103	-0.005	-0.175																														
SWT	**0.390	***-0.422	***0.749	***0.649	-0.232	***0.479	*-0.313	***-0.437	***0.574																													
DO	0.180	0.115	-0.161	-0.222	-0.138	-0.202	**0.3486	-0.174	-0.021	-0.227																												
TP	-0.004	*-0.266	**0.402	**0.400	-0.217	0.143	-0.061	-0.175	0.093	**0.372	*-0.270																											
TN	*0.296	-0.240	**0.389	0.249	**-0.347	0.152	-0.022	*-0.275	*0.271	**0.375	0.158	***0.455																										
Chl a	0.160	**-0.400	***0.445	0.226	***-0.573	0.081	0.031	-0.217	***0.497	*0.290	0.093	*0.341	**0.411																									
[TOC]	0.187	**-0.385	***0.488	***0.586	***-0.516	**0.336	-0.152	**-0.414	**0.416	***0.586	-0.136	***0.427	***0.518	***0.482																								
[Na]	*0.258	*-0.273	***0.567	***0.895	*-0.287	*0.263	-0.181	-0.220	***0.659	***0.721	-0.238	***0.429	**0.350	**0.373	***0.652																							
[K]	*0.315	*-0.269	***0.567	***0.870	-0.241	0.238	-0.127	-0.250	***0.693	***0.710	-0.208	**0.419	*0.280	**0.351	***0.615	***0.947																						
[Ca]	**-0.387	0.115	***-0.439	-0.073	0.023	-0.248	-0.008	***0.484	-0.227	**-0.407	0.106	0.088	-0.072	0.016	*-0.319	-0.216	-0.228																					
[Mg]	-0.016	0.217	0.051	*0.288	0.099	-0.128	-0.017	*0.285	0.256	0.014	-0.021	0.000	-0.246	0.085	*-0.256	0.240	*0.289	**0.388																				
[Sr]	-0.174	***0.467	-0.227	0.194	*0.311	-0.158	-0.097	***0.466	0.018	-0.254	-0.071	-0.058	*-0.290	-0.166	**-0.377	0.050	0.042	***0.593	***0.779																			
[Ba]	*-0.295	**0.351	-0.236	*0.286	0.172	0.091	-0.245	0.204	-0.119	-0.133	-0.151	0.134	-0.108	-0.134	-0.062	0.131	0.074	***0.433	0.427	***0.762																		
[Fe]	0.008	*-0.302	0.193	0.104	*-0.277	0.244	-0.127	*-0.292	-0.020	*0.275	0.002	-0.169	0.004	*0.321	**0.403	0.163	0.130	*-0.315	*-0.299	**-0.394	-0.163																	
[Mn]	-0.021	-0.193	0.095	0.117	*-0.283	0.168	-0.145	-0.122	0.001	0.141	-0.025	0.043	-0.012	**0.354	*0.305	0.043	0.034	0.045	-0.052	-0.110	0.063	***0.680																
[P]	0.045	-0.207	***0.493	***0.613	-0.171	0.245	-0.092	*-0.319	*0.302	***0.542	**-0.340	***0.762	0.220	*0.261	***0.612	***0.588	***0.619	-0.091	-0.005	-0.042	0.168	0.164	0.184															
[S]	0.096	*-0.258	**0.340	***0.470	-0.229	0.094	-0.112	0.014	**0.358	***0.521	-0.181	0.167	**0.393	0.165	***0.463	***0.530	***0.447	-0.157	-0.138	-0.194	-0.133	0.176	-0.103	*0.309														
[Si]	0.080	0.062	*0.282	**0.382	-0.106	-0.018	-0.074	0.149	*0.325	0.110	0.096	0.211	0.254	0.153	0.173	**0.351	*0.303	0.245	0.217	0.249	0.235	-0.036	0.053	0.238	0.201													
[F]	0.047	0.153	0.199	***0.839	-0.059	0.138	*-0.268	0.157	***0.443	**0.395	-0.208	0.129	0.035	0.110	**0.362	***0.736	***0.664	0.146	***0.502	***0.535	***0.591	-0.017	0.072	***0.454	***0.506	***0.454												
[Cl]	**0.365	*-0.259	***0.619	***0.849	*-0.297	0.202	-0.076	*-0.273	***0.704	***0.728	-0.211	***0.559	***0.482	**0.398	***0.664	***0.923	***0.918	-0.255	0.155	-0.049	0.057	0.091	0.023	***0.676	***0.501	*0.314	***0.661											
[DIC]	0.229	-0.172	**0.428	***0.947	*-0.264	0.231	-0.199	-0.131	***0.668	***0.642	-0.219	**0.382	*0.335	*0.339	***0.609	***0.929	***0.916	-0.068	*0.331	0.161	0.251	0.135	0.150	0.632	***0.578	**0.424	***0.842	***0.892										
Macrophytes	*-0.291	-0.063	-0.163	*-0.323	0.149	0.247	-0.170	-0.207	***-0.490	-0.151	-0.037	0.060	-0.256	*-0.275	-0.207	**-0.357	**-0.335	-0.071	-0.202	-0.103	0.079	0.103	-0.043	-0.043	-0.208	*-0.271	*-0.304	**-0.401	**-0.358									
sand	0.157	0.055	-0.133	0.179	-0.135	-0.132	0.052	0.170	**0.383	-0.027	0.219	-0.093	0.202	0.149	-0.019	0.024	0.074	*0.265	-0.053	0.058	0.028	-0.236	-0.147	-0.092	0.229	0.220	*0.277	0.139	*0.278	*-0.317								
emer	-0.099	0.024	-0.182	***-0.462	0.013	***-0.433	*0.290	**0.376	*-0.265	**-0.363	0.221	-0.118	0.040	-0.044	**-0.343	*-0.329	**-0.351	*0.290	0.061	0.086	-0.052	-0.177	-0.186	**-0.422	-0.064	0.140	-0.254	**-0.354	**-0.385	0.191	0.013							
subm	-0.178	0.049	-0.135	-0.220	0.231	*0.260	*-0.279	-0.073	*-0.275	-0.105	-0.103	0.039	*-0.282	-0.239	*-0.283	*-0.262	-0.196	-0.046	-0.011	0.015	0.147	0.085	0.041	-0.098	*-0.295	-0.161	-0.196	*-0.298	-0.231	***0.756	-0.251	0.199						
float	*-0.301	-0.111	-0.222	*-0.309	0.027	0.130	-0.042	-0.174	***-0.466	-0.156	0.082	-0.005	-0.138	-0.191	-0.092	**-0.349	**-0.347	0.010	*-0.275	-0.114	0.057	0.027	-0.051	-0.073	-0.094	*-0.307	*-0.274	**-0.361	**-0.360	***0.755	-0.143	0.148	0.243					
swamp	-0.157	-0.102	0.043	-0.180	0.052	0.150	-0.018	*-0.256	**-0.366	-0.062	-0.070	0.124	-0.125	-0.172	-0.048	-0.163	-0.199	-0.157	-0.186	-0.167	-0.070	0.141	-0.117	0.130	-0.029	-0.114	-0.226	-0.213	-0.212	***0.732	**-0.357	0.049	**0.372	**0.429				
Zcore	-0.042	***0.688	***-0.498	-0.236	***0.453	-0.250	-0.022	***0.524	-0.188	***-0.4395	0.044	**-0.391	**-0.393	**-0.382	***-0.495	*-0.325	**-0.347	0.235	0.232	**0.350	0.079	-0.240	-0.078	***-0.478	-0.219	-0.022	0.016	**-0.359	-0.252	-0.152	-0.018	0.016	0.014	-0.124	*-0.296			
Wc	-0.235	-0.052	-0.197	***-0.549	-0.005	-0.036	0.044	-0.013	*-0.284	**-0.380	0.055	-0.102	0.071	0.063	*-0.282	**-0.408	***-0.421	0.020	-0.039	-0.094	-0.138	-0.247	-0.117	***-0.496	**-0.400	***-0.454	***-0.501	**-0.383	***-0.512	0.189	-0.138	*0.292	0.170	0.180	0.040	0.033		
Omc	-0.212	*-0.297	-0.107	*-0.256	-0.153	0.175	-0.085	-0.208	-0.134	-0.164	0.165	-0.040	0.177	0.136	0.010	-0.174	-0.212	0.088	-0.168	-0.118	0.002	-0.039	-0.020	-0.255	-0.171	-0.165	*-0.328	-0.232	-0.256	**0.347	-0.011	*0.283	0.226	*0.327	0.214	**-0.402	***0.622	
Dmin	***0.711	-0.137	***0.589	***0.508	-0.186	**0.369	-0.184	**-0.427	***0.548	***0.542	0.121	0.201	**0.416	0.237	**0.369	**0.415	***0.450	**-0.399	-0.093	*-0.301	*-0.291	-0.036	-0.027	0.244	0.138	0.099	0.128	***0.518	**0.380	-0.197	0.092	*-0.331	-0.102	-0.233	-0.101	-0.164	-0.243	-0.206

*:$P < 0.05$

**: $P < 0.01$

***: $P < 0.001$

Appendix 2

Correlation table

	SA	Zmax	MAT	Scond	Secchi	LU_St	LU_Ag	LU_Fa	pH	SWT	DO	TP	TN	Chl a	[TOC]	[Na]	[K]	[Ca]	[Mg]	[Sr]	[Ba]	[Fe]	[Mn]	[P]	[S]	[Si]	[F]	[Cl]	[DIC]	Macrophytes	sand	emer	subm	float	swamp	Zcore	Wc	Omc
Zmax	0.111																																					
MAT	**0.405	**-0.362																																				
Scond	-0.053	0.191	0.005																																			
Secchi	0.119	***0.619	-0.226	-0.063																																		
LU_St	-0.029	-0.051	0.186	-0.139	0.165																																	
LU_Ag	0.075	-0.075	0.003	-0.048	*-0.303	***-0.849																																
LU_Fa	-0.081	0.229	**-0.358	**0.350	0.191	***-0.537	0.013																															
pH	***0.506	-0.002	**0.439	**0.383	-0.193	-0.159	0.187	0.018																														
SWT	*0.299	**-0.374	***0.695	-0.091	-0.071	*0.296	-0.165	*-0.295	*0.290																													
DO	*0.267	0.061	-0.049	0.123	-0.209	-0.118	*0.310	*-0.282	0.128	0.006																												
TP	-0.142	-0.253	*0.326	0.049	-0.240	0.033	0.019	-0.097	-0.026	0.150	-0.218																											
TN	0.237	-0.218	*0.320	-0.062	**-0.370	0.069	0.044	-0.225	0.207	0.212	0.260	*0.280																										
Chl a	0.138	**-0.393	**0.430	0.043	***-0.585	-0.002	0.101	-0.172	***0.449	0.171	0.083	***0.461	***0.496																									
[TOC]	0.019	*-0.324	*0.285	-0.174	***-0.528	0.096	0.061	*-0.289	0.038	0.104	0.120	*0.315	**0.443	***0.526																								
[Na]	0.091	-0.140	**0.405	***0.625	-0.186	-0.125	0.084	0.096	***0.458	0.259	0.028	0.175	0.145	*0.327	0.086																							
[K]	0.210	-0.136	**0.413	***0.589	-0.097	-0.148	0.168	0.020	***0.525	0.263	0.040	0.210	0.090	0.225	0.025	***0.836																						
[Ca]	*-0.330	0.039	*-0.345	***0.493	-0.055	-0.135	-0.107	**0.422	-0.067	-0.263	0.022	0.236	0.010	0.097	-0.121	0.126	0.079																					
[Mg]	0.018	0.225	0.094	***0.746	0.097	-0.117	-0.041	*0.298	*0.328	0.043	-0.099	0.102	-0.204	-0.039	*-0.324	***0.545	***0.573	**0.410																				
[Sr]	-0.133	**0.451	-0.178	***0.703	*0.293	-0.105	-0.149	**0.444	0.113	-0.230	-0.110	0.019	-0.262	-0.162	**-0.413	*0.339	*0.300	***0.581	***0.826																			
[Ba]	*-0.324	**0.384	*-0.303	***0.460	0.202	0.066	-0.234	0.243	-0.196	*-0.302	-0.130	0.169	-0.115	-0.163	-0.200	0.118	0.014	***0.490	***0.476	***0.788																		
[Fe]	-0.027	*-0.290	0.110	**-0.397	-0.215	0.192	-0.073	*-0.271	*-0.312	0.109	0.090	0.048	0.198	0.243	0.217	-0.234	*-0.327	*-0.302	**-0.438	***-0.481	*-0.271																	
[Mn]	-0.049	-0.159	0.021	-0.123	-0.237	0.116	-0.109	-0.074	-0.172	-0.010	-0.005	0.202	0.095	*0.275	0.195	*-0.283	*-0.316	0.118	-0.111	-0.109	0.035	***0.616																
[P]	-0.199	-0.056	*0.287	-0.001	-0.017	-0.038	0.137	-0.138	-0.114	0.048	-0.181	***0.697	0.038	0.179	0.191	-0.010	0.117	0.220	0.090	0.104	0.158	-0.070	0.073															
[S]	-0.045	-0.159	0.136	-0.016	-0.132	-0.140	0.033	0.232	0.102	0.206	-0.031	0.020	*0.317	0.054	0.122	0.175	0.019	0.026	-0.142	-0.139	-0.214	0.014	*-0.273	-0.114														
[Si]	0.015	0.146	0.242	***0.555	-0.048	-0.140	-0.012	*0.278	*0.287	-0.008	0.103	0.209	0.250	0.148	-0.048	*0.331	0.223	**0.405	**0.383	**0.368	0.254	-0.187	-0.026	0.083	0.135													
[F]	-0.153	**0.421	-0.126	***0.774	0.133	-0.184	-0.120	***0.529	0.137	-0.190	-0.034	-0.025	-0.104	-0.115	-0.243	**0.460	*0.282	***0.504	***0.727	***0.839	***0.697	**-0.460	-0.200	-0.007	0.187	***0.481												
[Cl]	*0.291	-0.114	***0.506	**0.435	-0.215	-0.227	*0.268	-0.011	***0.567	*0.271	0.071	*0.333	*0.301	**0.399	0.167	***0.754	***0.770	0.044	**0.373	0.148	-0.013	*-0.303	-0.262	0.236	0.113	*0.306	*0.300											
[DIC]	0.021	0.076	0.107	***0.842	-0.127	*-0.282	0.097	*0.356	***0.476	-0.015	0.079	0.098	0.098	0.212	-0.093	***0.733	***0.688	***0.476	***0.752	***0.599	*0.342	**-0.450	-0.248	0.050	0.145	***0.504	***0.742	***0.644										
Macrophytes	-0.242	-0.127	-0.065	*-0.310	0.099	**0.383	-0.251	*-0.313	***-0.458	0.024	-0.094	0.144	-0.235	-0.260	-0.093	**-0.359	*-0.314	-0.150	-0.239	-0.141	0.097	0.197	-0.008	0.145	-0.121	-0.261	-0.237	***-0.435	**-0.3858									
sand	0.141	0.078	-0.196	*0.264	-0.120	-0.182	0.078	0.212	**0.412	-0.136	0.255	-0.138	0.207	0.148	-0.108	-0.052	0.043	*0.305	-0.052	0.069	0.024	*-0.314	-0.172	-0.202	0.227	0.234	*0.322	0.145	***0.476	*-0.308								
emer	0.078	-0.143	0.112	0.084	-0.158	*-0.270	0.165	0.234	0.041	0.081	0.102	0.057	0.195	0.087	0.048	0.207	0.124	0.147	0.029	0.005	-0.016	-0.064	-0.120	-0.103	*0.285	**0.354	0.164	0.146	0.237	0.084	0.067							
subm	-0.127	-0.002	-0.045	-0.099	0.191	**0.385	**-0.359	-0.156	-0.206	0.071	-0.160	0.112	*-0.269	-0.224	-0.233	-0.213	-0.092	-0.114	-0.027	-0.015	0.164	0.166	0.081	0.045	-0.240	-0.136	-0.114	*-0.272	-0.168	***0.745	-0.241	0.108						
float	*-0.265	-0.165	-0.157	**-0.370	-0.019	0.228	-0.099	-0.257	***-0.453	-0.038	0.045	0.051	-0.114	-0.174	0.039	**-0.398	**-0.387	-0.049	*-0.315	-0.145	0.071	0.088	-0.024	0.058	-0.009	*-0.312	-0.219	**-0.421	**-0.436	***0.746	-0.132	0.062	0.215					
swamp	-0.135	-0.132	0.104	-0.224	0.028	0.211	-0.048	*-0.312	**-0.378	0.018	-0.099	0.181	-0.117	-0.170	0.026	-0.163	-0.226	-0.200	-0.209	-0.185	-0.064	0.205	-0.110	*0.275	0.022	-0.107	-0.219	-0.254	-0.266	***0.732	**-0.352	-0.006	**0.362	**0.420				
Zcore	0.061	***0.659	**-0.406	0.184	**0.400	-0.121	-0.138	***0.458	0.004	*-0.301	-0.041	**-0.388	**-0.378	**-0.356	**-0.400	-0.096	-0.146	0.142	0.245	*0.324	0.117	-0.166	0.001	**-0.370	-0.055	0.076	*0.320	-0.170	0.066	-0.253	0.010	-0.235	-0.062	-0.202	**-0.355			
Wc	-0.098	*-0.311	0.122	-0.165	*-0.271	*0.342	-0.194	*-0.345	0.029	-0.006	-0.110	-0.010	0.164	0.195	*0.315	0.069	-0.006	-0.233	-0.263	-0.264	-0.109	-0.027	0.045	-0.191	-0.213	-0.260	*-0.311	0.055	-0.181	0.080	-0.130	-0.080	0.072	0.107	-0.028	*-0.271		
Omc	-0.145	**-0.398	0.023	-0.061	-0.246	*0.335	-0.180	*-0.341	0.008	0.039	0.112	0.029	0.254	0.200	*0.314	0.059	-0.028	0.004	-0.240	-0.170	0.027	0.049	0.035	-0.110	-0.052	-0.083	-0.240	-0.064	-0.103	*0.306	0.011	0.164	0.182	*0.295	0.196	***-0.552	***0.639	
Dmin	***0.761	-0.002	***0.501	-0.086	-0.077	0.185	-0.020	*-0.329	***0.492	**0.394	0.249	-0.081	0.263	0.214	0.182	0.130	0.234	*-0.308	-0.066	-0.251	**-0.366	-0.014	-0.036	-0.096	-0.108	-0.017	-0.203	*0.339	0.020	-0.099	0.065	0.018	0.024	-0.188	-0.060	0.013	0.160	-0.089

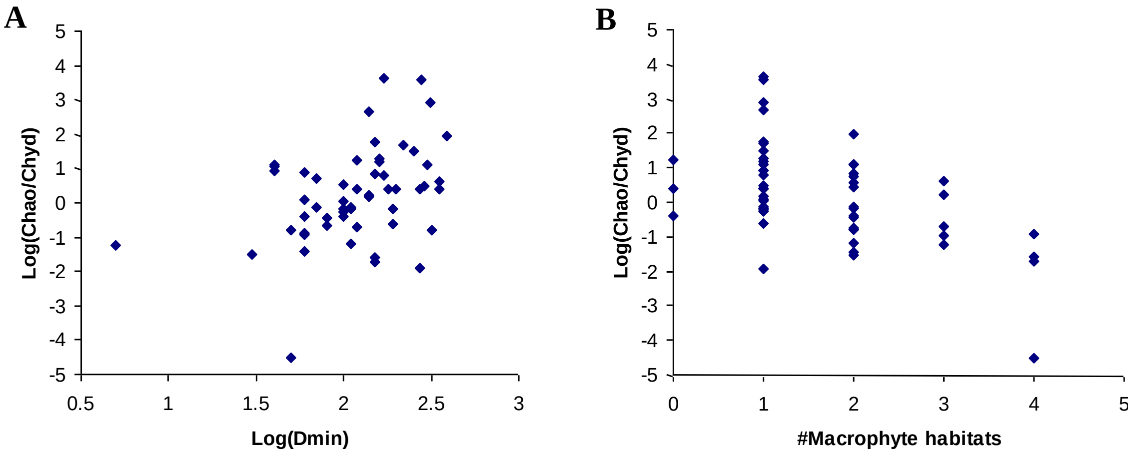
*: $P < 0.05$

**: $P < 0.01$

***: $P < 0.001$

Appendix 3

The following graphs illustrate the relationship in our dataset of freshwater lakes between the ratio of *Chaoborus* to chydorid cladocera and A) minimum distance to shore as well as B) the number of macrophyte habitats (r= 0.39, p< 0.005 and r=-0.54, p < 0.001, respectively).



5

A four thousand year history of crater lakes in western Uganda: response of the aquatic invertebrate fauna to climatic and anthropogenic impacts

Abstract

Increasing human pressure on East African lakes and their catchments threatens natural ecosystem functioning, and ultimately the quantity and quality of sustainable water resources. Detailed knowledge of the response of tropical African aquatic ecosystems to climate variability and human impact is therefore vital to properly understand current and future changes in the region's water resources. In this study, we use fossil assemblages of chironomid larvae, cladocerans, ostracods and other aquatic invertebrates preserved in the sediment records of two currently fresh crater lakes in western Uganda (Lake Wandakara and Lake Katinda) to reconstruct the response of aquatic communities to regional environmental change over the past 4000 years, and as such, to gain long-term data on ecosystem resilience. Synchronous changes in sediment composition and faunal assemblages indicate regionally widespread droughts centered at ~4000 cal.yr BP, ~2700 cal.yr BP, ~2000 cal.yr BP, ~AD 1100, ~AD 1300 and ~AD 1800. Changes in both the sediment and faunal composition at ~2200 cal.yr BP in Lake Katinda reflect increased input of clastic mineral sediments probably resulting from sedentary agriculture in the lake's surroundings. The Lake Wandakara aquatic community, on the other hand, shows little or no indications of human impact prior to the 11th century. Despite basin-specific factors influencing the sensitivity of each lake to climate variability and human impact, and thus the strength of signatures recorded by proxies, in both lakes a pronounced change in the mid-20th century can be attributed to the effects of intensifying human activity on aquatic productivity. This study illustrates the advantages of multi-proxy and multi-site reconstructions of past environmental change, and it validates screening for large (>150µm) remains of diverse aquatic invertebrates as a relatively fast method to characterize past changes in aquatic habitat.

Keywords: Uganda - tropical limnology – paleolimnology – human impact – late Holocene – *Chaoborus* – Cladocera – Ostracoda

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5.1 Introduction

In tropical Africa, climate during the late Holocene was characterized by a succession of wet and dry periods (Gasse 2000, Verschuren, 2004; Russell & Johnson, 2005). Evidence of (severe) drought affecting the entire East African region has been found in the sediment record of the African Great lakes Edward (Russell & Johnson, 2005), Turkana (Halfman *et al.*, 1994; Ricketts & Johnson, 1996), Victoria (Stager *et al.*, 1997) and Tanganyika (Cohen *et al.*, 2005; Stager *et al.*, 2009), as well as in smaller lakes and swamps such as Lake Naivasha (Verschuren *et al.*, 2000a), Mubwindi Swamp (Marchant *et al.*, 1997), Kabaka Swamp (Taylor *et al.*, 1999) and several Western Uganda crater lakes (Ssemmanda *et al.*, 2005; Ryves *et al.*, in review). About 2000 years ago and during the Medieval Climate Anomaly (MCA; ~1000-1300 AD) drought occurred broadly synchronously across East Africa. However, during the past millennium a contrasting climate evolution was recorded for the eastern and western parts. For example, during the main phase of the Little Ice Age (LIA; ~1500-1800 AD) relatively wet conditions were found in the easternmost part of the region, while studies based on lakes in the westernmost part of the region indicate prolonged and severe drought (reviewed in Verschuren & Charman, 2008). Although the exact geographical pattern of these decade- and century-scale droughts has yet to be established, it is clear that in the relatively recent past all regions of equatorial East Africa, from sub-humid western Uganda to arid northern Kenya, have experienced substantial water-resource variability that is not immediately evident from 20th-21st century historical weather data. Consequently, the modern-day hydrological balance (rainfall minus evaporation) is a poor guide to evaluate the long-term functioning and resilience of regional aquatic ecosystems, even in the absence of anthropogenic disturbance.

In this study, we analyse the changes in the aquatic biota of two small crater lakes in western Uganda (Lake Katinda and Lake Wandakara) during the late Holocene as they provide valuable insights on the extent and influence of these environmental changes on the lake ecosystems. Records of human history in the area are unclear before ~2000 BP, although some palynological and archeological studies show evidence of an ‘Early Iron Age’ in western Uganda starting at ~2500 BP, with Sudanic-speaking peoples herding cattle and growing grain (Taylor & Marchant, 1995, Taylor *et al.*, 2000). Widespread primary forest clearance and secondary forest regeneration starting at ~1000 AD has also been documented (Taylor *et al.*, 1999). Therefore, any changes in the sediment record from this time onwards can be seen as the result of climatic change, human impact or a combination of both (as climatic variation is presumed to have influenced human societies in pre-colonial western Uganda; Taylor *et al.,* 2000). Separating the effects of climate and human impact is particularly difficult in palynological studies. In many previous studies, climate during recent millennia was assumed stable, and any reduction in forest cover interpreted as evidence of anthropogenic deforestation (Robertshaw & Taylor, 2000). Here we combine stratigraphic data on bulk sediment composition and magnetic susceptibility, which sketch the long-term history of climate-driven hydrological change and local land use (Bessems, 2007), with community-level analyses of fossil aquatic invertebrate assemblages to study the response of the aquatic community in these tropical crater lakes to natural and anthropogenic disturbance. The historical perspective presented by this paleoecological analysis is equivalent to a series of ecosystem-level experiments that help to determine the relative sensitivity of indigenous aquatic communities to disturbance, and their likely ability to recover from current disturbance if conservation measures were put in place. The eventual goal of this study is to aid development of sound strategies for sustainable water resource management, biodiversity conservation and preservation of natural ecosystem functions in an area which suffers from increasing agricultural land use (Wakabi, 2006).

5.1.1 Study sites

Lakes Katinda and Wandakara are located in respectively the southern Bunyaruguru and northern Kasenda lake districts of western Uganda, and form part of a series of maar lakes associated with the western branch of the East African rift system (Melack, 1978). The climate is tropical sub-humid, with two wet seasons (March-May, October-December) mainly determined by the north-south passage of the Inter Tropical Convergence Zone (ITCZ). Additional precipitation can be delivered to the region when the Congo Air Boundary (CAB) reaches eastward during Northern Hemisphere summer. Mean annual evaporation (1750 mm) exceeds mean annual rainfall (1300 mm), resulting in a mildly negative local water balance (average data for Western Uganda, Russell & Johnson, 2006). The lakes are maintained against this negative water balance by surface run-off from inside the crater basin after heavy rainfall, supplemented during extreme lowstands by inputs from the shallow groundwater table. They have remained fresh despite strong lake-level fluctuation due to subsurface outflow, which counteracts the accumulation of dissolved salts. Natural vegetation is semi-deciduous lowland forest (White, 1983). However, as both lakes are situated outside national parks, most natural vegetation around the crater basins has now been replaced by an agricultural landscape, dominated by small-scale plots of banana, maize, cassava and millet. Routine burning of secondary vegetation and intense subsistence agriculture inside the steeply sloping crater basins has augmented their phosphorus loading, often causing eutrophication (Kizito *et al*., 1993).

Lake Katinda (0°13’ S, 30°06’ E, 1036 m a.s.l.) is a 0.44 km², 18m deep, circular freshwater lake (743 $\mu S.cm^{-1}$ in 2001) in a crater with a topographic catchment area of 2.2 km² and crater rim heights varying between 30 and 107 m above lake level (Fig. 1). The very scarce natural vegetation now remaining inside the crater is all secondary growth, and aquatic macrophyte vegetation is limited to a narrow fringe of emergent species (*Paspalidium geminatum* and *Cyperus alternifolius*) because of the steeply sloping near-shore lake bottom and low water-column transparency. Submerged tree trunks covered with calcium-carbonate deposits confirm that at some point in the lake’s recent history, lake levels have been significantly lower for an extended period of time. At some areas within the crater basin, heavy soil erosion has laid bare the underlying bedrock. There are fairly intensive fishing activities in both Lake Katinda and the nearby Lake Mirambi, predominantly on small haplochromine cichlids (*Haplochromis* sp.) and stunted tilapias (*Oreochromis* sp). The lake is currently highly eutrophic, with low transparency (Secchi depth: 0.5 m), high Chl *a* (42.6 µg/l), total nitrogen (TN; 55 µM) and total phosphorus (TP; 1.4 µM).

Compared to Lake Katinda, the kidney-shaped Lake Wandakara (0° 25’ N, 30°16’ E, 1170 m. a.s.l.) is much smaller (0.04 km²) and slightly shallower (12 m). It has a higher conductivity (1125 µS.cm^{-1} in 2001), a smaller topographic catchment area (0.13 km²) and crater rim heights varying between 19 to 103 m above lake level (Fig. 2). As in Lake Katinda, most natural vegetation has been replaced by plots for subsistence agriculture although more secondary natural vegetation remains, including *Euphorbia* trees. Also, a fairly well-developed littoral fringe of emergent macrophytes (including *Typha australis*, *Phragmites mauritianus* and *Paspalidium geminatum*) is present along the gently sloping north shore. Lake Wandakara can also be considered eutrophic, despite a slightly higher transparency (Secchi: 0.7 m) and lower Chl *a* (9.8 µg/l) at the time of our survey. TN (54 µM) is similar to Lake Katinda, while TP (1.9 µM) is slightly higher.

Both lakes were stratified during at the time of our survey, resulting in bottom anoxia and pronounced differences between surface water pH and bottom water pH (9.5 versus 7.6 in Lake Katinda, 8.8 versus 7.7 in Lake Wandakara).

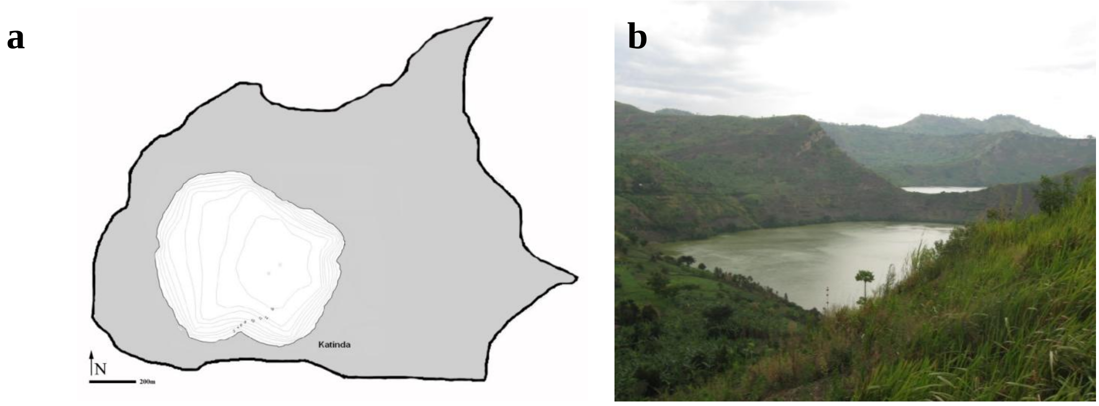

Figure 1: Lake Katinda: bathymetric map with indication of core sites and catchment area (a), general area (b).

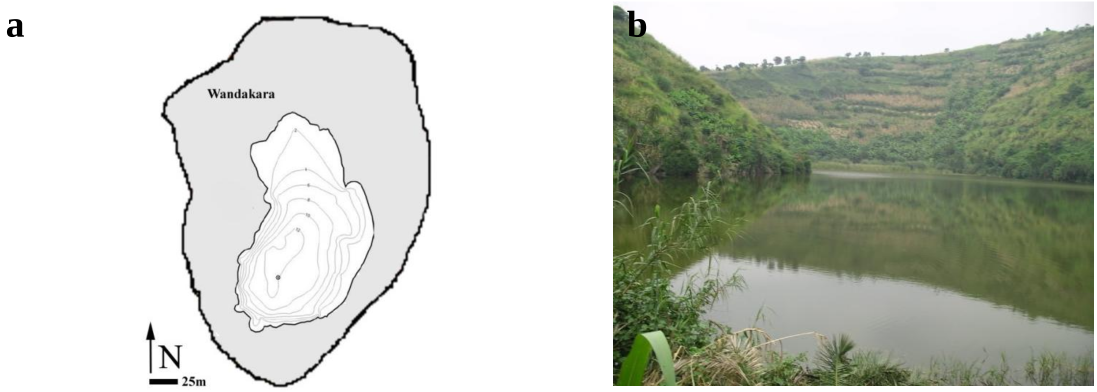

Figure 2: Lake Wandakara: bathymetric map with indocation of core site and catchment area (a), general area (b).

5.2 Material & Methods

5.2.1 Field sampling and laboratory analyses

Sediment cores were collected from the deepest part of Lakes Katinda and Wandakara in January 2001 and 2002. Cores were retrieved using a rod-operated single-drive piston corer (Wright, 1980) and a square-rod piston corer (Wright, 1967). The sediment-water interface and unconsolidated recent sediments were extruded in the field in 1-cm increments using a fixed-interval sectioning device (Verschuren, 1993), and transferred to Whirl-Pak® bags for transport. More consolidated sediments were transported in PVC or polycarbonate tubes. After shipping to Ghent University (Belgium), all cores were stored in the dark at a constant temperature of 4 °C. Multiple cores were taken to ensure overlap between adjacent core sections. These core sections were subsequently correlated by a combination of visual stratigraphy, data from loss-on-ignition (LOI, Bengtsson & Enell, 1986) and magnetic susceptibility to construct a single, continuous master profile. After splitting the cores lengthwise in two halves, the stratigraphy of each core was described by colour (Munsell, 1954) and texture following Schnurrenberger *et al.* (2003). Magnetic susceptibility (χ, in 10^{-6} m^3/kg) was measured non-destructively on 7.7 cm^3 plastic boxes filled with sediment from contiguous 1-cm or 2-cm intervals. These data are an indicator for changes through time in the source (and thus composition) of clastic sediment input, caused either by natural lake-level fluctuation and landscape changes or anthropogenic land-use change (Thompson, 1986; Dearing, 1999;). The chronology of the cores was determined using a combination of ^{210}Pb, ^{137}Cs and ^{14}C dating. In Lake Katinda the age of pre-20th century deposits was based on eight AMS ^{14}C dates obtained on bulk organic mud and on one terrestrial plant macrofossil. In Lake Wandakara AMS ^{14}C dates obtained on four samples of bulk organic mud and on two terrestrial plant macrofossils were supplemented with published ^{14}C ages on terrestrial plant macrofossils from two intervals of cores analyzed by Ssemmanda *et al*. (2005), which were cross-correlated to our cores using visual lithological markers and LOI data. Further details of dating techniques and sedimentological analyses are provided in Bessems (2007).

A total of 164 sediment samples (Lake Katinda: 111, Lake Wandakara: 53) were prepared for analysis of invertebrate remains by deflocculation in a 10% solution of potassium hydroxide (KOH) at 70°C (Walker & Paterson, 1985). Resulting in a ~55 and ~24-year resolution for the bottom (786-386 cm) and top (386-0 cm) section of Lake Katinda respectively, and a ~35-year resolution for Lake Wandakara. Deflocculated samples were rinsed on a 150-µm mesh sieve (Verschuren & Eggermont, 2007). The retained organic residue was transferred to a transparent counting tray and scanned at 20-80× magnification under transmitted light. All chironomid remains were picked out with a fine needle, mounted in glycerine (50% glycerol and water) on microscope slides, and analysed at 400× magnification with an Olympus BH-2 compound microscope. The remains of other invertebrate groups were identified directly during scanning of the sample at lower magnification, and only those specimens whose identification was ambiguous were picked out and mounted on microscope slides for confirmation. For all groups, the minimum number of individuals present in a sample was determined by the most abundant skeletal fragment or by the minimum number of individuals from which the remains could have originated. For chironomids, criteria for counting fragmentary fossils followed Walker (1987). Chironomid identification follows the East African regional inventory of Eggermont & Verschuren (2004a; 2004b), while ostracod identification was based on Rumes (Chapter 2) and comparison with a 22-species reference collection from Lake Naivasha, Kenya (Verschuren 1996). Cladoceran remains were identified using Szeroczyńska & Sarmaja-Korjonen (2007) for chydorids, Mergeay *et al*. (2005) for *Daphnia* ephippia and Dumont *et al.* (1981) for *Moina* ephippia. Remains of chydorid (benthic) cladocerans were identified to species level only in a subset of intervals (five in Lake Katinda and 18 in Lake Wandakara) to trace broad changes in the local composition of this fauna through time. Remains of other groups of aquatic invertebrates (including various types of insect larvae) were identified using Rumes *et al.* (2005) and the primary references mentioned therein. We also counted fish scales and aquatic macrophyte remains. Two types of unidentified chitinous remains, type Z and type δ, were regularly recovered. Type Z is a slender, claw-like structure (length: ~150µm) with a prominent dark, apical tooth and a large number of smaller, lighter sub-apical teeth placed in a single row (Fig. 3a). Type δ, most likely part of an ephemeropteran mandible, consists of two rigid parts connected by transparent and more flexible membrane: a dark structure (canine) with one apical and one subapical tooth, and a molar surface with parallel ridges (Fig. 3b).

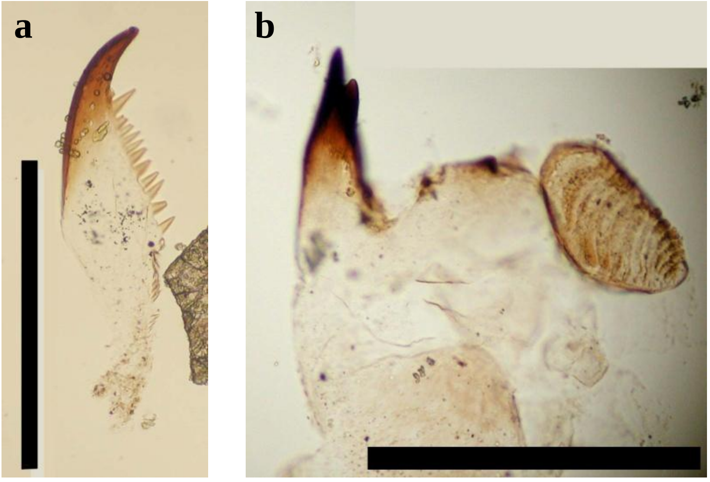

Figure 3: Unidentified chitinous remains, type Z (a) and type δ (b) (scale is 100 µm for a, b).

Between 0.1 and 17.9 g of wet mud was processed per depth interval to yield identifiable fossils from at least 50 chironomids (range 25–179.5, mean 77). Given the relatively low local species richness, this number met the criteria for numerical analysis (Quinlan & Smol 2001). The same samples were simultaneously analysed for other aquatic invertebrate remains (range 17-966, mean 118). Very low densities of fossil remains were limited to a sandy, inorganic core section (115-155 cm) in the Lake Wandakara record.

All chironomid taxa recovered from the Lake Katinda record are morphologically identical to taxa documented in a regional survey of modern-day larval chironomid faunas in East African lakes (Eggermont & Verschuren, 2004a,b), except for a single morphotype, Chironomini indet. type Katinda. This taxon (Fig. 4a,b) has a uniformly dark brown mentum with four median teeth of which the outer teeth are largest, and six pairs of lateral teeth. The first laterals are smaller than the second and third laterals, the fifth laterals are strongly reduced, and the sixth laterals are pointing outward. Ventromental plates are broadly fan-shaped, about as wide as the mentum, and medially separated by the width of all four median teeth and the first laterals; they have pointed anteromedian ends, and fine striae running over the entire surface. This species resembles *Kiefferulus chloronotus* in the general shape of the mentum and ventromental plates. However, the four median teeth make it unlikely that this is just an aberrant form or worn specimen of *Kiefferulus*. We found a single specimen of this morphotype in the Lake Katinda record, but it was also encountered in the sediment record from nearby Lake Mirambi (Rumes, unpublished data). Also all except one chironomid taxon recovered from the Lake Wandakara record have been found previously (Eggermont & Verschuren 2004a,b). This taxon, Orthocladiinae type Wandakara, has a uniformly coloured mentum, with a single median tooth ~3× as wide as the first laterals, and four (possibly five) pairs of lateral teeth, gradually diminishing in size and with their apices pointing forward (Fig. 4c). Ventromental plates are well-developed and wide, extending a little beyond the mentum, and with straight lateral margin. Seta submenti are positioned at the base of the ventromental plates. Diagnostic characteristics are incomplete because only one specimen of this morphotype was found and the fifth pair of lateral teeth was not unambiguously visible, possibly by wear. Analysis of further specimens may confirm the presence of this fifth pair of lateral teeth, in which case this taxon would belong to either the genus *Smittia* or *Parasmittia.* All other aquatic invertebrate taxa recovered from the Lake Katinda and Wandakara records have previously been documented from the region (Rumes *et al*., 2005; Rumes Chapters 1, 2 and 4).

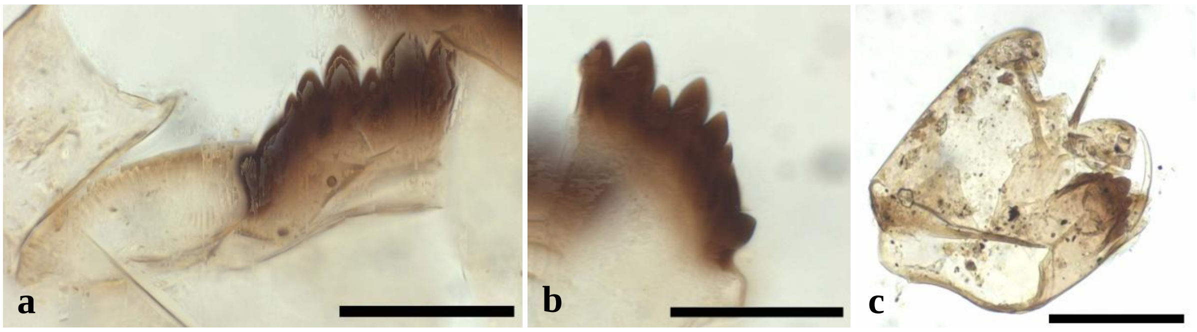

Figure 4: Sub-fossil remains of Chironomini indet. type Katinda (a, b), and Orthocladiinae type Wandakara (c)(scale is 50µm for a,b and 100 µm for c)**.**

5.2.2 Numerical analyses

Percent-abundance diagrams were made for all taxa that reached 2% in at least one interval and were present in at least two intervals. We also retained Ephemeridae, of which the abundance never reached 2% but which was found in more than four intervals.

Stratigraphic diagrams were produced with TILIA version 2.0.b.4. (Grimm, 1993) and TGView version 2.0.2 (Grimm, 2004). Stratigraphically constrained sum-of-squares cluster analysis CONISS (Grimm, 1987) applied to squared-root transformed species data identified major changes in invertebrate communities through time. Stratigraphic zonation was further accomplished by optimal sum-of-squares zonation (Birks & Gordon, 1985), using the broken-stick model proposed by Bennett (1996) to estimate the number of statistically significant zones. This analysis was performed using ZONE version 1.2 (Juggins, 1991) and BSTICK version 1.0 (J.M. Line and H.J.B. Birks, unpublished software).

Multivariate ordination techniques were used to determine the main patterns of variation underlying the fossil data. To determine whether linear- or unimodal-based numerical techniques were most appropriate (ter Braak, 1986), we analyzed each dataset by Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980) with non-linear rescaling, detrending-by-segments and down-weighing of rare taxa. Because the gradient along the first DCA axis was always less than 1.5 SD units, principal component analysis (PCA) was used for further data exploration (Lepš & Šmilauer, 2003). Multivariate analyses were performed using CANOCO v. 4.5 (ter Braak & Šmilauer, 2002).

Salinity inferences were obtained in C2 version 1.3.4. (Juggings, 2003) using chironomid-based transfer functions based on weighted-averaging (WA) optima, 2-component weighted-averaging partial least squares (WA-PLS(2)), and a weighted modern analogue technique (WMAT) (Eggermont *et al*.,2006). The reliability of chironomid-inferred paleosalinity estimates was evaluated using two diagnostic statistics available in C2 version 1.3.4. (Juggins 2003). Using MAT with squared chi-square distance as the dissimilarity coefficient, we assessed if a fossil assemblage had a good modern analogue assemblage in the modern calibration data set; the used cut-off dissimilarity value for a good modern analogue is the 10th percentile of the distribution of dissimilarities between calibration dataset samples (Clarke et al. 2006). Second, we calculated sample-specific errors (Birks 1995) with 999 bootstrapping cycles.

5.3 Results

5.3.1 Lake Katinda sediment stratigraphy

The 788-cm long composite sediment record of Lake Katinda consists of a black sapropel in the lower half, and clayey to silty sediments interrupted by a peaty layer in the upper half of the sequence (Fig. 5). Based on this diversity in texture and composition, the sediment can be divided into eight successive units. Throughout the sediment core, carbonate content is very low (~6.6%). At certain levels, namely at 600-580 cm (~2800-2700 cal. yr BP), 242-186 cm (~1000-780 cal. yr BP) and 56-29.5 cm (~225-120 cal. yr BP) depth, the values are slightly elevated (~7%, ~7.11% and ~7.5%, respectively). At 359-337 cm (~1500-1400 cal. yr BP) and 151-122 cm (~600-500 cal. yr BP) nearly doubled carbonate values occur (~14% and ~11%, respectively).

Magnetic susceptibility shows large variations throughout the sediment core: below 377 cm depth, measured χ is very low or even negative (~-9 10^{-6} m³/kg). Intermediate values ranging between 600 and 1350 10^{-6} m³/kg occur between 377-293 cm and 151-71 cm, with a peak value of 2900 10^{-6} m³/kg at 366 cm (~1600 cal. yr BP). The highest values are measured at 293-151 cm and from 71 cm to the surface (up to 8100 and 6058 10^{-6} m³/kg, respectively).

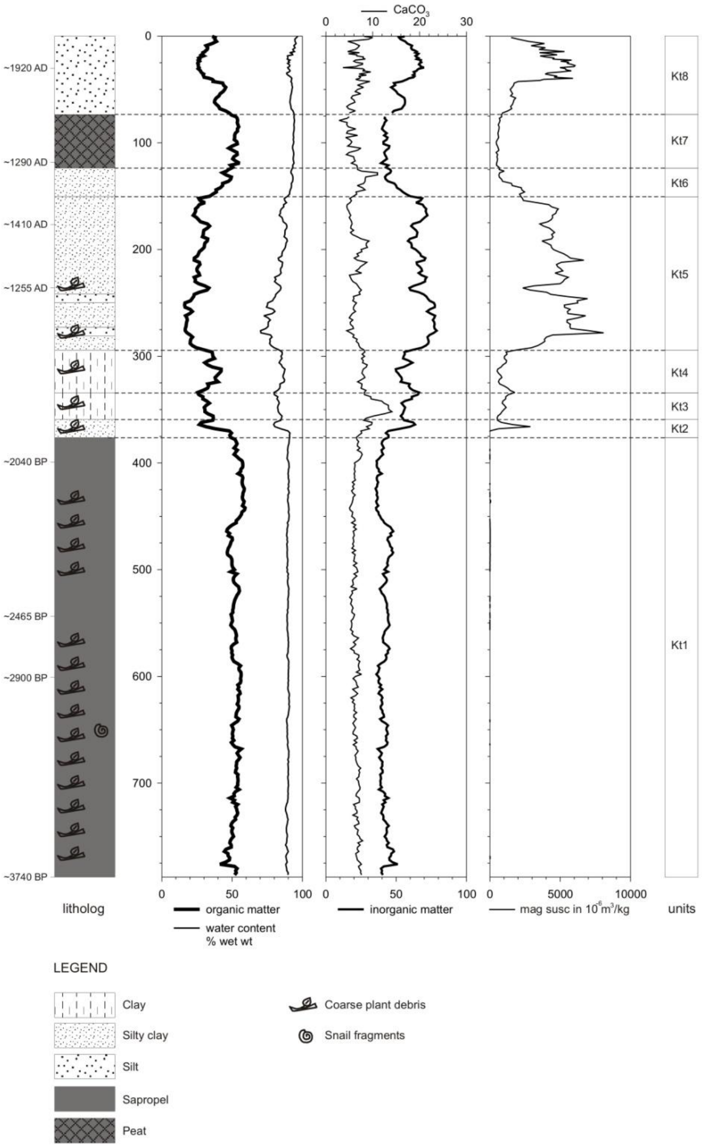

Figure 5: Lithostratigraphy and sediment composition of Lake Katinda. All sediment components are expressed as % of dry mass, unless otherwise indicated (Modified from Bessems, 2007)

5.3.2 Lake Katinda faunal stratigraphy and zonation

A total of 57 chironomid taxa were present among ~9000 specimens recovered from the 4000-year sediment record of Lake Katinda, as well as 26 other aquatic invertebrate taxa among which are 12 non-chironomid insect taxa and eight ostracod taxa (Table 1).

Table 1: Overview of the aquatic invertebrate groups encountered in the sediment records of Lake Katinda and Lake Wandakara. *Abundance data not included in the analyses due to their presumably mixed terrestrial and aquatic origin.

	Katinda	Relative abundance		Wandakara	Relative abundance	
	Records	Mean	Max	Records	Mean	Max
Cladocera						
Bosmina sp.	0	-	-	1	0.0	0.9
Moina micrura	0	-	-	4	1.3	57.9
Chydoridae	82	11.6	64.7	52	31.6	91.6
Ostracoda						
Darwinula stevensoni	0	-	-	26	1.2	6.3
Limnocythere notodonta.	1	0.0	4.0	0	-	-
Cytheridella chariessa	1	0.0	0.2	7	0.5	9.7
Candonopsis africana	20	0.7	15.4	22	2.1	26.0
Physocypria capensis	0	-	-	1	0.0	0.7
Hemicypris fossulata	9	0.3	8.8	0	-	-
Potamocypris mastigophora	0	-	-	1	0.0	0.5
Zonocypris costata	49	1.6	18.2	48	19.7	81.4
Oncocypris sp. type Katanda	12	0.2	5.6		-	-
Oncocypris sp. type Kyaninga	9	0.1	3.1	2	0.0	1.4
Ostracoda indet.	13	0.5	13.0	15	0.9	7.5
Insecta						
Diptera - *Chaoborus ceratopogenes*	111	77.4	100.0	53	28.9	71.6
Diptera - *Bezzia* type	3	0.0	0.9	1	0.0	1.0
Diptera - *Dasyhelea* type	0	-	-	13	0.4	5.4
Ephemeroptera - Baetidae	60	1.9	11.1	52	6.2	21.2
Ephemeroptera - Caenidae	56	3.0	31.7	41	2.2	11.4
Ephemeroptera - Ephemeridae	5	0.0	1.4	7	0.1	1.4
Trichoptera - Hydropsychidae	18	0.5	9.1	21	0.6	3.6
Trichoptera - *Ecnomus* sp.	2	0.0	4.5	8	0.3	3.0
Trichoptera - *Oecetis sp.*	6	0.1	3.1	0	-	-
Trichoptera - indet.	1	0.0	0.7	0	-	-
Coleoptera	1	0.0	1.1	0	-	-
Hemiptera - Notonectidae	1	0.0	1.0	1	0.0	1.5
Odonata	1	0.0	0.9	2	0.1	3.0
Acari						
Oribatida - Macropylina type	36	*	*	41	*	*
Hydracarina	8	*	*	10	*	*
Neorhabdocoela						
Neorhabdocoela - Type 1	99	*	*	36	*	*
Bryozoa						
Plumatella sp.	20	0.5	9.1	3	0.1	1.9
Thecamoeba						
Centropyxis sp.	1	0.0	2.5	15	1.0	5.4
Arcella vulgaris	25	0.9	15.8	23	0.5	4.8
Indet.						
Type Z	29	0.6	9.1	35	2.3	16.7
Type Delta	1	0.0	2.8	1	0.0	0.5

Species-level identification of chydorid Cladocera in selected samples yielded 10 taxa, but given the limited scale of the analysis this number likely underestimates past chydorid diversity in Lake Katinda. The density of fossil chironomid remains ranged between 71 and 8423 (mean value 2145 ± 2260) head capsules/g dry sediment (hc/g), with the highest values (>6000 hc/g) concentrated in the upper quarter of the core sequence, and mostly lower densities (<1000 hc/g) in the lower half (Fig. 6a, b). Densities of non-chironomid invertebrate remains varied from 26 to 6715 specimens/g dry sediment (average 1364 ± 1384). Similar to chironomids, highest densities (>2000/g) are concentrated in the upper quarter of the record, whereas the bottom half is characterized by lower densities. Very low concentrations are mostly limited to a few distinct intervals between 154 and 282 cm (Fig. 7a, b) that are typically low in organic matter content (Fig. 5). CONISS identified five chironomid assemblage zones (KatC5-KatC1; Fig. 6a,b), all of which were determined to be distinct by the broken-stick model. We further divided KatC3 into two subzones based on stratigraphic patterns in some taxa causing deep branching in the CONISS dendrogram (Fig. 5). The depth distribution of non-chironomid invertebrate taxa is divided in eight assemblage zones (KatI8-KatI1; Fig. 7a, b). Two of these, KatI8 and KatI4, consist of a single interval. In the bottom half of the record (786 - ~370 cm) there is little correspondence between the zonation of chironomid and that of non-chironomid assemblages. However, from ~370 cm onwards, there is a fairly good correspondence with synchronous changes recorded at ~370 cm, ~230 cm, ~130 cm and in the top 50 cm.

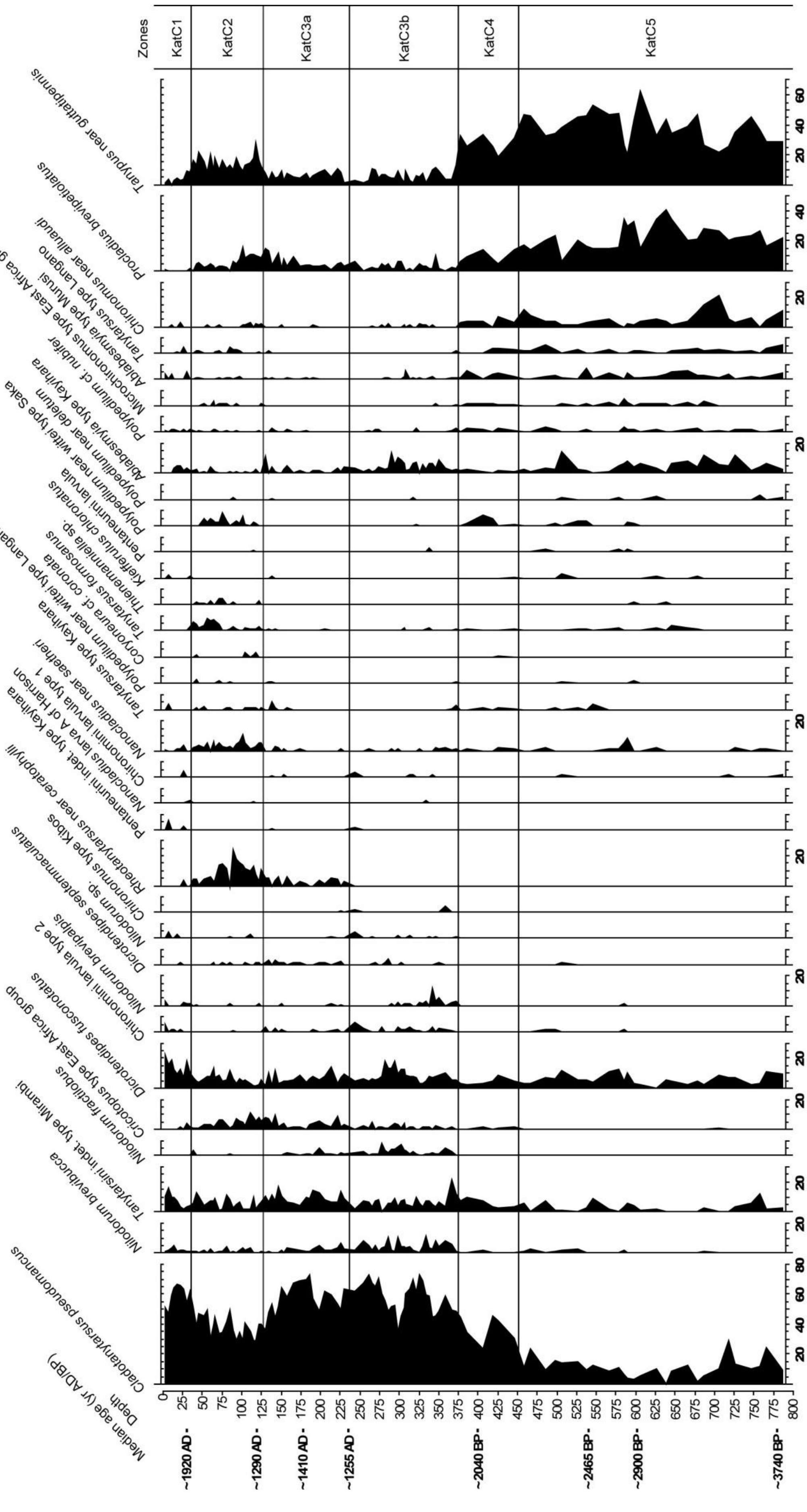

Figure 6a: Chironomid stratigraphy in Lake Katinda. Chronology based on ^{210}Pb-dating and radiocarbon dating (Bessems, 2007)

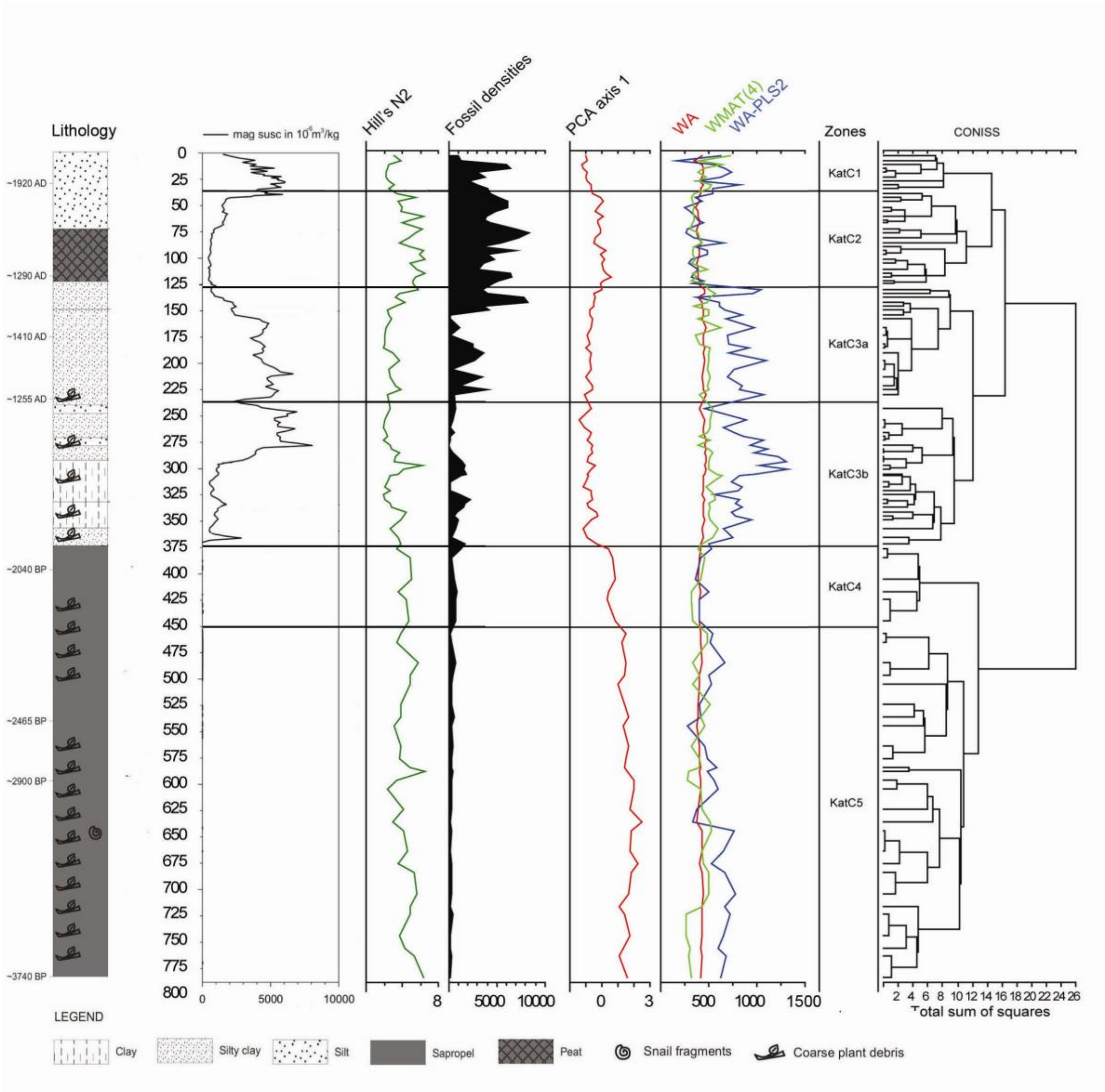

Figure 6b: Lake Katinda: litholog, magnetic susceptibility, Hill's N_2 diversity index, number of headcapsules per gram dry weight of sediment, PCA axis 1-sample scores, chironomid-based salinity reconstructions using weighted averaging (WA) optima, weighted-averaging partial least squares (WA-PLS(2)), and a weighted modern analogue technique (WMAT), zonation as determined BSTICK and CONISS.

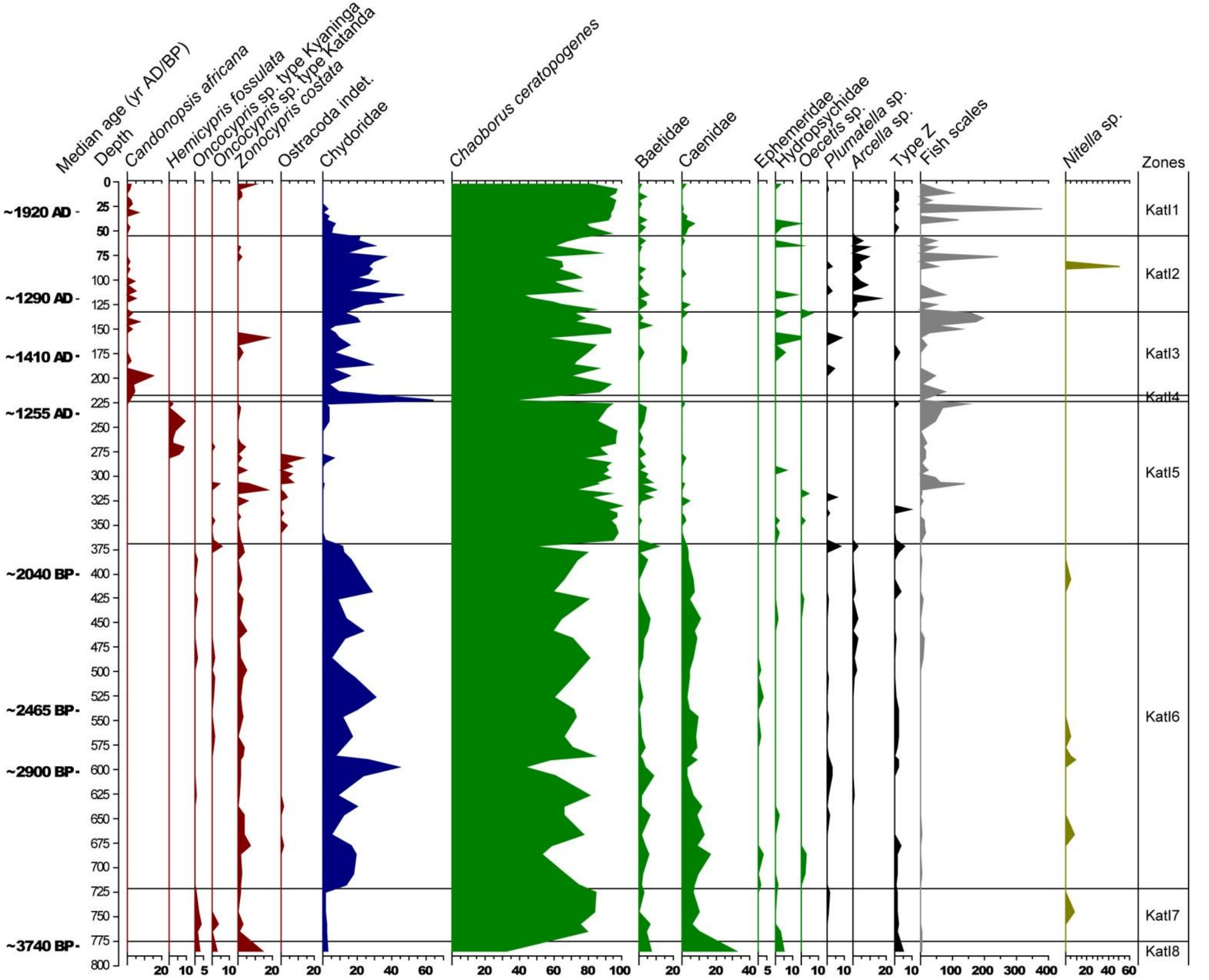

Figure 7a: Stratigraphic distribution of Ostracoda (red), Cladocera (blue), Insecta (green) and other aquatic invertebrate taxa (black) in Lake Katinda, fossil densities of fish scales and *Nitella* expressed as number of remains per gram dry weight. Chronology based on ^{210}Pb-dating and radiocarbon dating (Bessems, 2007).

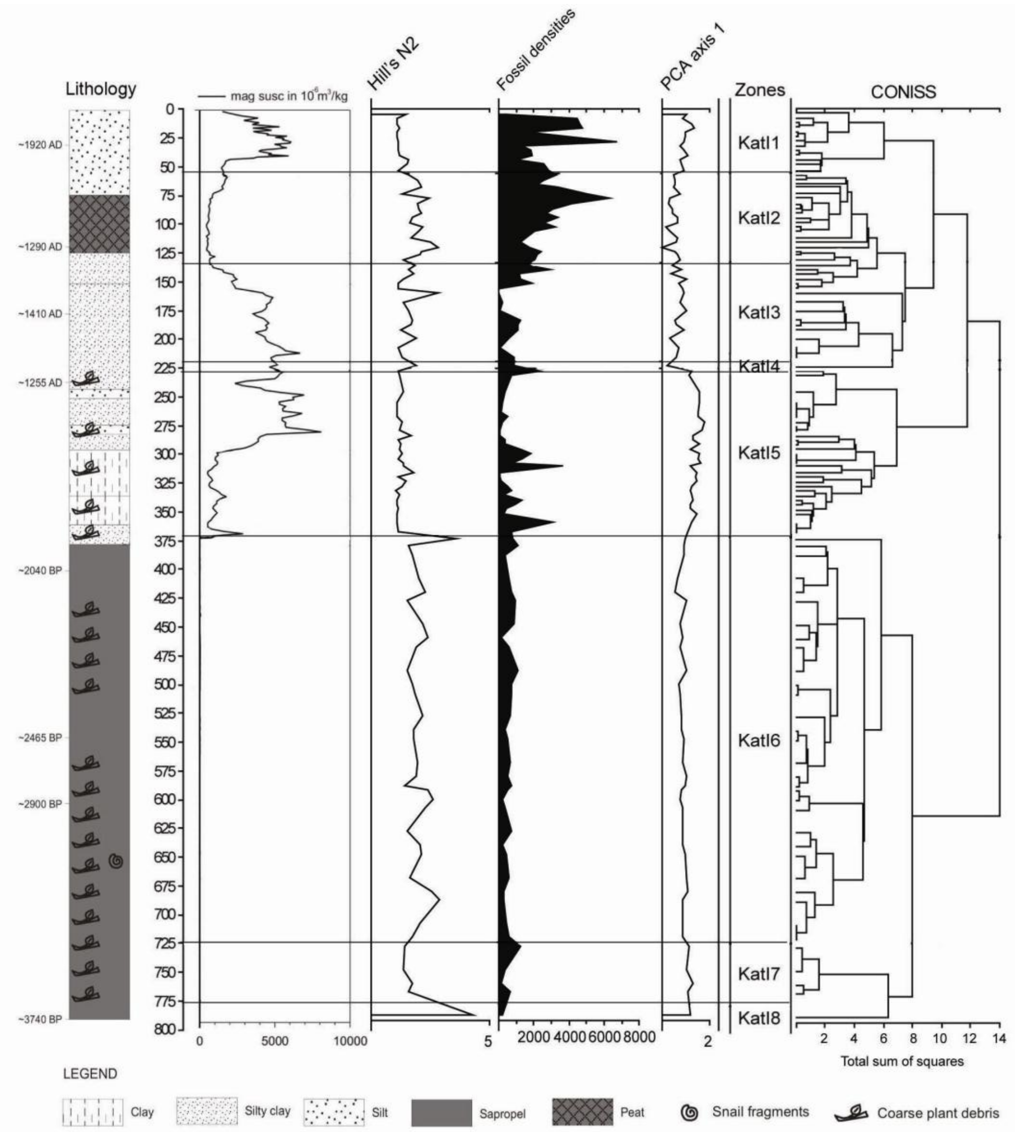

Figure 7b: Lake Katinda: litholog, magnetic susceptibility, Hill's N_2 diversity index, overall invertebrate fossil densities expressed as number of remains per gram dry weight of sediment, PCA axis 1-scores, zonation as determined BSTICK and CONISS.

5.3.3 Evolution of the chironomid community in Lake Katinda

Zone KatC5 (786-452 cm, ~3740-2150 cal. yr BP) is typified by a low abundance of *Cladotanytarus pseudomancus* (11 ± 6.7%), and relatively high abundances of *Tanypus* near *guttatipennis* (38 ± 10.1%), *Procladius brevipetiolatus* (23 ± 7.9%), *Ablabesmyia* type Kayihara (5 ± 3.7%) and *Ablabesmyia* type Murusi (2 ± 1.9%). *Dicrotendipes fusconatatus* (6 ± 3.4%) and *Chironomus* near *alluaudi* (5 ± 4.7%) are the most common Chironomini. *Nilodorum brevibucca* is sporadically present in the lower part of this zone, whereas in the upper part (from ~2450 cal.yr BP) it occurs more continuously though still at modest abundances (~1.5-2%).

In zone KatC4 (452-375 cm, ~2150-1900 cal. yr BP), numbers of *C. pseudomancus* increase markedly reaching 43.5% at its top. *T.* near *guttatipennis* and *P. brevipetiolatus* fall back significantly, and *Ablabesmyia* type Kayihara is reduced to a mean abundance of 1 ± 0.9%. Otherwise this zone is again typified by *Chironomus* near *alluaudi* (5 ± 0.5%) and *Dicrotendipes fusconotatus* (4 ± 1.0%).

Zone KatC3b (375-237 cm, ~1900-750 cal. yr BP) is characterized by strong and synchronous reductions of several chironomid species, including the Tanypodinae *T.* near *guttatipennis*, *P. brevipetiolatus* and *A.* type *murusi;* the Chironomini *C.* near *alluaudi, Polypedilum* cf. *nubifer* and *Microchironomus* type East Africa; and the Tanytarsini *Tanytarsus* types Langano and Kayihara. *C. pseudomancus*, on the other hand, typically reaches 50% or more (up to 73%), establishing itself as the dominant chironomid species up to the present. *Nilodorum* spp. also become an important component of the local chironomid fauna: *N. brevibucca* increases markedly from 366 cm onwards ; *N. fractilobus* appears for the first time and remains present throughout this zone; and *N. brevipalpis*, previously only recovered from a single KatC5 interval, is continuously present in the lower half of KatC3a (Fig. 6a, b). *Ablabesmyia* type Kayihara, *Dicrotendipes septemmaculatus*, Tanytarsini type Mirambi and *Cricotopus* type East Africa also increase markedly. Most of these abundance patterns are maintained in KatC3a (237-127.5 cm, ~750-400 cal. yr BP). The main differences with the previous subzone include the near-absence of *C.* near *alluaudi*, reductions in all three *Nilodorum* spp. and *A.* type Kayihara, and the appearance of *Rheotanytarsus* near *ceratophylli* (3 ± 2.3%). *C. pseudomancus* remains present in high densities (57 ± 9.9%), but decreases down to 35% at 134 cm.

Zone KatC2 (127.5-36.5 cm, ~400-100 cal. yr BP) resembles KatC4 in that *C. pseudomancus'* abundance is reduced to 30-40%, whereas numbers of *P. brevipetiolatus*, *T.* near *guttatipennis, Tanytarsus* type Langano, *Microchironomus* type East Africa and, to a lesser extent, *C.* near *alluaudi* increase. Tanytarsini indet. type Mirambi, *Nilodorum fractilobus* and *Nilodorum brevibucca* decreased in abundance to levels prior to KatC3. This zone is further characterized by high numbers of *Cricotopus* type East Africa and *R. near* *ceratophylli*, alongside *Nanocladius* near *saetheri*, *Tanytarsus formosanus* and *Polypedilum* near *wittei* type Saka. Towards the top of this zone, numbers of *C. pseudomancus* again increase up to 50% or more, while *R.* near *ceratophylli* and *P. brevipetiolatus* fall back.

In Zone KatC1 (36.5-0 cm, ~1900-2001 AD), *C. pseudomancus* is again the dominant chironomid (59 ± 7.3%), occurring alongside sizable numbers of Tanytarsini type Mirambi (7 ± 4.4%) and *Dicrotendipes fusconatatus* (14 ± 4.8%). *Tanypus* near *guttatipennis* is still common at the base of this zone, but it becomes a minor component in recent samples. *P. brevipetiolatus*, *Nanocladius* near *saetheri*, *P.* near *wittei* type Saka, *T. formosanus* and *R.* near *ceratophylli* are strongly reduced.

The PCA axis 1 score and Hill's N2 diversity index of the fossil chironomid assemblages in Lake Katinda (Fig. 6a, b) show a down-core pattern that is fairly similar to abundance trends of *Tanypus* near *guttatipennis* and *Procladius brevipetiolatus*, and that is inversely related to that of *C. pseudomancus* (i.e., high values in KatC5, KatC4 and KatC2; and lower values in KatC3 and KatC1). The small peak in Hill's N2 diversity in the middle of zone KatC3b (at 298 cm) corresponds with low numbers of *C. pseudomancus*.

5.3.4Evolution of other aquatic fauna in Lake Katinda

Zone KatI8 (786 cm, ~3740 cal.yr BP) consists only of the interval at the very bottom of the core sequence and is characterized by low numbers of the phantom midge *Chaoborus ceratopogenes* (32%), and fairly high abundances of the ostracods *Zonocypris costata* (15%), *Oncocypris worthingtoni* and *O.* sp. type Kyaninga (both 2%), and mayfly larvae belonging to the Caenidae (32%) and Baetidae (7%). The presence of fish is evident from a single fish scale.

In zone KatI7 (786-722 cm, ~3740-3400 cal.yr BP), *C. ceratopogenes* shows a major increase (81 ± 4.5%) while numbers of Caenidae (8 ± 2.2%), Baetidae (3 ± 2.6%) and *Z. costata* (1 ± 1.4%) were reduced. *Oncocypris* type Kyaninga maintains its numbers, and chydorid cladocerans are present but scarce (1 ± 0.5%).

Zone KatI6 (722-369 cm, ~3400-1900 cal.yr BP), which covers most of KatC5 and the entire KatC4, is characterized by stable but somewhat lower numbers of *C. ceratopogenes* (67 ± 10.0%), and high abundances of Chydoridae (17 ± 8.6%). The abundances of these two taxa are more or less inversely proportional, but neither shows a clear trend through time. Two analysed samples (638 and 426 cm) yielded valves and headshields of seven chydorid species: *Chydorus parvus*, *Coronatella* cf. *rectangula*, *Dunhevedia crassa*, *Euryalona orientalis*, *Karualona iberica*, *Notoalona globulosa* and *Pseudochydorus* cf. *globosus*. This assemblage is supplemented by modest abundances of Caenidae (7 ± 3.4%), Baetidae (3 ± 2.7%) and *Zonocypris costata* (2 ± 1.7%). The pelagic ostracod species *Oncocypris* type Kyaninga occurs sporadically, as do *Oncocypris worthingtoni*, *Plumatella* sp., Type Z and

Ephemeridae. The thecamoeban *Arcella* is largely absent in the lower half of this zone, but it is continuously present in the upper section.

In zone KatI5 (369-224 cm, ~1900-900 cal.yr BP), chydorid cladocera (0.6 ± 1.4%) and the mayfly family Caenidae (1 ± 1.1%) are a minor component. The pelagic *C. ceratopogenes*, on the other hand, increases markedly with values up to 72-100% (mean of 91 ± 6.4%). Baetidae are absent from the bottom part of this zone (369-328 cm), except for a single occurrence at 346 cm. The abundance of fish scales increases and rises to ~150 remains per gram dry sediment at the top of the zone. *Hemicypris fossulata* is limited to the top of this zone (278-224 cm). The charophyte *Nitella* is completely absent from this zone.

Zone KatI4 comprises a single interval (222 cm, ~750 cal.yr BP) in which chydorid remains outnumber *C. ceratopogenes*, and *H. fossulata* (which was common in the upper part of KatI5) is replaced by *C. africana*.

Zone KatI3 (218-132 cm, ~700-350 cal.yr BP) is dominated by *C. ceratopogenes* (79 ± 11.0%) alongside significant numbers of chydorid cladocerans (12 ± 7.8%). Fish scales are also common (57 specimens ± 69/gram dry sediment).

Zone KatI2 (132-54 cm, ~350-150 cal.yr BP) comprises most of chironomid zone KatC2, except for the top. It is characterized by slightly lower but still increasing numbers of *C. ceratopogenes* (65 ± 11.5%; from 41% at 114.5 to 76% at 56 cm). This zone is also typified by high concentrations of chydorid remains, reaching a peak value of 2300 per gram at 75.5 cm. Three analyzed samples in this zone yielded five chydorid taxa: *Alona cambouei/guttata, Alona* cf. *verrucosa, Chydorus parvus, Coronatella* cf. *rectangula*, and *Pleuroxus* cf. *varidentatus*. Zone KatI2 is also typified by the highest abundances of *Arcella* (4 ± 4.3%), and includes the only record of the thecamoeban *Centropyxis*. Caddisfly remains (belonging to the Hydropsychidae), and oospores of *Nitella*, occur sporadically.

Zone KatI1 (54-0 cm, ~1850 AD-2001 AD), which broadly corresponds to KatC1 and the very top of KatC2, is characterized by peak abundances of *C. ceratopogenes* (91 ± 6.2%), the disappearance of chydorids and simultaneous reduction of Caenidae towards the present.

The Hill’s N2 of non-chironomid invertebrate fauna in Lake Katinda is generally higher in the bottom half of the record compared to the top half; it is quite low in KatI7 and fluctuates strongly throughout KatI6. The lowest values of Hill’s N2 are recorded in KatI5 and KatI1. The PCA axis 1 score gradually decrease from KatI8 towards the top of KatI6. From KatI5 onwards, PCA axis 1 scores follow the abundance trend of *Chaoborus* with high scores in KatI5 and KatI1, and low scores in KatI4 and KatI2.

5.3.5 Lake Wandakara sediment stratigraphy

The 481-cm long core sequence of Lake Wandakara (Fig. 8) mainly consists of dark to olive brown carbonate clays (carbonate content: 10-35%, mean ~16%) with vague to clear lamination alternating with mostly massive sapropelic clays (organic content: 10-57%, mean ~39%). Besides these clays, there is also a black massive sandy silt at 115-150 cm depth and a peat-like section of fibrous silty clay at the base of the core. In total we recognize 15 distinct lithostratigraphic units, suggesting strong variation in lake level and hydrology through time.

The magnetic susceptibility profile of the Lake Wandakara sequence comprises four broad zones. The first zone comprises 481-320 cm (~1900-1000 cal. yr BP) with a mean χ value of ~1150 10^{-6} m³/kg and four peaks (at 431, 421, 409 and 327 cm) of which the bottom- and topmost correspond with silty horizons. The second zone comprises 320-161 cm (~1000-400 cal. yr BP) with χ values generally less than 200 10^{-6} m³/kg except in four minor peaks corresponding to silty horizons (at 253, 233, 215 and 180 cm). The third zone at 161-114cm (~400-~250 cal. yr BP) starts in laminated carbonate clay (at 161-150 cm) but mostly comprises a massive silt unit (150-114 cm) with extremely high χ values averaging 10,600 10^{-6} m³/kg. The fourth zone comprises the section 114-0 cm (~250 cal. yr BP-2001 AD), displaying modest values averaging ~1700 10^{-6} m³/kg after a minimum of ~500 10^{-6} m³/kg in the sapropel at 110-100 cm. The χ signal increases until around 60 cm depth after which the values decrease again to reach a value of 1300 10^{-6} m³/kg at the surface.

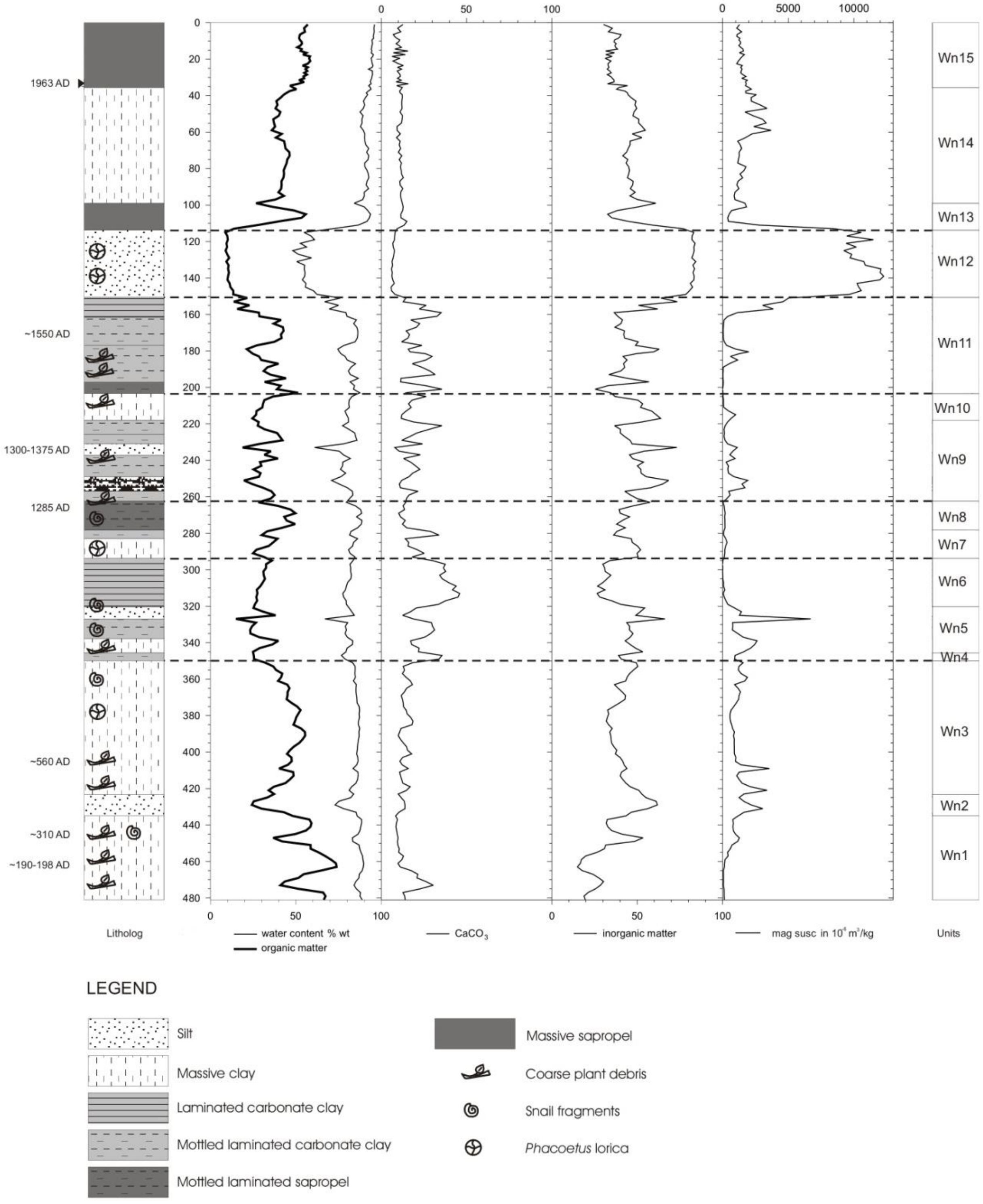

Figure 8: Lithostratigraphy and sediment composition of Lake Wandakara. All sediment components are expressed as % of dry mass, unless otherwise indicated (Modified from Bessems, 2007)

5.3.6 Lake Wandakara faunal stratigraphy and zonation

A total of 53 chironomid taxa were present among 3573 specimens recovered from the 2000 year sediment record of Lake Wandakara, as well as 26 other aquatic invertebrate taxa among which are ten non-chironomid insect taxa, eight ostracods and two non-chydorid cladocerans (Table 1). Species-level identification of chydorid Cladocera from 18 selected samples yielded 15 taxa.

The concentration of chironomid head capsules mostly varied between ~200-300 hc/g, with very low densities (<25 hc/g) in the unit of massive sandy silt between 115 and 155 cm, and high densities (>500 hc/g) in a rather limited number of intervals (411-381, 235, 187-163, 105-82,5 and 34,5-8.5 cm, see Fig. 9a, b). Concentrations of non-chironomid remains varied extremely from 9 to ~6800 remains/g dry sediment, with the highest densities found near the bottom of the record (475-381 cm) and, as for the chironomids, with very low densities (<40 remains/g) between 115 and 155 cm (Fig. 10a, b). To a certain degree, the density patterns of both chironomid and other aquatic invertebrate fossils seem to follow the organic matter content of the sediments. CONISS and the broken-stick model identified six significant chironomid assemblage zones (WanC6 to WanC1). We additionally divided the top zone in two sub-zones based on deep branching in the CONISS dendrogram (Fig. 9a, b). For the non-chironomid invertebrates, five significant assemblage zones were identified (WanN5-WanN1; Fig. 10a, b).

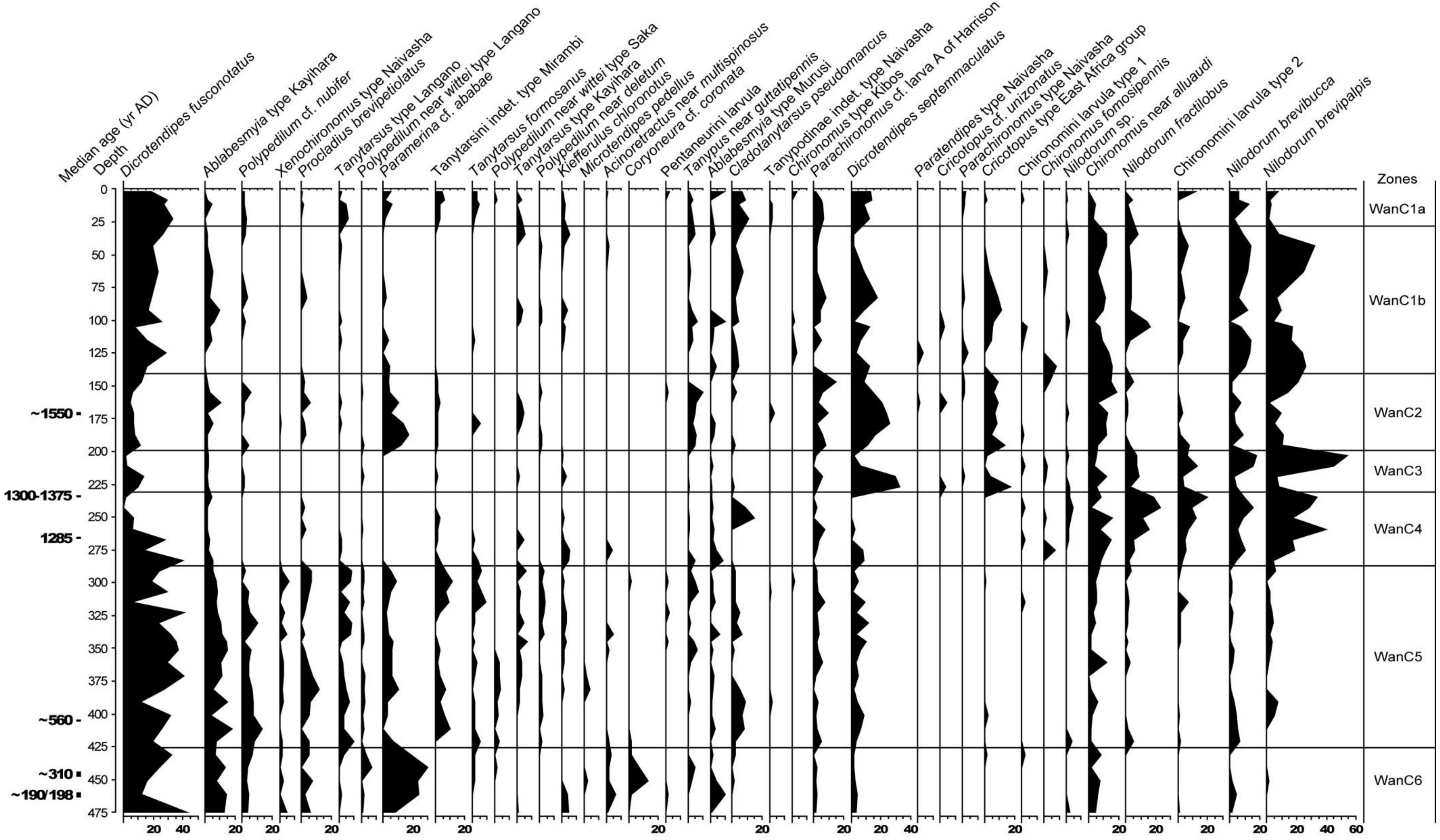

Figure 9a: Chironomid stratigraphy in Lake Wandakara. Chronology based on ^{210}Pb-dating and AMS ^{14}C ages (Bessems, 2007).

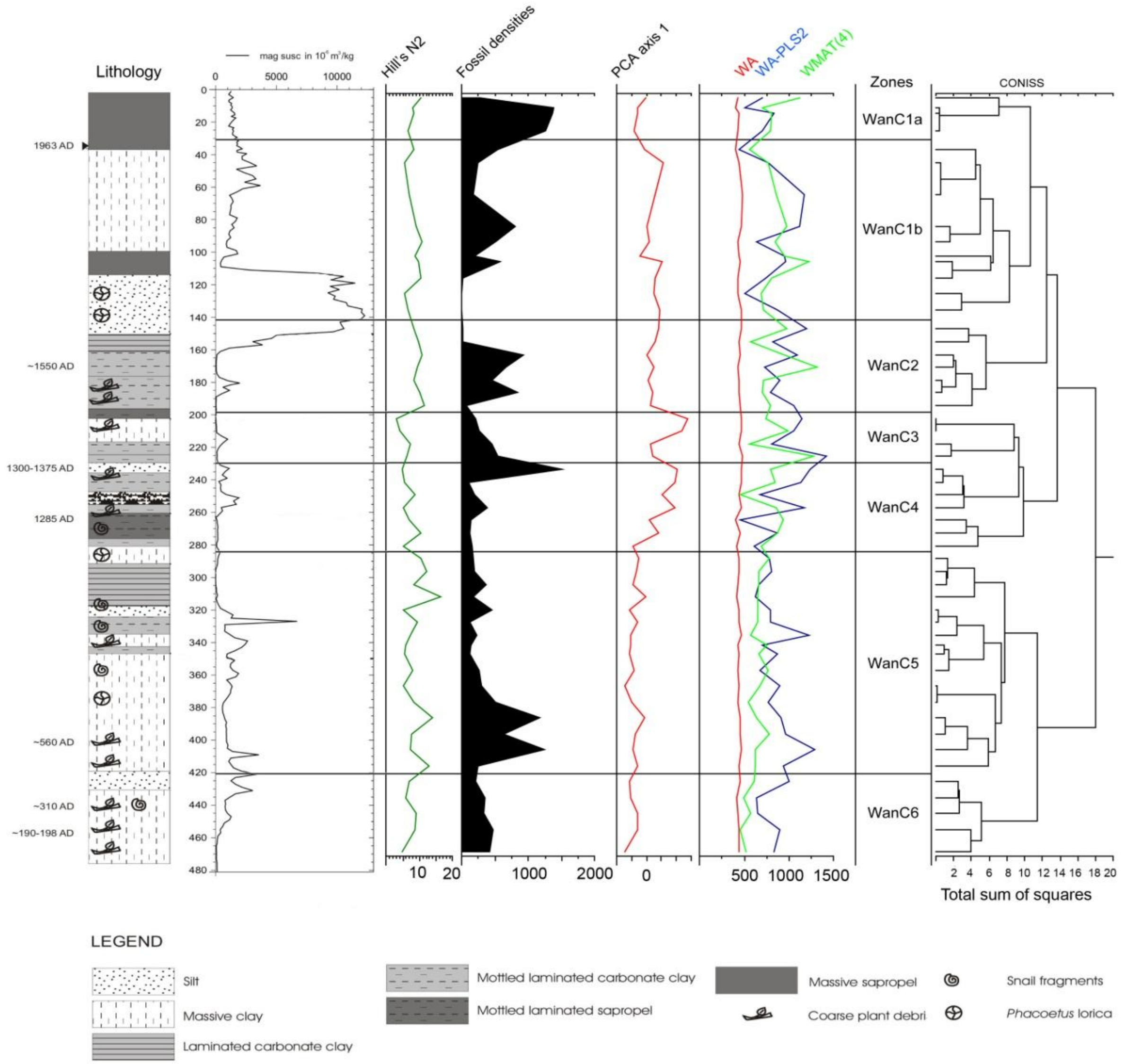

Figure 9b: Lake Wandakara: Litholog, magnetic susceptibility, Hill's N_2 diversity index, number of headcapsules per gram dry weight of sediment, PCA axis 1-sample scores, chironomid-based salinity reconstructions using weighted averaging (WA) optima, weighted-averaging partial least squares (WA-PLS(2)), and a weighted modern analogue technique (WMAT), zonation as determined BSTICK and CONISS.

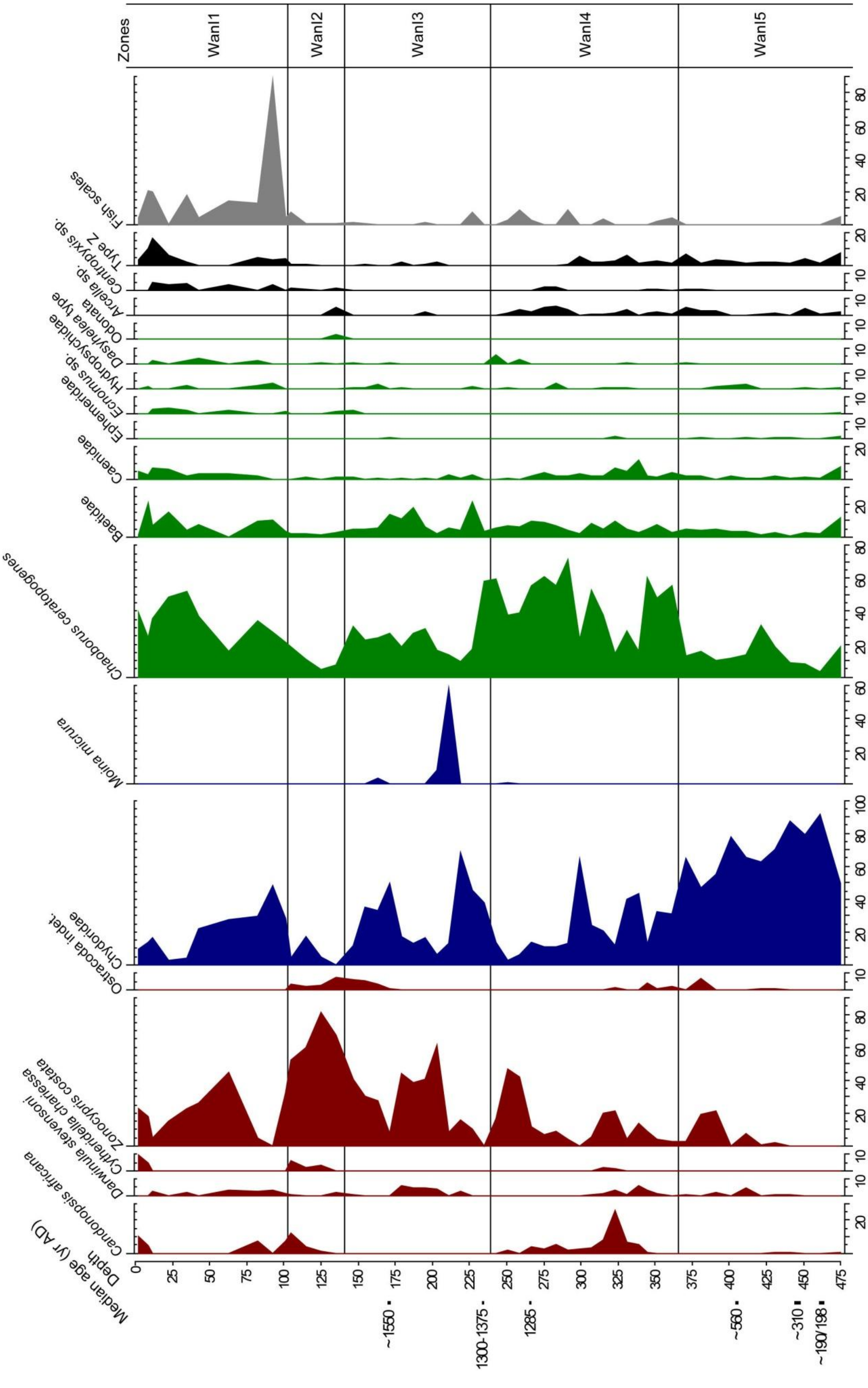

Figure 10a: Stratigraphic distribution of Ostracoda (red), Cladocera (blue), Insecta (green) and other aquatic invertebrate taxa (black) in Lake Wandakara, fossil densities of fish scales expressed as number of remains per gram dry weight. Chronology based on ^{210}Pb-dating and AMS ^{14}C ages (Bessems, 2007).

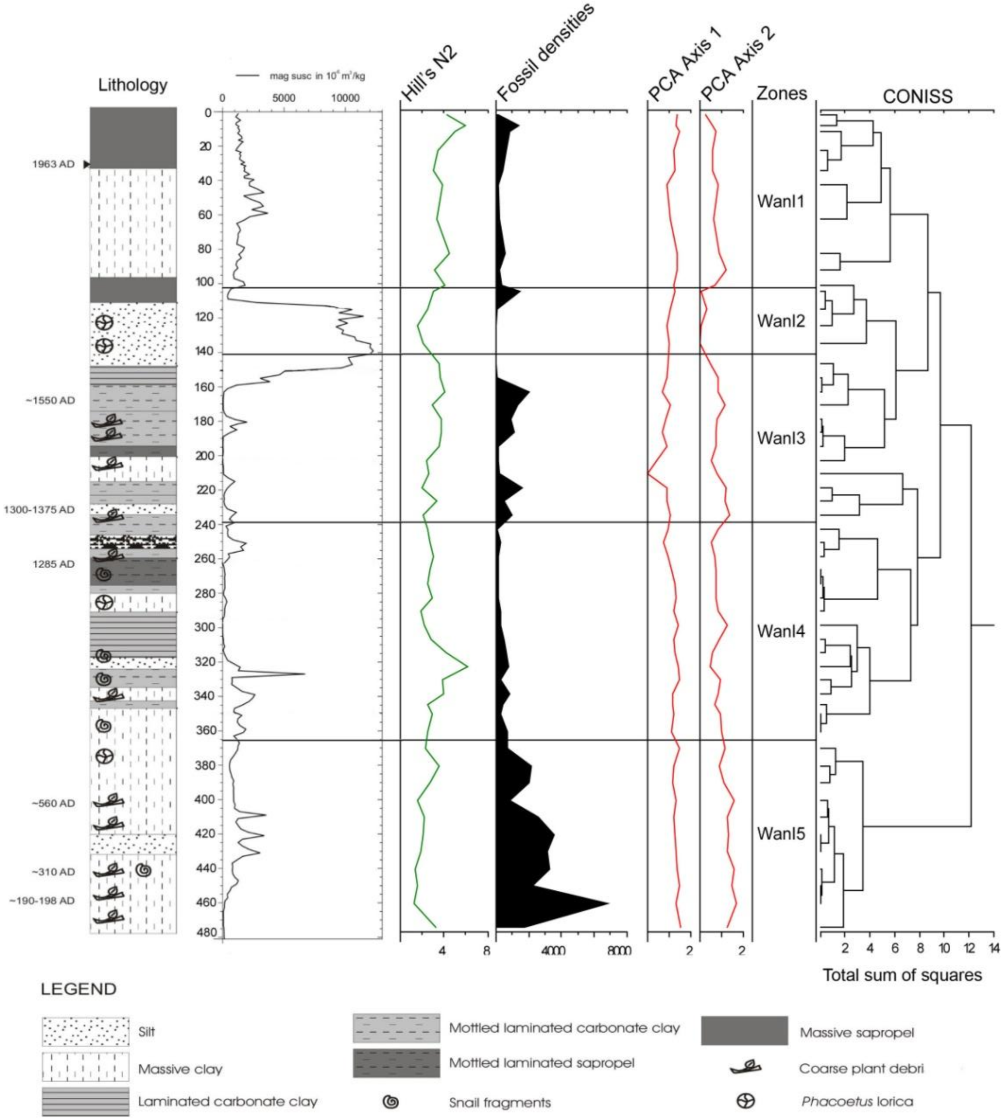

Figure 10b: Lake Wandakara: Litholog, magnetic susceptibility, Hill's N_2 diversity index, overall invertebrate fossil densities expressed as number of remains per gram dry weight of sediment, PCA axis 1-scores, PCA axis 2-scores, zonation as determined BSTICK and CONISS

5.3.7 Evolution of the chironomid community in Lake Wandakara

Zone WanC6 (475-426 cm, ~1900-1600 cal.yr BP) is characterized by relatively high numbers of *Dicrotendipes fusconatatus* (25 ± 12.2%), *Paramerina* cf *ababae*, *Ablabesmyia* type Kayihara and *Ablabesmyia* type Murusi. *Corynoneura* cf *coronata* and *Acinoretractus* near *multispinosus* are present in most intervals, whereas *Cladotanytarsus pseudomancus* and *Nilodorum* spp. occur only sporadically.

In zone WanC5 (426-287 cm, ~1600-900 cal.yr BP), numbers of *D. fusconatatus* (28 ± 10.0%) and *A.* type Kayihara remain high, although the latter falls back towards the top of this zone. *Paramerina* cf *ababae* significantly decreases in favor of *Tanytarsus* types Langano, *T.* type Kayihara, Tanytarsini indet. type Mirambi, *Cladotanytarsus pseudomancus* and, to a lesser extent, *Polypedilum* cf *nubifer*.

The distinct decrease in chironomid diversity within zone WanC4 (Hill's N2: 10.3 at 275 cm to 4.8 at 235 cm) is linked to the disappearance of several taxa, such as *Polypedilum* cf. nubifer and *Paramerina* cf. *ababae,* in favor of *Nilodorum* spp. and Chironomini larvula type 2 (which probably comprises all juvenile *Nilodorum*; Eggermont and Verschuren, 2004b). *Dicrotendipes fusconatatus* gradually decreases whereas *Chironomus* near *alluaudi* becomes more abundant.

Zone WanC3 (231-199 cm, ~650-525 cal.yr BP) shows pronounced differences between top and bottom intervals, as reflected by deep branching in the CONISS dendrogram. The lower part of the zone holds low numbers of *Nilodorum* and Chironomini larvula type 2, but high numbers of *Dicrotendipes* spp. and *Cricotopus* type East Africa group. Chironomid species composition in the upper part of the zone resembles that in the top sediments of WanC4 with high abundances of *Nilodorum* spp. and Chironomini larvula type 2, and low abundances of *Dicrotendipes*.

Some of the taxa that were absent in WanC4 and WanC3 reappear in zone WanC2 (199-141 cm, ~525-325 cal.yr BP). These include *Paramerina* cf. *ababae*, *Polypedilum* cf. *nubifer* and *P.* near *deletum*. This zone is further typified by relatively high numbers of *Tanypus* near *guttatipennis*, *Parachironomus* cf. larva A of Harrison and *C.* type East Africa group. *D. fusconotatus*, on the other hand, slightly falls back.

In subzone WanC1b (141-28.5 cm, ~325-50 cal.yr BP), both *D. fusconatatus* (20 ± 6.4%) and *C. pseudomancus* (3 ± 2.0 %) show an increase from the bottom to the top, while numbers of *D. septemmaculatus, A.* type Kayihara and *Cricotopus* type East Africa decrease. *Nilodorum brevibucca*, *N. brevipalpis* and *C.* near *alluaudi* are also an important component of the chironomid fauna in this subzone. Subzone WanC1a (28.5 cm – top, ~1960 AD – 2001 AD) is dominated by *Dicrotendipes fusconatatus* and *D. septemmaculatus*. *Nilodorum brevipalpis,* Chironomini larvula type 2 and *Chironomus* near *alluadi* are strongly reduced compared to the other subzone, whereas *C. pseudomancus,* Tanytarsini indet. type Mirambi, *Tanytarsus formosanus, Tanytarsus* type Langano and *Paramerina* cf. *ababae* show an increase.

The Hill's N2 diversity index varies strongly in zone WanC5, which is likely related to fluctuating numbers of *D. fusconotatus.* The index shows a pronounced increase at the transition between WanC3 and WanC2 (~525 cal.yr BP). Throughout the core, PCA axis 1 scores follow the abundance pattern of *N. brevipalpis*.

5.3.8 Evolution of other aquatic fauna in Lake Wandakara

Zone WanI5 (475-366 cm, ~1900-1250 cal.yr BP) is dominated by chydorids, although their relative abundance decreases towards the top of this zone (from 92% at 461 cm down to 47% at 381 cm). *Notoalona globulosa* dominated all five samples identified to species level. The 14 other chydorid species recovered from this zone are *Alona cambouei/guttata, Alona sp., Alonella excisa, A. exigua, Chydorus eurynotus, C. parvus, Coronatella* cf. *rectangula, Dunhevedia crassa, D. serrata, Euryalona orientalis, Karualona iberica, Pleuroxus toumodensis, P.* cf. *varidentatus,* and *Pseudochydorus* cf. *globosus*. Ostracod abundance gradually increases from 431 cm upwards. Fish remains are absent except for a single scale in the deepest interval (475 cm). *Chaoborus ceratopogenes* is present but in rather low abundance (14 ± 7.4%).

In zone WanI4 (366-239 cm, ~1250-650 cal.yr BP), chydorids are significantly less abundant than in WanI5, except for a pronounced peak at 299 cm (~900 cal.yr BP). From the single sample identified to species (259 cm) only two chydorid taxa were recovered: *P.* cf. *globosus* and *Alona* sp. The relative abundance of *Chaoborus ceratopogenes* (45 ± 17.4%), Baetidae and Caenidae is higher than in WanI5. Other aquatic invertebrate taxa frequently present in this zone are mayfly larvae of the family Ephemeridae, the caddisfly larvae *Ecnomus* sp. and Hydropsychidae, the biting midge (Ceratopogonidae) *Dasyhelea* type, the thecamoeban *Arcella* sp. and type Z. The ostracods *Candonopsis africana* and *Zonocypris costata* are fairly abundant, with relative abundances reaching 26 and 47%, respectively. Fish remains are also more common compared to the previous zone.

In zone WanI3 (239-141 cm, ~650-325 cal. yr BP), the density of *Chaoborus* remains is fairly high compared with WanI4 (on average 148 and 163 pairs of mandibles /g dry sediment, respectively), but their percent abundance decreases to 24% (± 12.7%) in favor of mostly littoral species such as chydorid cladocerans, *Z. costata* and Baetidae. *Moina micrura* ephippia are so abundant in the single interval at 211 cm (~570 cal.yr BP) that they dominate the fossil assemblage. *Dunhevedia crassa* is the most abundant chydorid species in four out of five samples from this zone identified to species level. The seven other chydorid species are *Alona cambouei/guttata, Alona* sp., *Alonella exigua, Chydorus eurynotus, C. parvus, Pleuroxus toumodensis* and *Pseudochydorus* cf. *globosus*.

Zone WanI2 (141-103 cm, ~325-230 cal.yr BP) is dominated by the ostracod *Z. costata*, and also *Cytheridella chariessa* is encountered more frequently in this zone than in any other zone. In two chydorid samples identified to species, four taxa were present: *Alona* sp., *Chydorus eurynotus*, *Dunhevedia crassa* and *Pseudochydorus* cf. *globosus*.

Zone WanI1 (103-0 cm, ~1780-2001 AD) is characterized by relatively high numbers of the thecamoeban *Centropyxis* sp., mayflies of the Caenidae family, the biting midge (Ceratopogonidae) *Dashylea* type and the caddisfly *Ecnomus* sp. This zone is also characterized by fairly high numbers of fish scales. The start of subzone WanI1b (103-39 cm, ~1750 – 1950 AD) is typified by relatively high abundances of chydorids, mayflies belonging to the Baetidae and the ostracod *Candonopsis africana*. *Chaoborus ceratopogenes* abundance (27 ± 9.0%) is similar to that in WanI3. In three chydorid samples analysed we encountered in total six species: *Alona* sp., *Chydorus eurynotus, C. parvus, Dunhevedia crassa, D. serrata* and *Pseudochydorus* cf. *globosus.* In subzone WanI1a (~1950-2001 AD) there is a switch to higher abundances of *Chaoborus* (40 ± 11.2%), while abundances of chydorids and *Z. costata* decrease. Only three chydorid species were recovered from the two samples analysed in this subzone: *Alona* sp., *Karualona iberica* and *Pseudochydorus* cf. *globosus*.

The Hill’s N2 diversity index starts at low values in WanI5 (as this zone is strongly dominated by chydorids, which are not included in its calculation), and rises in WanI4 and WanI3. It decreases in WanI2 (due to the dominance of *Z. costata*), but recovers again in WanI1. PCA axis 1 scores are rather invariable and dominated by the effect of the mass occurrence of *Moina micrura* at 211 cm. PCA axis 2 scores (Figure 9) seem to be determined by the distribution of littoral aquatic insect species.

5.3.9 Chironomid-inferred salinity changes in lakes Katinda and Wandakara

Excluding unidentifiable specimens, five of the 57 fossil chironomid taxa recovered from Lake Katinda are not represented in the Eggermont *et al.* (2006) calibration dataset. These five taxa (*Stempellina johanseni*, *Zavriella* type Amboseli NP Pool 3, near *Paradoxocladius* type Kifuruka, Chironomini indet. type Katinda and *Polypedilum* type Mirambi) are too rare, also in our dataset (together comprising 0.07% of the total Lake Katinda inventory), to be included in quantitative analyses. Quantitative salinity reconstructions based alternatively on WA, WA-PLS(2) and WMAT-4 show some differences, particularly in zones KatC1, KatC3a-b and near the base of the record in KatC5 (Fig. 5). These may be due to the weak correlation between chironomid species distribution and salinity in a broad range of fresh waters (Eggermont *et al.*, 2006). However, the general trends indicate that Lake Katinda remained fresh (ranging between ~400 and 1000 µS/cm) throughout the past 4000 years (Fig. 5). The present-day conductivity of Lake Katinda (743 µS/cm in 2001) is estimated reasonably well when inferred from surface-sediment chironomid assemblages using the WA-PLS(2) and WMAT-4 methods (629 µS/cm and 724 µS/cm), but the WA estimate of 437 µS/cm is significantly lower. All Lake Katinda chironomid assemblages have good modern analogues in the calibration dataset and sample-specific error for the model outputs is similar throughout the record (on average 0.35 log10 conductivity units). All three inference models reconstruct elevated conductivity in zone KatC3a-b, and comparable values in the top 38cm of zone KatC1. The change is most pronounced in the WA-PLS(2) reconstruction, because peak abundances of *C. pseudomancus* and *Ablabesmyia* type Kayihara exert greater influence on inferred conductivity using this method. The salinity changes inferred on the basis of chironomid community composition are associated with changes in aquatic invertebrate composition: episodes with elevated conductivity correspond to zones with peak abundances of *Chaoborus* (KatI7, KatI5-3 and KatI1).

Of the 48 identifiable chironomid taxa encountered in the Lake Wandakara record, two are not represented in the Eggermont *et al.* (2006) calibration dataset due to their general scarcity. Here the salinity reconstructions based alternatively on WA, WA-PLS(2) and WMAT-4 differ more substantially. The present-day conductivity of Lake Wandakara (1125 µS/cm in 2001) is estimated reasonably well when inferred from surface-sediment chironomid assemblages using the WA-PLS(2) and WMAT-4 methods (698 µS/cm and 1120 µS/cm), but the WA estimate of 432 µS/cm is significantly lower. Also WA estimates based on the fossil samples are systematically below the WA-PLS(2) and WMAT-4 estimates, and rather invariant (total range 398 to 481 µS/cm). This is probably because Lake Wandakara is one of the more concentrated freshwater lakes in the Eggermont *et al.* (2006) calibration dataset. Most freshwater chironomid taxa found there, both today and in the past, have modelled conductivity optima significantly below the present-day Lake Wandakara conductivity, and approach their upper tolerance limit at this site. WA-PLS2 and WMAT-4 indicate that salinity varied between 400 and 1500µS/cm, but reconstruct some rather strong flip-flops between intervals. These flip-flops reflect the sometimes large changes in abundance of dominant chironomid taxa between intervals. WMAT-4 suggests a fairly gradual increase in conductivity between ~800-700 cal.yr BP, and again in the last century (Fig. 6a, b). Although sample-specific errors for the various model outputs are similar to those for the Lake Katinda record (on average 0.35 log10 conductivity units), the salinity reconstruction for Lake Wandakara is somewhat problematic since 15 samples (28% of the total) do not have good modern analogues in the calibration dataset (mainly in core sections 155-187 cm and 361-441 cm).

5.4 Discussion

5.4.1 Lake Katinda – lake history

Our record of the environmental history of Lake Katinda starts at about 3740 cal. yr BP. The fossil assemblage of the aquatic invertebrate community inhabiting Lake Katinda at that time (KatI8) is dominated by littoral insects and ostracods. In western Uganda crater lakes, the proportion of pelagic *Chaoborus* to littoral insect remains in mid-lake surface sediments depends mainly on lake depth and distance to shore (Rumes, Chapter 4). In conjunction with the relatively high abundance of the chironomid *Dicrotendipes fusconotatus*, known to inhabit submerged weedbeds (Verschuren, 1997), this suggests that lake level was low and that a well-developed fringe of aquatic macrophytes was present. That relatively few chydorids were encountered may be due to a prior phase of elevated conductivity, as most chydorids in the region are limited to dilute freshwater lakes (Rumes, Chapter 1). However, no such salinity signature can be inferred from the species composition of the chironomid assemblage.

Between ~3740 and 3400 cal.yr BP (KatI7), the fossil assemblage is clearly dominated by *Chaoborus*. In the chironomid fossil assemblage, numbers of *Dicrotendipes* decrease in favour of Tanytarsini indet. type Mirambi, *Procladius brevipetiolatus* and *Tanypus* near *guttatipennis*. Both Tanypodiinae have been found together in a wide variety of habitats (Verschuren, 1997 and primary references therein), but the predatory *Procladius* is known to occur in higher densities on stable mud bottoms (Darlington, 1977; Clark *et al.*, 1989). Tanytarsini indet. type Mirambi is widespread in Ugandan and Kenyan lakes (Eggermont & Verschuren 2004a) and highest abundances of this species were usually found in more productive lakes (based on species distribution data from Eggermont, 2004; and environmental data from Rumes, Chapter 1). However, we have no other indication that Lake Katinda was particularly eutrophic at that time. Overall the fossil assemblage suggests a significant transgression shortly after ~3740 cal.yr BP, with a strong increase in lake depth and expansion of stable mud bottom habitat and retreat of aquatic macrophyte cover. After ~3400 cal.yr BP (KatI6) *Chaoborus* abundance decreased somewhat in favour of littoral insects and chydorids which indicates a decrease in lake level. However *Chaoborus* still dominates the invertebrate assemblage between ~3400 and 2150 cal.yr BP, with the exception of a short interval around 2800 cal.yr BP. At this time, *Chaoborus* abundance decreased in favour of chydorids and littoral insects, resulting in a temporary increase in the recorded species diversity of the local aquatic invertebrate community (peak in Hill's N2; Fig. 5). Abundances of both Baetidae and *Plumatella* increased, indicating that submerged weedbeds are approaching the core site (Rumes, Chapter 4). This implies the presence of a well-developed fringe of aquatic macrophytes, suggesting a temporary decrease in lake level. Also some rare chironomid species are recorded from this period: *Polypedilum* near *wittei* type Saka, *Polypedilum* near *wittei* type Langano, and *Thienemanniella* cf. sp. D of Epler. *Polypedilum* is a genus whose Holarctic (Pinder & Reiss 1983) and African (Harrison 1987; Kibret & Harrison 1989) representatives are most often associated with vegetated near-shore habitat. This zone corresponds with a slight increase in sedimentary carbonate content, which can be explained by evaporative concentration and/or reduced groundwater outflow causing calcite to precipitate from the water column.

At ~2150 cal.yr BP (shortly before the transition to KatI5), the abundance of *Cladotanytarsus* starts to increase considerably, at the expense of *Procladius brevipetiolatus* and *Tanypus* near *guttatipennis*. This change in abundance probably reflects a gradual change in the texture of local shallow-water substrates, since the former species is known to have a preference for sandy substrates with coarse organic matter (Petr, 1971; Eggermont *et al.*, 2007), whereas the two latter species are known to occur in highest densities on stable mud bottoms. During this shift, the proportion of *Chaoborus* remains to littoral insect remains remains fairly stable up to ~2000 cal.yr BP, which suggests that lake level did not vary dramatically. From ~2000 cal.yr BP (at the start of KatC3 and KatI5), a pronounced change in sediment composition occurs, from clayey sapropel to silty and peaty clay. At the next sampled interval (372 cm) *Chaoborus* abundance decreased dramatically in favour of Baetidae, *Plumatella*, and unknown insect mandible Type Z. This coincides with the presence of several *Polypedilum* spp. and *Tanytarsus* spp., two genera which are often associated with vegetated near-shore habitat (Harrison, 1987; Verschuren, 1997; Verschuren *et al.*, 2000). The fact that vegetation-dwelling chydorid Cladocera were not able to profit from this apparent decrease in lake level suggests that the change in bottom habitat was accompanied by a reduction in transparency, which would have negatively affected aquatic macrophytes. Whether this reduced transparency was mostly due to increased mineral turbidity or algal biomass is unclear. In the sediment record this period is also marked by an increase in both inorganic matter content and magnetic susceptibility, which are indicative of increased erosion. A study of the modern-day aquatic communities in the Uganda crater lakes found a negative correlation between chydorid abundance (and species richness) and lake trophic state, and explained it as due to the associated reduction of aquatic macrophyte habitat (Rumes, Chapter 1).

The most distinct change in both chironomid and non-chironomid fossil assemblages throughout Lake Katinda's recorded history occurs ~1900 cal.yr BP. At that time, mud-dwelling *Procladius* and *Tanypus* strongly decrease in favour of *Cladotanytarsus*, *Nilodorum* and Tanytarsini indet type Mirambi. In lakes Naivasha and Oloidien in central Kenya, both *Cladotanytarsus pseudomancus* and *Nilodorum brevibucca* were found to prefer sandy substrate with coarse organic material (Eggermont *et al.*, 2007). Among the other aquatic biota, abundances of both *Chaoborus* and fish remains increase strongly, whereas chydorid Cladocera virtually disappear, and Caenidae and Baetidae are strongly reduced. Strikingly the abundance of *Zonocypris costata*, an ostracod species able to flourish under a wide range of environmental conditions (Rumes, Chapter 2, 3), remains fairly constant. Overall the diversity of both the chironomid fauna and the aquatic invertebrate community is reduced. Simultaneously, magnetic susceptibility of the sediments increases and the percent inorganic matter continues to rise, which is indicative of an increased input of clastic mineral material. We therefore infer that substantial clearing or disturbance of terrestrial vegetation inside the crater basin caused erosion of topsoil which was flushed into the lake and resulted in coarser-grained and less organic lake-bottom sediments. High mineral turbidity hampered development of aquatic macrophytes, resulting in an impoverished aquatic invertebrate fauna. Given the frequent peaks in fossil density from this level onward, high turbidity may have benefited *Chaoborus* directly by curtailing visual predation by fish. The density of fish scales also increases, however, suggesting either that human catchment disturbance enhanced total lake productivity, or that the early settlers favourably managed the lake's fisheries.

This situation remains fairly stable until ~700 cal.yr BP (KatI4), when chydorid abundance exceeds that of *Chaoborus* and very few non-chironomids are present. In the chironomid assemblage, the small reduction in *Cladotanytarsus* and the relatively high numbers of *Cricotopus* type East Africa suggest expansion of stable mud bottoms (Verschuren, 1997). A further increase in stable mud bottom habitat from ~700 to 350 cal.yr BP (KatI3) is suggested by increases of *Procladius*, *Tanypus* and *Cricotopus* and is accompanied by a gradual decrease in magnetic susceptibility. This suggests that the changes bottom habitat are determined by changes in erosion rather than by changes in lake depth. From ~500 cal.yr BP (the upper part of KatC3a) the abundance of *Cladotanytarsus* and *Nilodorum,* both preferring sandy substrate with coarse organic material, starts to decrease. At the same time there is a drastic decrease in magnetic susceptibility of the sediments. Both of these provide evidence for significantly reduced input of coarse-grained eroded soils. In KatI3, high abundances of *Chaoborus* are centred about ~650 and ~450 cal.yr BP, while *Zonocypris* and several littoral insects (Hydropsychidae, Baetidae, and Caenidae) become more abundant towards ~500 cal.yr BP. The results suggest relatively high lake levels from ~700 to 350 cal.yr BP interrupted by a minor dry phase, centred ~500 cal. yr BP, during which anthropogenic erosion significantly decreased.

The next zone (~350 to 200 cal.yr BP, KatI2) is comprised of black silty peat, and characterized by low magnetic susceptibility. The abundance of chydorids and *Arcella* is higher than in any other part of the record, while chironomids associated with vegetated near-shore habitats (*Cricotopus, Dicrotendipes, Tanytarsus, Polypedilum, Nanocladius*) thrive. Increased abundance of *Rheotanytarsus* may also indicate lower lake levels (Eggermont, 2004). Both magnetic susceptibility and *Cladotanytarsus* abundance are low, and levels of inorganic matter content are similar to those prior to anthropogenic erosion (Fig. 4). Numbers of both fish and *Chaoborus* decrease, while the abundance of littoral insect taxa hardly changes. The increase of chironomids associated with stable mud bottom (*Procladius, Tanypus*) is not related to an increase in lake level, but rather reflects a reduction in coarse sandy habitats. Overall abundance trends reflect a significant reduction in lake level. However, at no point the lake became a swamp. Lake level increased again between ~200 and 100 cal. yr BP, which is reflected by a decrease in chydorids and *Arcella.*

Changes in the fossil chironomid assemblages at ~100 cal. yr BP include new reduction or disappearance of species associated with stable mud bottom (*Procladius* and *Tanypus),* and species associated with vegetated near-shore habitats (*Cricotopus, Tanytarsus, Polypedilum, Nanocladius*). Numbers of both *Cladotanytarsus* and *Dicrotendipes fusconotatus* increase, as does magnetic susceptibility and the inorganic matter content. Aquatic invertebrate assemblage diversity also decreases due to the very high abundance of *Chaoborus* remains.

Chydorids are absent from the top sediments, and abundance of most other littoral species is reduced. *Zonocypris* remains are more abundant in the surface sediments. As at ~1900 cal. yr BP, increased disturbance of terrestrial vegetation in the crater basin probably resulted in soil erosion and enhanced turbidity. This recent evolution of the fossil assemblages is consistent with the modern-day status of Lake Katinda, a highly eutrophic ecosystem with low water-column transparency and poorly developed aquatic vegetation.

To summarize, our record starts at ~3900 cal. yr BP with shallow lake conditions and a fairly diverse fauna of aquatic invertebrates. Diversity indices fluctuate between ~3740 and 2150 cal. yr BP as episodes of higher lakes level result in a lower proportion and lower diversity of littoral taxa being recovered, and episodes of lower lake level are characterized by a more diverse assemblage of both littoral and pelagic taxa At ~2150 cal. yr BP, changes in chironomid composition indicate soil erosion in the catchment area. Following a short drought centred ~2000 cal. yr BP, the effect of increased soil erosion is confirmed by pronounced changes in the other invertebrate fauna and sediment composition. High levels of soil erosion and low aquatic diversity continued until ~500 cal. yr BP, at which time both lake level and erosion decreased resulting in a higher number of aquatic macrophytes and associated invertebrates. Lake levels again increased between ~200 and 100 cal. yr BP, as reflected by a decrease in species diversity and the lower number of littoral taxa. From ~100 cal. yr BP onwards, agricultural activity appears to have recommenced as reflected by a further reduction in species diversity and high magnetic susceptibility of the sediments.

5.4.2 Lake Wandakara – lake history

In Lake Wandakara the recovered sediment record starts at about 1900 cal.yr BP, with an aquatic invertebrate community characterized by various benthic chydorid Cladocera and littoral aquatic insects. In combination with a relatively low abundance of *Chaoborus* and in consideration of the gently sloping northern shore (Fig. 1), this could be interpreted as low lake-level conditions permitting the development of a broad fringe of aquatic macrophytes. This is also reflected in the chironomid fauna dominated by *Dicrotendipes fusconotatus* and *Paramerina* cf. *ababae*, which are both known to inhabit submerged weedbeds (Kibret & Harrison, 1989; Eggermont 2004; Rumes Chapter 1). This lasted until ~1600 cal.yr BP (WanC5), when the deposited sediments changed from clay to silt (435-424 cm), and there was a series of three peaks in magnetic susceptibility of the sediment. In the chironomid assemblage *Paramerina* abundance decreased drastically in favour of *Cladotanytarsus*. Chydoridae as a group temporarily decreased, as did some other littoral taxa (*Arcella*, Hydropsychidae). At the same time, there was a small peak in *Chaoborus* abundance and *Zonocypris costata* increased. A short transgression, with intensive run-off created by heavy rainfall, may have brought an increased amount of terrestrial coarse debris into the lake. However, at no point did high turbidity or an increase in lake trophic state prevent the development of aquatic macrophytes, as evidenced by the chironomid faunal assemblage. For the remainder of WanI5 (~1600 to 1250 cal. yr BP), chironomid assemblages remained fairly stable, dominated by species associated with stable mud bottoms and aquatic macrophytes. In the aquatic invertebrate assemblage lower *Chaoborus* abundance and higher diversity of littoral invertebrates indicate a return to lower lakes levels, which is confirmed by the presence of snail fragments and coarse plant debris in the sediment record.

In the bottom part of WanI4 (~1250 up to 900 al. yr BP), at first high lake levels persist as indicated by high numbers of pelagic *Chaoborus*; followed by low lake levels when chydorid numbers briefly exceeded those of *Chaoborus* and there is a small increase in chironomid taxa associated with submerged macrophytes (*Tanytarsus, Paramerina,* and *Polypedilum*). At ~900 cal.yr BP, chironomid species associated with vegetated near-shore habitats (*Xenochironomus, Tanytarsus, Paramerina* and *Polypedilum*) and species associated with stable mud bottoms (*Procladius* and *Tanypus),* were replaced by species which prefer sandy substrate with coarse organic material *(Nilodorum, Chironomus* near *alluaudi,* and to a lesser extent *Cladotanytarsus*) (chironomid habitat preferences based on Verschuren, 1997; Eggermont, 2004; Eggermont *et al.*, 2007). These changes, coupled with an increase in the inorganic matter content of the sediment, are indicative of increased land use and associated erosion in the crater basin. During this period (the upper part of Wan I4; ~900 up to 650 cal.yr BP) *Chaoborus* dominated the non-chironomid assemblages, chydorid abundance was very low and the tolerant *Zonocypris* becomes more abundant.

Zone WanI3 (239-141 cm, ~650-325 cal. yr BP), comprises both WanC3 (~650-525) cal.yr BP and WanC2 (~525-325 cal.yr BP). The former starts out with high abundances of chydorids, Baetidae mayflies and chironomids associated with vegetated near-shore habitats (*Cricotopus, Dicrotendipes*) which are all indicative of lower lake levels. It is later characterized by chironomid species which prefer sandy substrate with coarse organic material, sediment with high inorganic matter content, and a series of peaks in magnetic susceptibility, which are indicative of increased erosion in the crater basin. As such, an initial decrease in lake level was followed by an increase in erosion during conditions of low lake level. In WanC2, there is a general decrease in chironomid species which prefer sandy substrate with coarse organic material in favour of chironomids associated with vegetated near-shore habitats, as well as a decrease in inorganic matter content. Both are suggestive of a decrease in erosion. The proportional increase of the pelagic *Chaoborus* to littoral could reflect an increase in lake level rather than in trophic state as Chydoridae and Baetidae remain abundant.

In WanI2 (~325 and 250 cal.yr BP) fossil densities are very low, and their poor state of preservation suggests that some of them may have been reworked. Magnetic susceptibility in this interval is very high, and Bessems (2007) suggested that it may be defined as an instantaneous input, the result of intensive run-off created by heavy rainfall, which brought an immense amount of terrestrial coarse debris into the lake. If true, this event would likely represent the region-wide lake transgression dated to ~1815 AD in the central Kenya Rift Valley (Verschuren *et al.*, 2000b). An instantaneous deposit would agree with some of our results, since the chironomid assemblage is dominated by species which prefer sandy substrate with coarse organic material *(Nilodorum, Chironomus* near *alluaudi*) and the other aquatic invertebrate assemblage is dominated by detritivore ostracods. Chironomid-based salinity inference indicates that conductivity may have increased (from ~500 µS/cm to 1000 µS/cm) during deposition of these sediments. *Cytheridella chariessa* which is encountered in this zone more often than in any other zone, is also more common in freshwater lakes with slightly elevated conductivities (between 500-1000 µS/cm; Rumes, Chapter 2). Alternatively, high abundances of Ostracoda and the presence of a number of rare littoral taxa (*Ecnomus,* Odonata) in combination with low *Chaoborus* abundances suggest that this massive unit was deposited during lake low stand. In this scenario, the near-absence of chydoridae could be explained by the slightly elevated conductivities mentioned above.

In subzone WanI1b (from ~250 to 50 cal.yr BP), littoral insect remains are fairly abundant and diverse (Baetidae, Caenidae, *Ecnomus,* Hydropsychidae, *Dasyhylea* type, type Z). The ratio of chydorids to *Chaoborus* remains fairly stable throughout the zone. Both indicate that lake level probably remained relatively constant. Since significantly higher numbers of fish remains are found in this zone, one might expect that zooplanktivore haplochromines would have suppressed the *Chaoborus* abundances. That this is not clear from our record is could be due to the fact that both *Chaoborus* and plankton feeding fish benefited from the same conditions. An increase in magnetic susceptibility of the sediments at the start of the 20th century is probably due to the return of human-induced soil erosion. Increased nutrients tend to benefit green algae and cyanobacteria, which form a major part of the natural diet of tilapia in the study area (Bwanika *et al.*, 2004). Deep-water anoxia will also be increased by eutrophication resulting from excess nutrient input. The presence and size of an anoxic hypolimnion where *Chaoborus* can avoid fish predation during the day positively benefits *Chaoborus* abundance in tropical lakes (Lewis, 2000; Rumes *et al.*, 2005). A pronounced peak in fish scales ~200 cal. yr BP (at 87cm core depth) may reflect the deposition of a fish carcass near the core site, but it may also reflect a deliberate introduction of non-indigenous fish. The latter is supported by continuous recovery of fish scales from this point onwards, at abundances above those recorded at any previous time in lake history. The chironomid assemblage in this zone is dominated by species associated with vegetated near-shore habitats (*Dicrotendipes*) and species which prefer sandy substrate with coarse organic material (*Nilodorum, Chironomus* near *alluadi*).

In subzone WanI1a (~1960-2001 AD) there is a gradual increase in chironomid species preferring sandy substrate with coarse organic material *(Nilodorum, Chironomus* near *alluaudi, Cladotanytarsus*) at the expense of species associated with vegetated near-shore habitats. In the non-chironomid invertebrate community there is a pronounced decrease of chydorids in favour of *Chaoborus*. However this trend is somewhat inverted in the upper two intervals. In the top intervals, the chironomid assemblage is dominated by *Dicrotendipes septemmaculatus* and *D. fusconotatus* (associated with vegetated habitats), and most species preferring a sandy substrate with coarse organic material (*Nilodorum* and *Chironomus* near *alluaudi*) decrease in the top intervals (with the exception of *C. pseudomancus*). This would suggest that, even with the largest part of the crater basin currently used for agriculture, the input of coarse terrestrial material into the lake is limited by the presence of a significant buffer of terrestrial vegetation and emergent aquatic vegetation at the lake shore.

In short, from ~1900 to 1600 cal. yr BP the aquatic invertebrate community in the shallow Lake Wandakara is dominated by taxa associated with littoral macrophyte habitats. Contrary to Lake Katinda, this does not result in high species diversity of aquatic invertebrates, which is due to the numerical dominance of the multi-species chydoridae taxon. At ~1600 cal. yr BP, there is a change in sediment composition and chironomid assemblage which seems to indicate increased erosion, although it more likely reflects a threshold increase in lake depth at which certain littoral habitats were replaced. Low lake levels again predominate from ~1600 and are followed by a transgression ~1250 cal. yr BP. At ~900 cal.yr BP a reduction in lake levels coincides with the onset of intensive human activities around Lake Wandakara (Russel *et al.*, 2009), resulting in a clear shift in the chironomid faunal assemblage and a reduction in Chydoridae. The combined effects of variable anthropogenic impact and natural climate variability directly influenced the aquatic invertebrate community of Lake Wandakara for the next 550 years. At ~325 cal. yr BP, a strong drought, which dramatically reduced lake level and probably elevated conductivity, marks the end of anthropogenic erosion. From ~250 to 50 cal.yr BP, a diverse invertebrate fauna suggests intermediate lake levels and abundant Chydoridae reflect high water transparency. At the start of the 20th century *Chaoborus* benefits from an increase in turbidity as a consequence of renewed anthropogenic erosion. At ~1960 AD there is a pronounced shift in the aquatic invertebrate fauna which probably reflects an increase in lake trophic state related to anthropogenic erosion.

5.4.3 Human impacts and climate change in western Uganda from ~4000BP

The broad patterns of late-Holocene climate history in western Uganda has recently been elucidated by investigations of the sediment archives of Lake Edward (Russell & Johnson, 2003, 2005) and crater lakes in the area (Russell *et al.,* 2007; Bessems, 2007; Bessems *et al.,* 2008). Integrating this information with our data on aquatic biota allows us to determine how climate change and human impacts have influenced the aquatic ecosystems of lakes Katinda and Wandakara. In the period ~4000 BP to ~2200 BP, for which only the record from Lake Katinda is available, there is no indication of significant human impact. Evidence for lower lake levels is found at ~2800 BP and possibly also just before ~4000 BP, which both correlate well with drought periods recorded in Lake Edward (Russell & Johnson, 2005).

In the catchment of Lake Katinda, anthropogenic erosion commenced at ~2200 BP and increased drastically after a period of lower lake levels at ~2000 BP. This drought, which is also evidenced at the start of the Lake Wandakara record, may have caused the human population in the area around Lake Katinda to congregate near the lake and could thus have intensified human pressure on the lake. In both lakes, lake levels increase and appear to remain relatively stable up to ~900 BP. At ~900 BP and ~750 BP changes in composition of fossil assemblages indicate lower lake levels. The first of these droughts also marks the start of human impact on the crater basin of Lake Wandakara. There is evidence for human impact during wetter conditions up to ~500 BP, after which both lake levels and human impact decrease. From ~250 to ~150 BP, aridity was wide-spread throughout equatorial East Africa (Verschuren *et al.*, 2000, Bessems *et al.*, 2008). This is the time when large nucleated settlements in Western Uganda were abandoned in favour of pastoralism (Taylor *et al.*, 2000). Although this drought has no clear signature in the pollen record of Lake Wandakara (Ssemmanda *et al.*, 2005), clear indicators for lake-level changes occur in both the sedimentological parameters and the composition of aquatic invertebrate assemblages, as they do in Lake Katinda. After this period, lake levels increase and changes in lake trophic state as a consequence of human impact are noticed from ~1920 AD in Lake Katinda and from ~1960 AD in Lake Wandakara.

In both lakes, diversity of fossil aquatic invertebrate assemblages decreased during periods of increased erosion which was probably the result of human impact. In the case of chironomids, a few species associated with sandy habitats and coarse organic debris dominated the fauna. Higher densities of *Chaoborus ceratopogenes* and fish remains associated with these changes in bottom fauna probably reflect the increase in general aquatic productivity and turbidity associated with excess nutrient input, although the abundance of fish remains may have been influenced by deliberate introductions. Our analysis indicates that the aquatic biota in these lakes have been subject to strong natural fluctuations in environmental conditions in the course of the last 4000 years. Human impact starting ~2200 years ago in Lake Katinda and ~900 years ago in Lake Wandakara changed the composition of the aquatic invertebrate fauna, which partly recovered in Lake Katinda when humans vacated the area for over 150 years. For lakes Wandakara and Katinda, the effects of natural environmental change on the aquatic biota over the last few thousand years were subordinate to the effects of changes in anthropogenic land use.

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6

Climatic and hydrological instability in semi-arid equatorial East Africa during the late Glacial to Holocene transition: A multi-proxy reconstruction of aquatic ecosystem response in northern Tanzania

Abstract

This paper reports new multi-proxy palaeoenvironmental data on the late Glacial-Holocene transition (c. 14.8–9.3 ka) in equatorial East Africa, in the form of microfossil assemblages (chironomids, diatoms and ostracods) recovered from the sediment record of Lake Emakat, Empakaai Crater, northern Tanzania. In the context of available palaeoclimatic and palaeoecological information from the region and previously published fossil pollen and carbon and nitrogen isotopic data for the same sediment sequence, we here reconstruct local lake-system response to regional climatic and hydrological instability during the period of post-glacial warming. The aquatic biological proxy indicators suggest that the water level and chemistry of Lake Emakat evolved, first from a shallow freshwater body at 14.8 ka to a deeper freshwater phase between c.14.4 and 10.3 ka and then to a markedly shallower, alkaline-saline environment after c.10.3 ka. The lake appears to have been deepest between 13.2 and 12.0 ka, at a time of climatic drying when moist montane forest vegetation within the lake's crater catchment was being replaced by open wood-and scrubland. Some palaeohydrological changes reconstructed for Lake Emakat are in phase with lake evolution elsewhere in the region and thus apparently track broad-scale climate changes, but others are not. Collectively these multi-proxy paleolimnological data indicate a complex adjustment of the local aquatic ecosystem to temporal variations both in total annual effective precipitation and its seasonal distribution. The lake's hydrological response was further conditioned by local factors, notably its geological and topographic setting.

Keywords: Climate change - Crater lake – Chironomids – Diatoms - East Africa – Empakaai-Multi-proxy reconstruction – Ostracods

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6.1 Introduction

The late Glacial to Holocene transition was a period of warming-induced climatic instability recorded in ice core data from both the Arctic and Antarctic regions, with the degree of synchrony between events in the Northern and Southern hemispheres being a major issue of debate (Sowers and Bender, 1995, Bard et al., 1997, Blunier et al., 1998, Steig et al., 1998 and Denton et al., 1999). Although most studies of this period have focused on the North Atlantic region and the adjacent landmasses, there is increasing evidence that climatic instability associated with the overall warming trend was felt worldwide, with phases of climatic reversal also reported for many low-latitude locations in South America (e.g., Rigsby et al., 2005), Asia (e.g., Mingram et al., 2004), and Africa (Bonnefille et al., 1995, Beuning et al., 1997, Gasse and Van Campo, 1998, Maley and Brenac, 1998, Abell and Plug, 2000, Gasse, 2000, Talbot, 2001, Barker et al., 2002, Johnson et al., 2002, Gasse, 2002 and Lezine and Cazet, 2005). Despite this apparent multitude of data, significant uncertainty remains about the exact sequence and timing of events in most tropical regions, partly due to insufficient geographical coverage and partly due to the difficulty of extracting past patterns in rainfall and temperature variation from local paleohydrological proxy indicators.

In this paper we report the results from analyses of diatoms, chironomids and ostracods in an AMS ^{14}C-dated lake-sediment sequence from a relatively poorly studied and climatically sensitive region in equatorial East Africa. These biological proxy indicators provide information on fluctuations in water level and chemistry, which together with data on the content and isotopic composition of carbon and nitrogen in the lake sediment (Muzuka et al., 2004) and pollen data of past vegetation change (Ryner et al., 2006) permit a coherent, multiple-proxy reconstruction of climate and environmental change in northern Tanzania during the late Glacial to Holocene transition.

6.2 Study site

The Empakaai, or Embagai, Crater (2°55′ S, 35°50′ E) belongs to a chain of volcanoes known as the Crater Highlands (2100–2800 m above sea level, a.s.l.) associated with the Gregory (eastern) arm of the East African rift system in northern Tanzania (Fig. 1). Empakaai Crater is an intact caldera of the Elanairobi volcano, believed to have been active during the late Pliocene (Hay, 1976) and located 10 km south of Oldoinyo Lengai, an active carbonatite volcano. The caldera is about 6 km in diameter and covers an area of about 35 km^2. Its rim rises 400–900 m above the floor of the caldera, situated at 2300 m a.s.l.

As elsewhere in eastern equatorial Africa, maximum cloud cover and rainfall on the windward eastern slopes of the mountains occur at 2000–3000 m a.s.l., while conditions become increasingly drier above that elevation (Hastenrath, 1984). In the Crater Highlands the eastern slopes receive up to 1000 mm of rainfall/yr, while plains to the west are drier and receive about 600 mm/yr (Homewood and Rodgers, 1991); the topographical mosaic within the Crater Highlands creates enhanced local patterns of water-balance variation. Precipitation is strongly seasonal and generally occurs between November and May, with most rain falling from March to May (Homewood and Rodgers, 1991; Nicholson, 2000). Homewood and Rodgers (1991) computed an adiabatic lapse rate for the Crater Highlands of c. 1 °C 200 m^{-1} and noted that diurnal temperature variations were greater than monthly variation through the year. Ambient temperatures on the rim of Empakaai Crater ranges from a daily mean of 15 °C in November to 22 °C in March, while night-time temperatures can fall below 0 °C in August (Frame et al., 1975).

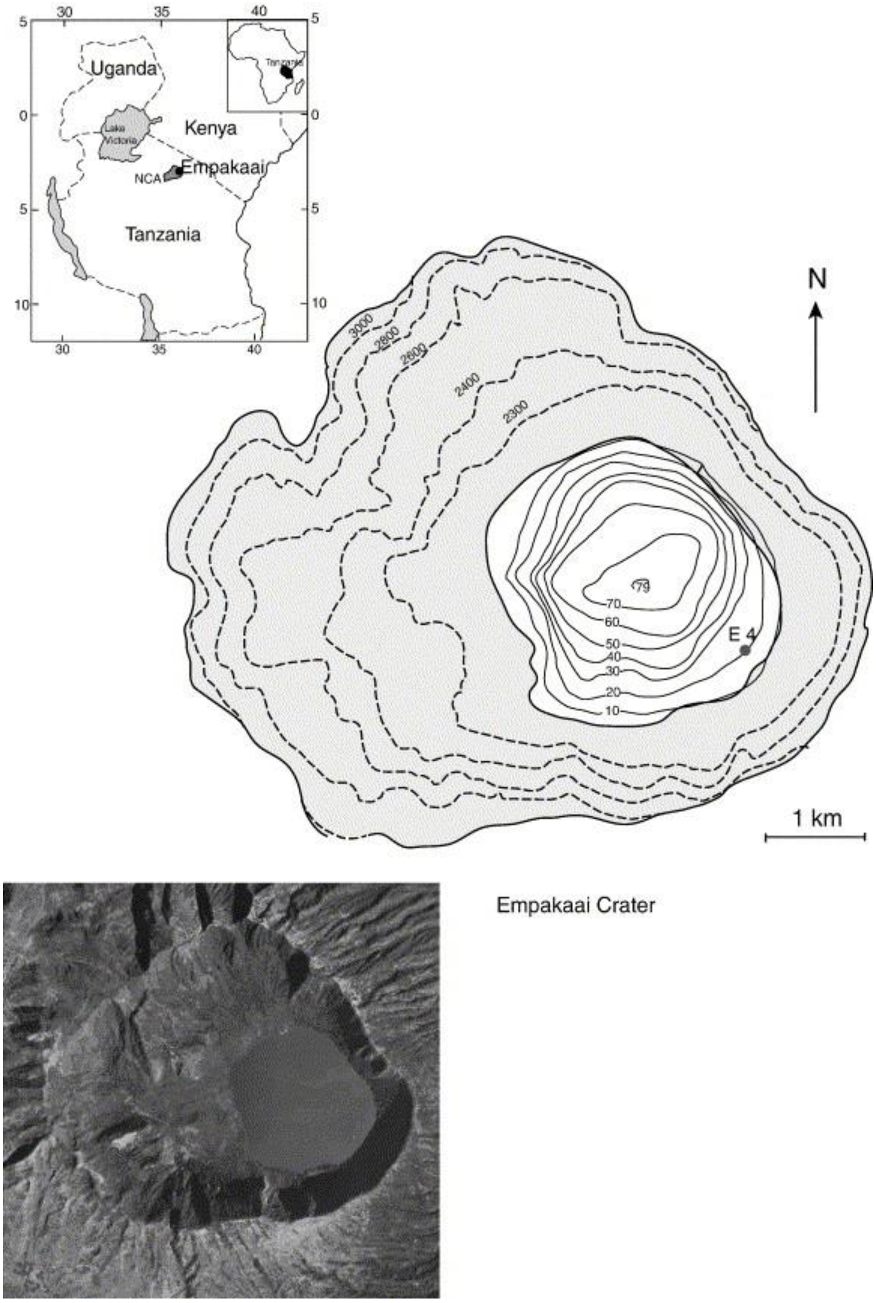

Figure 1: Location of study site Empakaai Crater in Ngorongoro Conservation Area (NCA) in northern Tanzania, and topography and bathymetry of Lake Emakat based on, respectively, the map sheet Oldoniyo Lengai (Y/42–39/4) and Frame et al. (1975). The aerial photograph was taken in 1972.

The area of Empakaai Crater is located mainly within the Afromontane phytochoria (White, 1983), which along a gradient of increasing altitude comprises a range of vegetation types from semi-deciduous woodland to evergreen forest and afroalpine grassland. The outer wall of the caldera and surrounding landscape have undergone livestock grazing and dry-season burning since the beginning of the 20th century, but patches forest and woodland do remain. Vegetation on the inner caldera slopes consists of a mosaic of thicket (highland shrubs), wooded grassland, and evergreen moist montane forest. Patches of this moist montane forest located in hollows on the steep southern and eastern slopes inside the caldera include isolated individuals of *Hagenia abyssinica* (Frame et al., 1975; Rånge, 2001), a taxon that is well represented in open canopy Montane Forest in East Africa (*sensu* Hamilton, 1982).

Part of the floor of Empakaai Crater is occupied by Lake Emakat, an alkaline saline lake (pH 10; 26,000 μScm^{-1}) with a maximum depth of c. 80 m (Fig. 1). Immediately south of the lake a small sheltered shallow pond (7 m deep in 1974) occurs that has similar chemical and thermal properties as Lake Emakat itself (Frame et al., 1975). At present the lake is fed mainly by direct precipitation and water from a few permanent and seasonal streams within the caldera, and it is hydrologically closed except for some springs, both permanent and seasonal, present on the outer slope of the caldera (Frame et al., 1975). Former higher lake levels are represented by old shorelines along the present lake shore. Local photographs from 1921 and 1974 (Barns, 1923 and Frame et al., 1975) and aerial photographs from 1958, 1972 and 1983 suggest that these shorelines may well be less than a century old. The intact caldera wall could potentially support a highstand more than 200 m above present lake level. Field measurements in August 2000 as part of the current study indicated stable temperature stratification, and relatively high concentrations of the major cations and total dissolved solids (Muzuka et al., 2004). Presence of H_2S below 15 m together with a change in dissolved Ca content at 20 m (Muzuka et al., 2004) indicate anoxic deep water and stable meromictic (permanently stratified) conditions. The living phytoplankton community encountered during fieldwork was dominated by cyanobacteria of the genera *Spirulina*, *Lyngbya* and *Oscillatoria* (Muzuka et al., 2004).

6.3 Methods

6.3.1 Lithological, mineralogical and chronological analyses

During fieldwork in August 2000, a 210 cm-long sediment core labelled E4 was retrieved from 20 m water depth in the southeastern part of the lake (Fig. 1) using a modified Livingstone corer. The core was sealed in the field and transported intact to the University of Stockholm. There the core was run through a GEOTEK multi-sensor core logger to determine down-core variations in magnetic susceptibility. Whole-core magnetic susceptibility measurements provide a non-destructive means of identifying and quantifying iron-bearing, allochthonous mineral matter in the sediments usually representing phases of inwash

(Dearing, 1986). In Africa, the technique has been used mainly as a tool to identify the source and transport pathways of clastic material to lake basins (e.g., Thevenon et al., 2002, Barker et al., 2003 and Peck et al., 2004).

Core E4 was then split lengthwise, described macro-and microscopically (the latter using smear-slides), and sampled for AMS ^{14}C dating. Choronological control is provided by ^{14}C ages on ten samples of bulk organic carbon (Ryner et al., 2006) Down-core variation in carbon (C) content was determined gravimetrically on freeze-dried, ground samples by combusting at 550 °C (organic C) and 900 °C (inorganic C) in an ELTRA CS 500 carbon/sulphur analyser. In hydrologically stable lakes, sedimentary organic C content provides a proxy for lake productivity and/or influx of terrestrial organic debris. In the climatically sensitive Lake Emakat, however, the principal controls on sedimentary organic C content are more likely temporal variation in the preservation of autochthonous organic matter and/or its dilution by mineral sediment components that is associated with lake-level change (Verschuren, 2001). The inorganic C content represents chemical precipitates (authigenic carbonate) and biotic remains (ostracods).

6.3.2 Microfossil analyses

Sediment samples (20 in total) were processed for diatom analysis using H_2O_2 to oxidise organic matter and HCl to remove carbonates. A known quantity of polystyrene microspheres was added to the diatom suspension for quantitative estimates of diatom concentration (valves mg^{-1} dry sediment; Battarbee and Keen, 1982), mounted in Naphrax and observed under a microscope at 1000x magnification. At least 380 and on average 488 diatom valves were counted per sample. Identification of diatom taxa was facilitated through reference to Africa-specific (Hustedt, 1949, Gasse, 1986 and Cocquyt, 1998) and general (Krammer and Lange-Bertalot, 1986, 1988, 1991a,b) taxonomic manuals. Fossil diatom assemblages preserved in lake sediments are widely used as biological indicators of water chemistry and quality (Gasse, 1986, Stoermer and Smol, 1999 and Battarbee et al., 2001). In this study, transfer functions established from a large African dataset of modern diatom-environment relationships (Gasse et al., 1995) were used to produce quantitative estimates of water conductivity (C_d), pH, the cation ratio (the ratio of alkali to alkaline earth metals, (Na K)/(Ca Mg)), and the anion ratio alkalinity/ (Cl + SO_4); all ions expressed in meq l^{-1}, supplemented by qualitative paleoecological interpretations based on the ecology and distribution of diatom taxa in East Africa (Gasse et al., 1983 and Gasse, 1986). Most diatom taxa encountered in the Emakat sediment record are included in the modern reference dataset (Gasse et al., 1995), consequently diatom-inferred calculation of chemical variables could be based on 82 to 99.8% of the fossil diatom assemblages.

Chironomid and ostracod remains were isolated from the sediment by deflocculation in 10% potassium hydroxide (KOH) heated to 70 °C (Walker and Paterson, 1985), followed by rinsing on stacked 250- and 150-μm mesh sieves. Retained organic residues were transferred to a transparent counting tray and scanned separately at 30x magnification under transmitted light. All distinctive animal remains were identified and counted directly or picked out with a fine needle, mounted in glycerine (50% glycerol and water) on microscope slides, and analysed at up to 400x magnification. Reference literature on African Chironomidae included Verschuren (1997), (Eggermont and Verschuren, 2003a), (Eggermont and Verschuren, 2003b), (Eggermont and Verschuren, 2004a) and (Eggermont and Verschuren, 2004b), Eggermont et al. (2005); ostracods were identified using the primary taxonomic literature (Klie, 1933, Lowndes, 1936, Klie, 1939, Lindroth, 1953 and Martens, 1993) and direct comparison with original specimens described in these papers. Chironomidae were counted as halves when at least half of the mentum was present and processed samples were searched completely.

Fossil species assemblages of aquatic invertebrates such as chironomids and ostracods have been extensively used as indicators of climate-driven changes in their aquatic habitat. Ostracods (Crustacea: Ostracoda) are common in both permanent and temporal waters. Their mainly benthic lifestyle, strong niche specificity and rapid generation turnover make them sensitive indicators of changes in ambient physical and chemical conditions (Park et al., 2003). Chironomids (Insecta, Diptera: Chironomidae) occur over a wide geographical and ecological range of permanent standing waters (Walker, 1995 and Walker, 2001). The remains of their larvae preserved in lake sediments can be used to quantitatively reconstruct climate-induced changes in temperature (Walker et al., 1997, Lotter et al., 1997 and Brooks and Birks, 2001) and water chemistry (Walker et al., 1995 and Heinrichs et al., 2001). In Africa the use of chironomids as palaeoenvironmental indicators is relatively recent (Mees et al., 1991; reviewed in Verschuren and Eggermont, 2006) but has proven to be a useful complement to diatom studies. Here a new 73-lake East African calibration data set with root-mean-squared errors of prediction (RMSEP) ~0.3 $\log_{10}$ conductivity units (Eggermont et al., 2006) was used for quantitative chironomid-based salinity reconstruction on selected samples; see Verschuren et al. (2004) for a comparison of chironomid-based and diatom-based salinity reconstruction in African lakes.

6.4 Results

6.4.1 *Sediment chronological, lithological and mineralogical analyses*

Down-core variations in lithology, magnetic susceptibility and (organic and inorganic) carbon are summarised in Fig. 2, in relation to sediment chronology (cal yr BP) based on the ten AMS ^{14}C dated sediment horizons presented in Table 1 (and see Muzuka et al., 2004 and Ryner et al., 2006). These dates indicate that the 210–89 cm section of the cored E4 sequence covers Lake Emakat history through the late Glacial to Holocene transition from c. 14.8 to 9.3 ka (× 1000 calibrated ^{14}C years before present). Linear regression of the weighted-average probability distributions of all ten ^{14}C dates versus core depth indicates a more-or-less linear rate of sediment accumulation of 0.23 mm/yr at the E4 core site.

Lithologically the sediment sequence comprises three major stratigraphic units. Unit 1 (between the core base and 195 cm depth) is composed of fine clay laminae (1–4 mm thick) grading to somewhat thicker laminae in the lowermost 5 cm. Unit 2 (195–109 cm) consists of more coarsely laminated organic clays with two bands of inorganic material (silt, sand, and volcanic debris) at 131–130 cm and 123–116 cm. Unit 3 (109–89 cm) sediments are mostly silty clays. Less organic core horizons tend to have higher magnetic susceptibility, but the relationship is not clear-cut (Fig. 2). The inorganic C content is variable but generally low and not correlated with organic C content, indicating temporally variable chemical conditions within the lake and/or input of eroded carbonates from the catchment.

Calendar age conversion was done using BCal (http://bcal.shef.ac.uk/, Stuiver et al. 1998). The calibrated date is the weighted average of the probability distribution for each radiocarbon date.

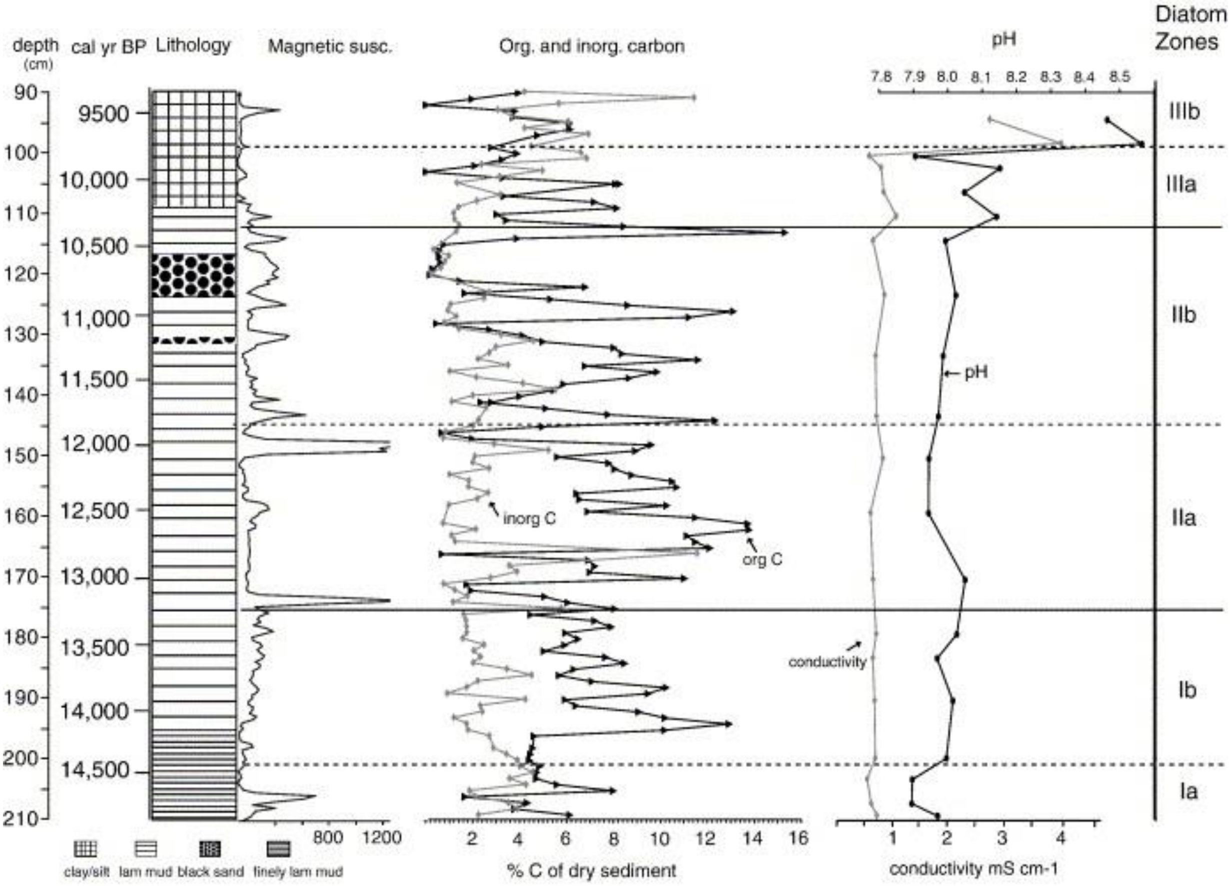

Figure 2: Down-core variations in lithology, magnetic susceptibility, C (organic and inorganic) and diatom-inferred conductivity and pH reconstructions based on the modern African diatom calibration dataset (Gasse et al., 1995), and stratigraphic zonation of fossil diatom assemblages (as in Fig. 3). Sediment chronology is in calendar year BP, based on linear regression of 10 AMS ^{14}C dates (see text).

Table 1: AMS radiocarbon dates on bulk sediment and plant macroremains from core E4, Lake Emakat, Empakaai Crater, Tanzania.

Lab ref Ua-	Sample depth (cm)	^{14}C year yr BP	$\delta^{13}C^{‰ (PDB)}$	Calibrated year Cal yr BP	2α (+/−)	Sample material
17,046	89–90	8640 ± 80	− 22.9	9626	194/139	Bulk
18,000	109–110	8690 ± 85	− 24.3	9783	327/232	Bulk
17,047	122–123	9440 ± 115	− 25.4	10,694	385/294	Bulk
18,001	129–130	9710 ± 95	− 26.1	11,047	197/289	Bulk
18,002	149–150	10,915 ± 105	− 26.3	12,486	226/143	Bulk
21,300	160–161	10,410 ± 95	− 26.8	12,577	158/186	Macro
18,003	169–170	9765 ± 110	− 26.9	12,683	46/12	Bulk
21,301	180–182	10,930 ± 190	− 24.0	13,001	317/318	Macro
18,004	189–190	12,185 ± 110	− 25.0	14,203	610/380	Bulk
17,048	203–204	12,450 ± 130	− 25.1	14,634	652/501	Bulk

6.4.2 Diversity and fossil distribution of aquatic biota

Although all analysed levels contained fossil diatoms, many valves were badly broken and their content varied from 36 to 1200 valves mg^{-1} dry sediment (Fig. 3). A total of 102 diatom taxa were identified. Most of the recovered taxa are widely distributed in East Africa today (see Gasse et al., 1983, Gasse, 1986 and Gasse et al., 1995), thus facilitating palaeoenvironmental reconstruction based on their modern ecology. Euplanktonic diatom taxa are poorly diversified in the fossil assemblages. The best represented is *Aulacoseira granulata* var. *angustissima* (O. Müller) Simonsen, which grows optimally in dilute shallow lakes of the calcium–sodium bicarbonate type, and tolerates highly turbid waters (Gómez et al., 1995). *Nitzschia lancettula* O. Müller is a common planktonic taxon of large freshwater lakes, but its frequency here does not exceed 8%. Many samples are characterised by facultatively planktonic freshwater taxa. The various species of small *Fragilaria* (*F. brevistriata* Grun. and varieties, *F. pinnata* Ehr., *F. construens* and its var. *venter* (Ehr.) Grun., *F. zeilleri* var. *elliptica* Gasse) encountered generally inhabit the shallow areas of lakes and rivers. *Nitzschia paleacea* Grun. and *N.* aff. *gracilis* Hantzsch are found as epiphytic, epipelic or planktonic forms in lakes, marshes and slowly running rivers. The ecology of *Cyclotella ocellata* Pant in eastern Africa is poorly known, due to its scarcity in the dataset of modern African diatom distribution (Gasse et al., 1995). However it is common in some Late Quaternary lake records from the region, e.g., during the early Holocene freshwater highstand of the present-day hyperalkaline Lake Abiyata, Ethiopia (Chalié and Gasse, 2002). Elsewhere, this species usually grows in the littoral zones of freshwater lakes, but can also enter the plankton and survive salinity variations (e.g., Patrick, 1970). Other common taxa in the E4 sediment sequence display clear preferences for epiphytic and/or periphytic environments. *Amphora libyca*, *A. pediculus* (Kütz.) Grun., *Cocconeis placentula* Ehr., *Epithemia adnata* (Kütz.) Bréb., *E. turgida* (Ehr.) Kütz., *E. sorex* Kütz., *Gomponema* *clevei* Fricke and its varieties, *G. intricatum* Kütz. and its varieties, and *Cymbella* spp. are most commonly observed as epiphytic. Several of the periphytic taxa present, e.g., *C. placentula*, *Gomphonema intricatum* var. *pusilla* Mayer and *G. clevei* var. *javanica* Hust., are known to tolerate enhanced salinity although they tend to be better represented in dilute waters. These taxa were found in the modern phytoplankton of the currently mesosaline Lake Emakat, albeit in low number (≤ 1% relative abundance). *Nitzschia inconspicua* is also salt-tolerant, being found in oligo-to mesosaline water. Only relatively few taxa in the fossil Lake Emakat flora live optimally in water of high conductivity. One of them is the periphytic *Craticula elkab* O. Müller, which thrives today in hyperalkaline lakes (e.g., Lake Elmenteita and Lake Abiyata) and is thus a good indicator of high concentrations of sodium and carbonate ions. *Cyclotella meneghiniana* Kütz. is a facultative planktonic form of carbonate or chloride-rich oligo-to mesosaline water. Surface-sediment diatom assemblages from the modern Lake Emakat are dominated by *Anomoeoneis sphaerophora* (Kütz.) Pfitzer, *Rhopalodia gibberula* (Ehr.) O. Müller and *Nitzschia liebetruthii* Rabenhorst, species which in core E4 are only represented by rare specimens.

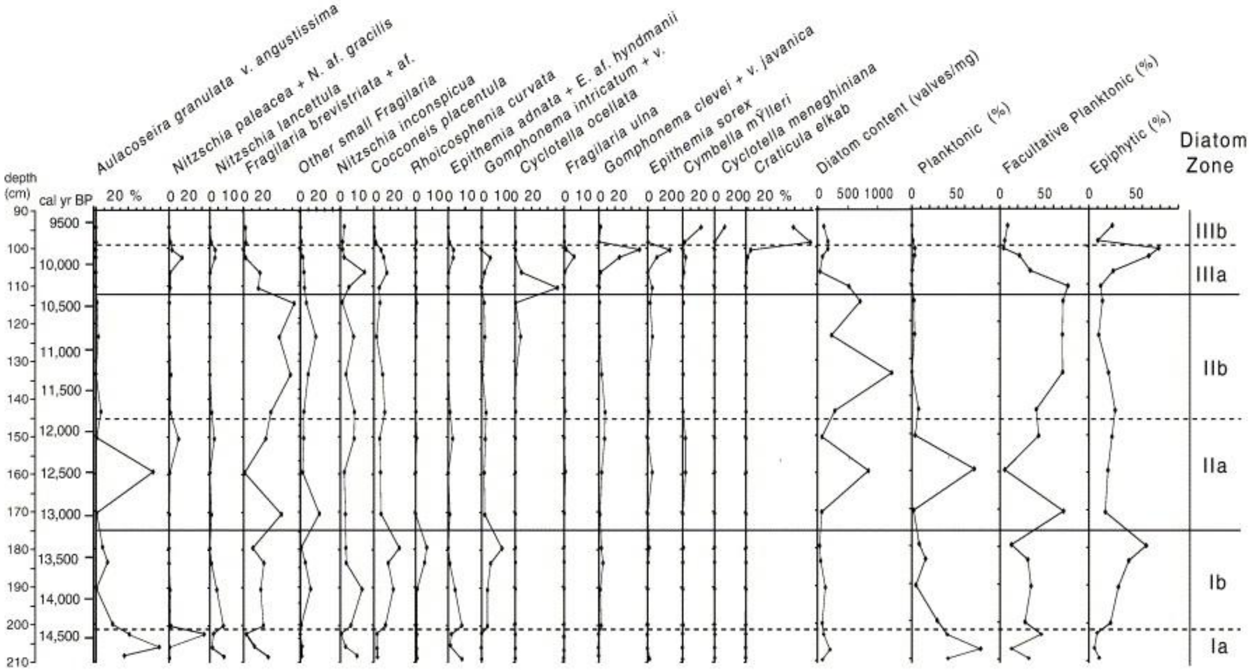

Figure 3: Down-core variations in diatom % species abundances, their broad habitat preferences, and diatom zonation based on stratigraphically constrained cluster analysis. Only diatom taxa with an abundance of > 5% in more than one sample are shown.

Based on the abundances of major taxa and their habitat preferences, we identified three diatom zones:

Diatom zone I, 210–175 cm (c. 14.8 to 13.2 ka)

Within zone I the diatom content is low. The zone is divided into sub-zones Ia and Ib. In sub-zone Ia (210–201 cm, c. 14.8 to 14.4 ka), peak relative abundance of the planktonic diatom *A.*

granulata var. *angustissima* (77%), bracketed by relatively high values of *F. brevistriata*, *N. lancettula* and *N. paleacea*, indicates a relatively wet phase. In sub-zone Ib (201–175 cm, c. 14.4 to 13.2 ka), the facultative planktonic, small freshwater *Fragilaria* species (mainly *F. brevistriata* and *F. pinnata*) increase in percentage, but the assemblage is dominated by periphytic forms. Among these, the relative abundance of taxa most commonly living as epiphytes (e.g., *C. placentula*, *E. adnata*, *G. intricatum*) increases progressively up to 180 cm, suggesting colonisation by macrophytes of a shallow or transparent water body. There are also relatively high proportions of the salt-tolerant taxa *N. inconspicua*, *C. placentula* and *G. intricatum*, likewise pointing to a phase with (at least seasonally) negative water balance.

Diatom zone II, 175–112 m (c. 13.2 to 10.3 ka)

Diatom content in zone II is generally much higher than in Zone I, reaching a maximum at 134 cm core depth. Marked shifts in diatom composition around 150–144 cm and 124 cm coincide with sand layers, suggesting either short-term increases in sedimentation rate or dilution by detrital material. Diatom assemblages in Zone II are characterised by planktonic and facultative planktonic taxa, indicating a water body of some depth. As with Zone I, we divide Zone II into two sub-zones. Sub-zone IIa (175–145 cm, c. 13.2 to 11.8 ka) includes a large peak of *A. granulata* var. *angustissima* (70%), bracketed by high values of small *Fragilaria* (including *F. brevistriata*) and followed by a moderate increase of *N. lancettula* and *N. paleacea*. Sub-zone IIb (145–112 cm, c. 11.8 to 10.3 ka) is dominated by facultative planktonic *Fragilaria* (mainly *F. brevistriata* and *F. construens* var. *venter*), while the total percentage of periphytic diatoms remains relatively low (< 35–40%).

Diatom Zone III, 112–94 cm (c. 10.3 to 9.3 ka)

Zone III is characterized by taxa that are poorly represented in earlier zones, an overall decrease in diatom abundance and an increase in diatom-inferred ionic concentration. Also this zone is divided into two sub-zones. Sub-zone IIIa (112–99 cm, c. 10.3 to 9.7 ka) starts with a narrow peak of the facultative planktonic diatom *C. ocellata* in association with small *Fragilaria* spp., which are subsequently, and abruptly, replaced by periphytic diatoms. The almost complete disappearance of open-water species and predominance of epiphytic taxa suggest a very shallow marsh environment, i.e., a substantial lowering of lake level. Several salt-tolerant freshwater taxa reach their maximum relative abundance in this sub-zone, namely *Nitzschia inconspicua*, *G. clevei* var. *javanica*, *E. sorex*, and the above-mentioned *C. ocellata.* Also notable are the presence of rare halophilic *Rhopalodia gibberula* (not shown in Fig. 3) and appearance, near the top of Sub-zone IIIa, of *Craticula elkab*. Sub-zone IIIb (99–94 cm, c. 9.7 to 9.3 ka) shows the most striking event of the whole record, with dramatic falls in abundances of previously common taxa coincident with a major increase in *Craticula elkab*. This sample at 99 cm depth exhibits the highest values of diatom-inferred conductivity (C_d: 4040 μS cm^{-1}), anion and cation ratios (> 1), and pH is close to 9, indicating concentrated water of the sodium carbonate type. At 95 cm, *C. elkab* is associated with the oligo-to mesosaline *Cyclotella meneghiniana*, which is common in alkaline, saline lakes in eastern Africa today, and with *Cymbella mulleri*, resulting in an assemblage generating a diatom-inferred conductivity of 2750 µS cm^{-1}. The low diatom content of Zone III may be due to high pH or frequent ionic content fluctuations, which leads to biogenic silica dissolution (Barker et al., 1994), or alternatively to the competition with cyanobacteria, the major component of algal biomass in many saline, alkaline lakes.

Among the invertebrates, 92 % of identifiable remains are ostracoda, while the remaining 8 % comprised Cladoceran resting eggs (3 %), chironomids (2.3 %), Turbellarian egg cocoons (2%), Acari (0.7 %) and sporadic other remains (together 0.4 %). Down-core variations in the main chironomid and ostracod taxa are summarised in Fig. 4 (see Appendix A for all ostracod taxa recovered). Aquatic invertebrate fossils were rather scarce overall (see total sum in Fig. 4) and their distribution erratic, thus precluding establishment of a stratigraphic zonation specific for invertebrate microfossils. We thus describe invertebrate distribution in relation to the diatom zone boundaries, as shown on Fig. 4.

The large majority of ostracod remains were found in the section of E4 above 112 cm depth (Diatom Zone III, i.e. after c. 10.2 ka). Taxa commonly encountered in this part of the core (e.g., *Candonopsis africana* Klie, *Gomphocythere obtusata* Sars, *Limnocythere* spp., *Stenocypris major* Ferguson and *Zonocypris costata* Vavra) today occur throughout eastern Africa in fluctuating shallow lakes (B. Rumes et al., unpublished data). *Gomphocythere* and *Limnocythere* (together representing 56 % of the fossil fauna, but mostly in a single depth interval at 106 cm) are peculiar for their lack of drought-resistant eggs, which theoretically restricts them to lakes with long-term permanency (Martens, 1993). Still the distribution of *Gomphocythere* in eastern Africa is poorly documented, with some species apparently endemic to individual lakes while others have a widespread distribution (Park and Martens, 2001). *Limnocythere* species are tolerant of waters with a wide range of salinity and alkalinity (Cohen et al., 1993 and Martens et al., 1996). In North America this genus is associated with both high salinity and high seasonal variability (Forester, 1991). Below 110 cm core depth (Diatom Zones I and II) ostracoda are scarce, except for the lowermost sample (209 cm) which contained a sizable number of *Sarscypridopsis* near *trigonella* and juvenile *Sclerocypris* specimens, indicating unstable bottom habitat conditions at the start of the sequence, i.e. around 14.8 ka. Above 110 cm, *Sarscypridopsis* near *trigonella* increases dramatically and is followed by peak abundances in, most notably, *Gomphocythere obtusata*, *Limnocythere* sp., *Stenocypris major* and *Zonocypris costata*. High absolute ostracod abundances may represent explosive population growth such as is known to occur during seasonal or longer-term lake regression, when hydrochemical conditions become unstable, and short-lived detritus-feeders, such as ostracoda, benefit from the disintegration of regular freshwater communities and food webs. Strikingly absent from the Emakat record is the planktonic ostracod species *Physocypria capensis* Sars, common throughout sub-Saharan Africa in lakes with sizable open-water habitat (Martens, 1984).

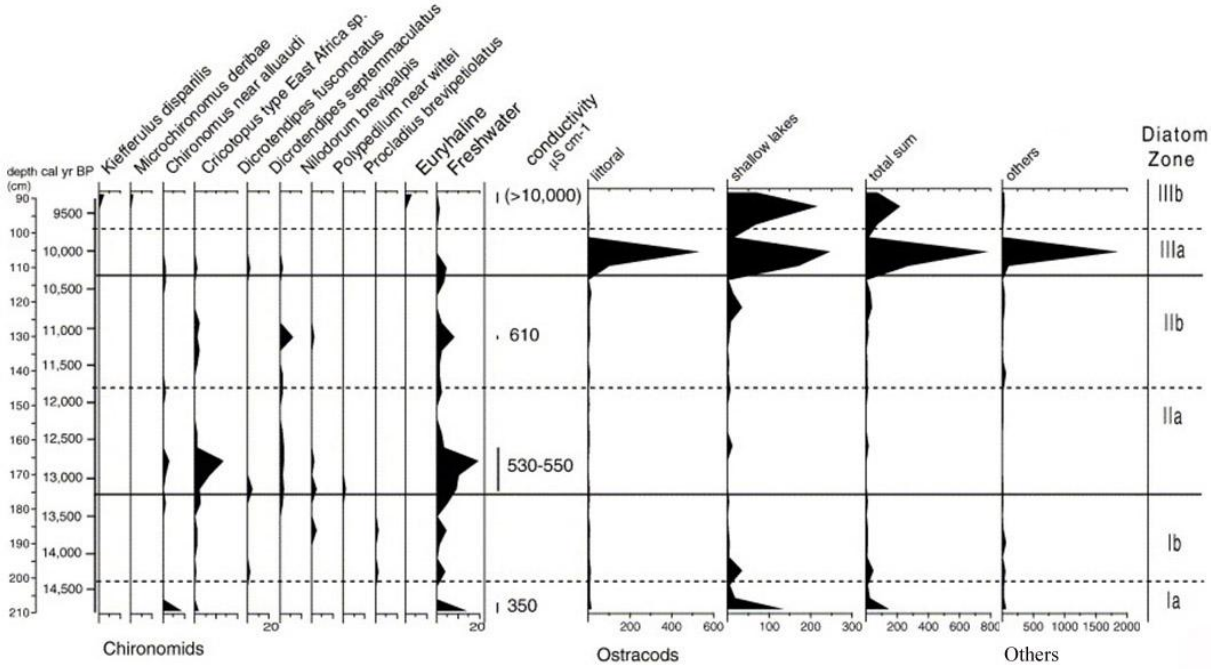

Figure 4: Down-core variations in absolute fossil abundances of the main chironomid taxa, the stratigraphic distribution of freshwater and euryhaline chironomid taxa, chironomid-inferred conductivity estimates for selected core intervals (see text) based on the modern African chironomid calibration dataset (Eggermont et al., 2006), and the broad habitat associations of recovered fossil ostracod assemblages. Ostracod taxa are listed in Appendix A

Of the 16 chironomid taxa recovered, all in low numbers, 14 are present in the East African calibration data set. Twelve of these taxa are stenotopic or eurytopic freshwater species, with conductivity optima between 210 µS cm^{-1} (*Tanytarsus* type Kayihara) and 620 µS cm^{-1} (*Dicrotendipes septemmaculatus* Becker). The most common taxon in E4 samples (*Cricotopus* type East Africa sp. group: 39 % of the fauna) is a morphotype that includes the two common African Orthocladiinae species *Cricotopus albitibia* Walker and *C. scottae* Freeman (Eggermont and Verschuren, 2004a). Based on its occurrence in 19 East African lakes, its conductivity optimum is estimated at 580 µS cm^{-1}. The two remaining taxa (*Kiefferulus disparilis* Goetghebuer and Microchironomus deribae Freeman) are halobiont species that typify African soda-lake environments (Verschuren, 1997) and have conductivity optima of, respectively, c. 10,750 and 16,020 µS cm^{-1} (Eggermont et al., 2006).

Due to the very low abundance of chironomid remains in all but a few samples and a root-mean-squared error of prediction (RMSEP) ~0.3 log10 conductivity units, estimates of inferred salinity have to be considered with caution. Notwithstanding this caveat, the chironomid record suggests a slight trend of increasing salinity up-core, from c. 350 µS cm^{-1} at the start of the sequence (c. 14.8 ka) to c. 530–550 µS cm^{-1} around 1.66–1.75 m depth (first half of Diatom Zone IIa, c. 13.2–12.6 ka) and to c. 610 µS cm^{-1} around 1.30–1.31 m depth (middle of Diatom Zone IIb, c. 11.0 ka; Fig. 4). All but one of the freshwater Chironomidae inhabiting the lake during this period are common eurytopic taxa. The only exception, *Tanytarsus* type Kayihara, has previously only been found in two steep-sided crater lakes in Uganda and a dilute (78 µS cm^{-1}) forest lake in Kenya. The latter occurrence reduces the modelled conductivity optimum of this species (210 µS cm^{-1}) to below average, but the single specimen found occurred in a sample (114–115 cm; not shown in Fig. 4) that yielded only two other chironomid fossils, too few to produce a meaningful value of inferred conductivity. No freshwater Chironomidae were found above 110 cm (Diatom Zone III). The only midge remains recovered from this zone are the halobiont species *K. disparilis* and *M. deribae* at the very top of the sediment sequence (94 cm), indicating a relatively sudden transition to a strongly alkaline soda-lake environment with conductivity exceeding 6000 µS cm^{-1}. Thus, the chironomid-and diatom-inferred water-chemistry evolution of Lake Emakat is in full agreement throughout the E4 sequence.

6.5 Discussion

6.5.1 Palaeoenvironmental reconstruction and regional comparisons

6.5.1.1 Prominent lake-level rise to a freshwater highstand: c. 14.8–14.4 ka

Pollen data of late Glacial vegetation change in the Empakaai area (Ryner et al., 2006) indicate that at the start of this period (~ 14.8–14.7 ka) vegetation in the caldera was characterised by relatively open grassland with scattered trees of *Hagenia abyssinica* and *Juniperus* sp., evolving to a more closed landscape (increasing AP/NAP ratio) around 14.4 ka. For the lake, a rapid increase to peak abundance of the euplanktonic freshwater diatom *Aulacoseira granulata* var. *angustissima*, bracketed by high values of the facultatively planktonic *F. brevistriata*, *N. lancettula* and *N. paleacea*, attest to a significant rise in lake level during this period and dilute water chemistry (200–300 µS cm^{-1}). However this open-water freshwater diatom assemblage is not in itself indicative of great water depth. The finely laminated sediments that characterise sediment deposition during this period, becoming even more finely laminated from c. 14.6 ka, reflect establishment of low-energy sedimentary conditions associated with permanent stratification in relatively deep water. Scarcity of *Potamogeton* seeds together with relative commonness of mud-dwelling Chironomidae, mainly *Chironomus* near *alluaudi* Kieffer, indicate poorly developed aquatic vegetation, consistent with high lake level in a steep-sided crater basin. Organic C content is moderate, but its C/N ratio is relatively low suggesting good organic matter preservation and a significant contribution from autochthonous sources (phytoplankton). The combined data indicate a climate trend of increasing humidity from ~ 14.8 to 14.6 ka, first reflected in a more positive lake water balance and followed by expansion of montane forest vegetation.

6.5.1.2 Inferred lake-level decline associated with a variable climate: 14.4–13.2 ka

According to the pollen data (Ryner et al., 2006), vegetation in the Empakaai Crater was dominated by moist montane forest characterised by *Hagenia abyssinica*, which in eastern Africa is commonly associated with moist upper montane forest including areas of regenerating montane forest (Hamilton, 1982). Diatom abundances were low throughout this period. Even so, small freshwater, facultative planktonic *Fragilaria* (mainly *F. brevistriata* and *F. pinnata*) increased in abundance, but periphytic forms tended to dominate, indicating that the core site lake floor was lying within the euphotic zone, and thus normally implying reduced lake level relative to the situation before 14.4 ka. This shallowing stimulated expansion of aquatic macrophytes, as suggested by high percent abundances of epiphytic diatom taxa. Remains of chironomids also indicate reduced lake levels: the few recovered specimens dating to this period (*Dicrotendipes fusconotatus, Tanytarsus formosanus*) are inhabitants of littoral vegetation and shredders of coarse plant detritus. The high proportion of salt-tolerant freshwater diatoms (*N. inconspicua, C. placentula* and *G. intricatum*) may reflect seasonal drought or significant inter-annual fluctuation in lake water balance, however diatom-inferred conductivity (300–400 cm^{-1}) remains well within the freshwater range. The sediment composition also changes during this period, from finely laminated sediments to a more homogenous gyttja containing bands of coarse material indicative of phases of carbonate precipitation and/or inwash, as would be expected to occur under conditions of varying water levels. The δ^{15}N values declined while δ^{13}C increased, suggesting a change in the predominant source of organic matter from autochthonous to allochthonous (Muzuka et al., 2004). C/N values are high at 18–22, indicating that the surrounding forest vegetation contributed significantly to organic matter sedimenting in the lake.

The basal sediments of core E4 representing these first two lake phases (together forming Diatom Zone I) accumulated during a period (14.8–13.2 ka) of substantial shifts in climatic conditions over the African continent (Street-Perrott and Perrott, 1993, Gasse, 2000 and Gasse, 2002). In eastern Africa (Fig. 5), lakes Victoria (Talbot and Laerdal, 2000), Tanganyika (Gasse et al., 1989), Magadi in Kenya (Roberts et al., 1993), and Manyara and Rukwa in Tanzania (Holdship, 1976, Barker and Gasse, 2003 and Haberyan, 1987) all began a pronounced transgression at ~ 15 ka, coeval with the lake-level rise recorded at Lake Emakat. In southeastern Africa, Lake Malawi appears to have risen to high level already before that time (Filippi and Talbot, 2005). The Empakaai pollen data, from 14.7 to 13.2 ka, show high abundance of *Hagenia* and peak AP/NAP ratio's (Ryner et al., 2006), indicate that this regional lake transgression (Beuning et al., 1997, Talbot and Laerdal, 2000, Barker et al., 2002 and Talbot et al., 2006) reflected establishment of a moister climate that persisted for about 1500 yr. This stands in apparent contradiction with the inference of lake-level decline at Lake Emakat after c. 14.4 ka. Perhaps the establishment of dense montane forest inside Empakaai Crater, by increasing evapotranspiration and reducing run-off, resulted in lake-level decline despite improved rainfall. It is also possible that our first-order inference of lake-level decline after 14.4 ka is erroneous. Indeed, coincidence of peak *A. granulata* var. *angustissima*, high ostracod abundances and absence of aquatic macrophytes in the period 14.8–14.4 ka may represent only the transgressive phase itself, when nutrient availability was high but water-column transparency low (as favoured by *A. granulata*) and a stable littoral environment lacking. Expansion of aquatic macrophytes, epiphytic diatoms and vegetation-dwelling chironomids after 14.4 ka may then reflect not a lake regression but rather a stabilisation of (high) lake level in a moist climate regime. In this scenario, forest development would have reduced nutrient and clastic mineral input to the lake, leading to improved transparency and a dominance of epiphytic diatoms and other vegetation-dwelling biota. It is also consistent with high mean organic C content in this section of the core, due to a combination of lessened dilution by clastics and good preservation, and a high C/N ratio because the lake's lower trophic state increased the relative proportion of terrestrial organic matter.

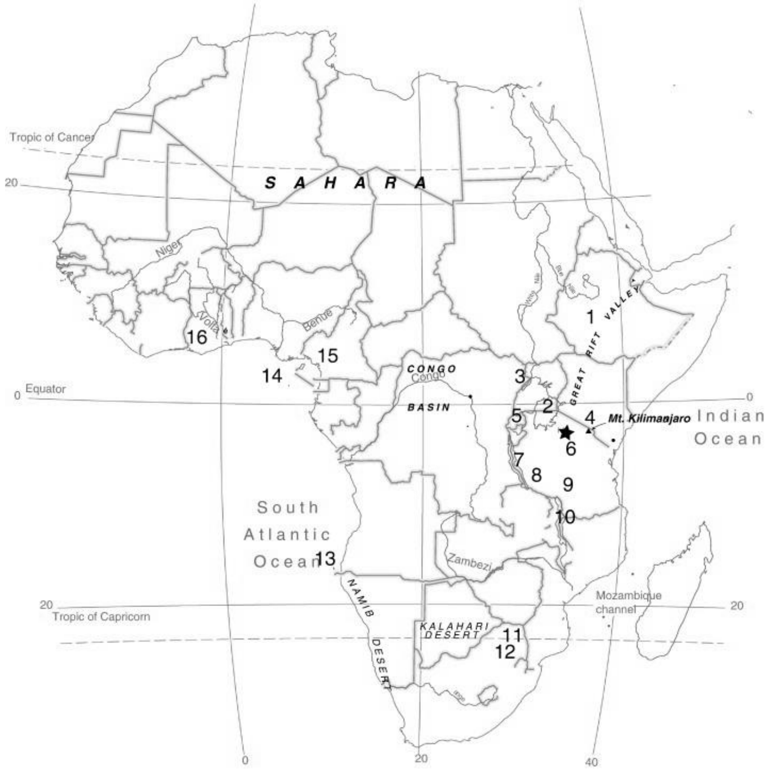

Figure 5: Map of Africa with locations of Lake Emakat (star) and other palaeoenvironmental records cited in the text. 1) Lake Abiyata, 2) Lake Victoria 3), Lake Albert, 4) Lake Magadi, 5) Rusaka swamp, 6) Lake Manyara, 7) Lake Tanganyika, 8) Lake Rukwa, 9) Lake Massoko, 10) Lake Malawi, 11) Makapansgat Valley 12) Wonderkrater, 13) Marine core GeoB1023-5, 14) Marine core KW31, 15) Lake Barombi Mbo, 16) Lake Bosumtwi.

Inference of a drier climate during this period is in eastern Africa only in agreement with evidence from Lake Massoko in southern Tanzania (Barker et al., 2003). Beyond eastern Africa, however, evidence for a drier interval beginning c. 14.4 ka is more common. In South Africa, Holmgren et al. (2003) and Scott et al. (2003) provide evidence of a dry phase from, respectively, speleothem records in Makapansgat Valley and pollen data from Wonderkrater. On the western side of the African continent, e.g., Lake Barombi Mbo in Cameroon (Maley and Brenac, 1998) and Lake Bosumtwi in Ghana (Talbot, 2001) as well as Atlantic Ocean sediments off the Angolan coast (Shi et al., 1998) have all yielded evidence of a dry interval from c. 15.0 ka–14.4 ka, linked to the Antarctic Cold Reversal (Blunier et al., 1998). The Lake Emakat record is ambiguous about whether this influence of the thermohaline circulation extended into eastern equatorial Africa.

6.5.1.3 Lake transgression within a drier climate: 13.2–11.8 ka

Pollen data indicate a decline in the extent of moist montane forest in the crater after c. 13.2 ka, and expansion of vegetation types associated with drier climatic conditions (Ryner et al., 2006). Enriched δ^{13}C in bulk organic matter suggests increased evaporation rates over precipitation, or alternatively the increased importance of C_4 plants (Muzuka et al., 2004) as seemingly reflected in slightly higher mean abundance of Cyperaceae pollen (Fig. 6). The diatom assemblages (Diatom Zone IIa), on the other hand, appear indicative of lake-level increase, with epiphytic taxa dwindling to the benefit of the facultative planktonic diatoms *N. lancettula* and *N. paleacea*, and around 12.5 ka a dramatic increase in the euplanktonic *Aulacoseira granulata*. Peak abundance of the chironomid *Cricotopus* type East Africa (Eggermont and Verschuren, 2004a and Eggermont and Verschuren, 2004b), an orthocladiine species, at that time suggests that the local standing-water habitat was well-oxygenated, i.e. with conditions of relatively low algal production and a dynamic unvegetated shoreline that are likely to have occurred during a transgressive phase.

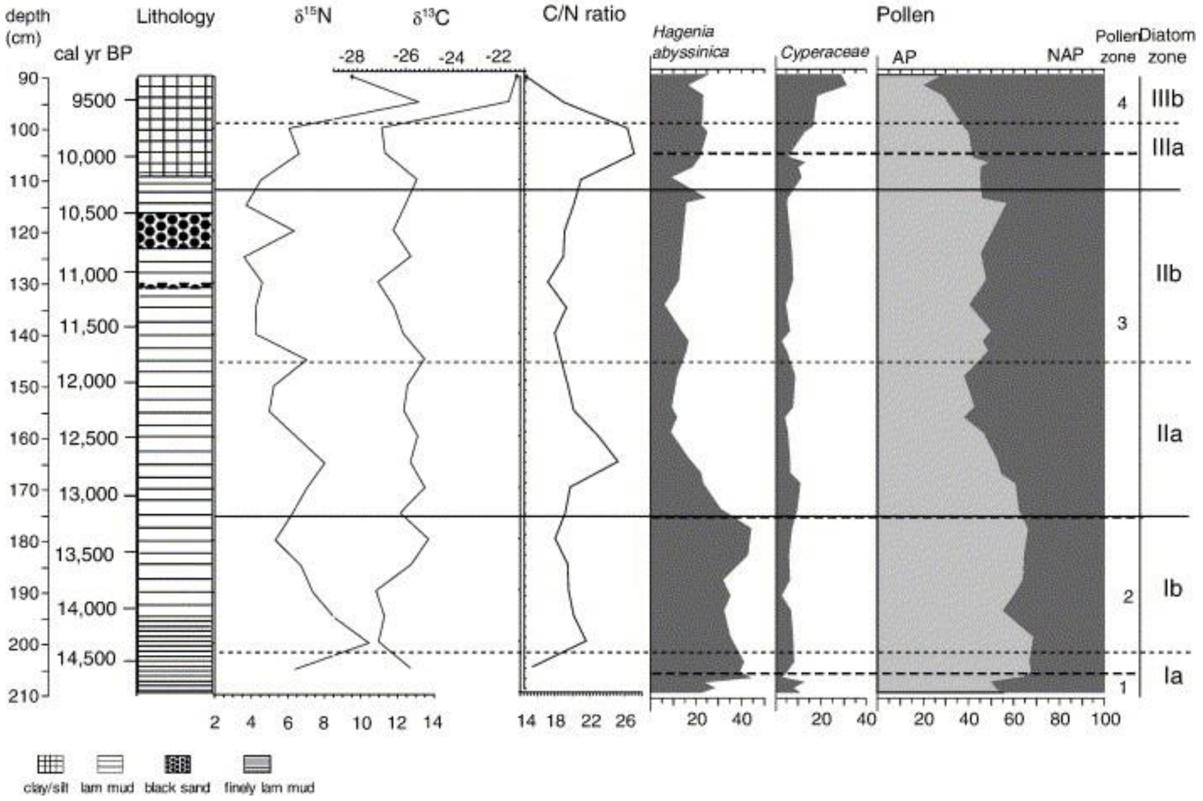

Figure 6: Down core variations in lithology, δ^{13}C, δ^{15}N, C/N ratio, and summarised pollen data originally published in Muzuka et al. (2004) and Ryner et al. (2006) compared to the diatom zonation established in this study. For comparison the pollen zones from Ryner et al. (2006) are indicated with dotted lines.

6.5.1.4 Increased inter-annual variability: c. 11.8–10.3 ka

The shift to slightly higher *Hagenia* abundance and AP/NAP ratio after 11.8 ka indicate the return of somewhat wetter conditions, although overall the pollen data still indicate predominance of forest and scrub communities that are today associated with climatically relatively dry conditions (Ryner et al., 2006). More variable magnetic susceptibility and organic C content, and more pronounced alternation of banded muds and sands already from c. 12.0 ka reflect enhanced periodic influx of clastic material from the crater catchment, presumably as a result of increased erosion, which may have been brought about by more pronounced dry and rainy seasons. Lake level at Emakat seems to have remained as high as before 11.8 ka: diatom assemblages during this period are dominated by the facultative planktonic *Fragilaria* species (mainly *F. brevistriata* and *F. construens* var. *venter*), while periphytic forms had relatively low abundances.

Taking the whole period c. 13.2–10.3 ka together (i.e. Diatom Zone II), substantial changes in the land cover of terrestrial vegetation combined with relatively continuous high Emakat lake level indicates an evolution of both total annual effective precipitation and its seasonal distribution as local expressions of global climatic instability during the late Glacial–Holocene transition. During this time interval, most paleoenvironmental records from northern and equatorial Africa show a dry interval interrupting a general trend of increasing humidity and often claimed to coincide with the Younger Dryas chronozone (Gasse, 2000 and Gasse, 2002). Records from the western Sahara and Sahel place this dry episode at c. 11.0–10.0 ^{14}C ka BP (Gasse and Van Campo, 1998), while a similar dry interval recorded at Lake Bosumtwi in Ghana (Talbot, 2001) and Lake Barombi in Cameroon is dated to between 11.5 and 10.4 ^{14}C ka (Maley and Brenac, 1998), and in a marine record from the Gulf of Guinea to 13.4–12.1 ka (Lezine et al., 2005). In eastern equatorial Africa, Lake Abiyata in Ethiopia recorded a dry phase around 12.0 ka (Chalié and Gasse, 2002) while Lake Magadi in Kenya (Roberts et al., 1993), Lake Albert in Uganda (Beuning et al., 2003) and Rusaka swamp in Burundi (Bonnefille et al., 1995) place it around 11.0 ^{14}C ka. Farther south, Lake Malawi experienced a dry episode between 12 ka and 10.5 ka (Johnson et al., 2002 and Filippi and Talbot, 2005). At present, chronological control on most above records is not sufficiently constrained to either claim or argue against the regional synchrony of this prominent late Glacial event.

In contrast with other East African sites recording a dry interval around 12 ka, pollen data from Lake Emakat provide no clear indication of a return to climatically wetter conditions at the onset of the Holocene, e.g. the expected re-expansion of moist montane forest (Ryner et al., 2006). The Emakat diatom stratigraphy does suggest a temporary rise in lake levels at c. 12.5 ka, but this highstand is clearly not sustained very long. Thus lack of a signal in the pollen record may simply reflect a muted vegetation response to short-lived changes in effective precipitation, however significant their temporary effect on lake water balance and local diatom assemblages.

6.5.2 Transition to a high-salinity environment: c. 10.3–9.3 ka

From c. 10.3 ka a number of significant changes occur in the Lake Emakat record that suggest an abrupt lowering of lake levels. The nature of the sediment changes from a predominantly organic-rich gyttja to a more minerogenic deposit with reduced organic C content, coincident with a marked transition to diatom assemblages reflecting decidedly shallow, saline–alkaline conditions. First occurs the almost complete disappearance of open-water taxa and growing dominance of epiphytic taxa, suggesting a very shallow marsh-like environment. Then at c. 10.0 ka taxa indicative of saline waters highly charged with sodium carbonate, most prominently *Craticula elkab* but also *Rhopalodia gibberula*, appear in the record for the first time while salt-tolerant freshwater diatoms such as *C. ocellata*, *Nitzschia inconspicua*, *G. clevei* var. *javanica* and *E. sorex* reach their maximum relative abundance. High ostracoda density from c. 9.8 ka, seemingly representing frequent occurrence of explosive population growth, is also indicative of pronouncded seasonal or longer-term lake regression. By the time the top of the E4 core sequence was deposited (c. 9.3 ka), diatom-inferred conductivity in Lake Emakat reached 6000 µS cm^{-1}; the chironomid-based estimate is even slightly higher, around or higher than 10,000 µS cm^{-1}.

Lack of information on the mid-and late-Holocene sediments deposited above the E4 sequence precludes evaluation of whether this early-Holocene high-salinity condition of Lake Emakat has continued uninterrupted into the saline environment (27,000 µS cm^{-1}) it is today. Prolonged climatic aridity starting c. 10.3 ka is not evident in records from elsewhere in eastern Africa, but is known from South Africa (starting c. 10.2 ka; Holmgren et al., 2003 and Scott et al., 2003). A short-lived dry event around this time is reported from West Africa (c. 9.6 to 9.4 ka; Lezine and Cazet, 2005).

That the dramatic fall in Lake Emakat levels at 10.3 ka represents a drastic change in tectonic and/or hydrogeological conditions in the Empakaai Crater, which could have led to abrupt draining of lakewater from the caldera, is a scenario that can be excluded. Geomorpholoical and bathymetric survey data (Frame et al., 1975 and own unpubl. field data) reveal no evidence of scoured sediments or an ancient breach in the caldera's closed hydrology.

6.5.3 Local aquatic ecosystem responses to climatic instability

In the context of global warming-induced hydrological instability in semi-arid regions, this paper commenced by stressing the need for greater understanding of the specific response of local surface-water systems to particular future climate change scenarios. Palaeolimnological approaches provide a means of examining lake response to climate change over a variety of time scales and independent of the pollen-based reconstruction of vegetation change.

Combination of palaeolimnological evidence from multiple aquatic biota inhabiting Lake Emakat with pollen and organic stable-isotope data has provided the opportunity to reconstruct its complex history during one such period of warming-induced climatic instability in the past: the late Glacial-Holocene transition.

The evidence presented suggests that at times Lake Emakat has responded in concert with other aquatic ecosystems in equatorial East Africa and beyond this region. However, at times the changes reconstructed for Lake Emakat have few or no homologues elsewhere (e.g., the abrupt fall in lake levels c. 10.3 ka). Furthermore, sometimes the hydrological evolution of the lake appears to contrast with terrestrial moisture-balance inferences based on vegetation history (e.g., the temporary rise in lake levels c. 12.5 ka coincident with drying of the terrestrial landscape). These non-synchronous responses may be more apparent than real, and hinge on the correct interpretation of particular ecological indicator taxa (e.g., whether the pelagic *Aulacoseira granulata* reflects high lake level, or the turbid high-nutrient conditions associated with the (possibly shallow) initial phases of a pronounced transgression episode) or physical limnology (whether dominance of epiphytic diatoms reflects a shallow lake with abundant aquatic macrophytes, or high transparency during a stable highstand in a forested catchment). Uncertain dating control and possible sedimentary hiatuses also limit intra-and inter-regional comparisons, and due to different response functions, vegetation records and lake-level records are not directly comparable. Still, as has been reported elsewhere (Landman et al., 1996) the contrast between lake and vegetation histories may have a true climatic meaning, for example increased levels of Lake Emakat can be a result of increased seasonality, and hence increased runoff, rather than an increase in the total amount of rainfall.

Sediments accumulating in Lake Emakat document part of the complex local responses to both regional and local drivers of change in water quality and catchment conditions. One reason why Lake Emakat appears out of phase with other regional lakes could be because the Empakaai Crater creates its own microclimate: the wall of the caldera acts as a wind break, while water vapour from the lake leads to the formation of low-lying clouds that restrict further heating and evaporation. These local features are likely to dampen the local response to regional climate forcing, particularly when the caldera walls are largely forested and create relatively stable environmental conditions when compared with surrounding areas. This is recognised today by local people, who move their livestock into the caldera during severe droughts in order to find forage and water. Because of this cushioning effect of local environmental conditions, then, all changes that have left a mark in the sedimentary record are likely to reflect response to forcing of substantial magnitude. Moreover, during periods of sparse vegetation cover in the catchment some of this cushioning effect will be lost and the steep, currently devegetated walls of the caldera are likely to enhance runoff and erosion, particularly if the majority of precipitation fall concentrated in short seasonal bursts.

In conclusion, for climate and paleohydrological change in equatorial East Africa during the late Glacial–Holocene transition, our multiple-proxy indicator palaeolimnological data from Lake Emakat reveal the following sequence of events:

1. Expansion of moist montane forest within the catchment was associated with a transgressive lake phase c. 14.8–14.4 ka, followed by stabilisation of this highstand or slight decline of lake level until c. 13.2 ka.

2. The spread of drier vegetation types in the catchment from c. 13.2 ka was associated with lake-level instability and increased turbidity, with apparent high lake levels c. 12.7–12.3 ka and continuing to 10.3 ka, which we interpret to result from higher runoff owing to increased seasonality of rainfall.

3. A substantial lake-level lowering after c. 10.3 ka leading first to shallow freshwater environment and from 9.7 ka an abrupt transition to high salinity and alkalinity.

4. The record from Lake Emakat partly accords with lake histories to both the south and the north of eastern equatorial Africa, with the specific local paleohydrological evolution possibly reflecting the separate regional influences of the Antarctic Cold Reversal in the Southern Hemisphere and the Younger Dryas in the Northern Hemisphere.

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Appendix A

Species list of the chironomids and ostracods encountered in the sediment core E4, Lake Emakat, Empakaai Crater.

Invertebrates	*Environmental preference* (when known)
Chironomidae	
Chironomini	
Chironomus near *alluaudi*	Freshwater
Chironomus near *imicola*	Freshwater
Dicrotendipes septemmaculatus	Freshwater
Dicrotendipes fusconotatus	Freshwater
Kiefferulus disparilis	Euryhaline
Microchironomus deribae	Euryhaline
Nilodorum brevibucca	Freshwater
Nilodorum brevipalpis	Freshwater
Polypedilum near *wittei*	Freshwater
Tanytarsini	
Cladotanytarsus pseudomancus	Freshwater
Genus cfr. *Paratrichocladius* type Kayihara	Freshwater
Tanytarsus formosanus	Freshwater
Tanypodinae	
Ablabesmia/Xenopelopia	
Procladius brevipetiolatus	Freshwater
Tanypodinae indet.	Freshwater
Orthocladiinae	
Cricotopus type East Africa sp. group	Freshwater
Orthocladiinae indet type Challa	
Orthocladiinae indet.	
Ostracoda	
Candonopsis cfr. *africana*	Shallow lake
Cypris puberoides	Shallow lake
Gomphocythere obtusata	
Limnocythere sp.	
Oncocypris mülleri	Littoral
Sarscypridopsis near *trigonella* type Naivasha	Shallow lake
Sclerocypris (juvenile)	Shallow lake
Stenocypris major	Shallow lake
Vestalenula cuneata	Shallow lake
Zonocypris cordata	Shallow lake
Zonocypris costata	Littoral
Ostracoda indet.	

7

Aquatic community response in a groundwater-fed desert lake to Holocene desiccation of the Sahara

Abstract

The finely laminated sediment record of a permanent, hypersaline, desert oasis lake in the Ounianga region of northeastern Chad presents a unique opportunity to document the hydrological evolution of this groundwater-fed aquatic ecosystem during mid- and late-Holocene desiccation of the Sahara. In this study we reconstruct long-term changes in zoobenthos and zooplankton communities of Lake Yoa as their early-Holocene freshwater habitat changed into the hypersaline conditions prevailing today. Chironomid production peaked during the fresh-to-saline transition period, then stabilized at about half that of the earlier freshwater ecosystem. Quantitative salinity inferences based on fossil chironomid assemblages indicate that the fresh-to-saline transition occurred fairly abruptly between ~4100 and 3400 cal yr BP, but that the ecosystem was buffered against shorter-term climate fluctuations due to continuous inflow of fossil groundwater. The mixture of tropical-African and southern Palaearctic chironomid faunas in the Lake Yoa fossil record required us to address several methodological issues concerning chironomid-based salinity reconstruction, and the applicability of a calibration dataset based on tropical East and West African lakes to this Sahara desert locality. The most coherent reconstruction was obtained with an inference model that applies a weighted best-modern-analogue (WMAT) transfer function to the African calibration dataset expanded with six Sahara lakes.

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7.1 Introduction

One of the most prominent environmental changes of the Holocene is the evolution of the North African continent from an early Holocene “green Sahara” (Claussen and Gayler, 1997) largely covered by tropical grassland (Hoelzmann *et al*., 1998) to the world's largest warm desert today. This mid-Holocene aridification of the Sahara is widely believed to have occurred abruptly around 5500 cal yr BP, based on a marine record of terrigenous dust deposition in the tropical Atlantic Ocean (deMenocal *et al*., 2000), that has received apparent support from climate model output suggesting strong biogeophysical feedback between climate and vegetation (Claussen *et al*., 1999). Knowledge of the true paleohydrological and landscape evolution of the Sahara during the later Holocene remains fragmentary, because under today's arid to hyper-arid climate regime, there has been almost no aquatic deposition, and most paleoenvironmental archives in earlier lake deposits have become eroded or truncated by intense wind deflation (Hoelzmann *et al*., 2004). Better documentation of the climate and environmental history of the Sahara is important to improve understanding of Holocene climate and ecosystem dynamics worldwide, because the Sahara is globally the most significant source of dust aerosols (Koren *et al*., 2006). These influence the Earth's climate by reflecting sunlight (Goudie and Middleton, 2001), affecting cloud formation (Graf, 2004), and fertilizing nutrient-limited regions (Koren *et al*., 2006 and Remer, 2006).

In northern Chad, between the Tibesti and Ennedi mountains, a handful of fairly deep, permanent desert lakes exist which potentially provide a continuous archive of Holocene environmental change in the Sahara (Kröpelin, 2007a). These Ounianga lakes are maintained against the extremely negative local water balance by continuous groundwater inflow from the Nubian Sandstone Aquifer, which was last recharged during the early-Holocene humid period (Hissene, 1986 and IAEA, 2007). The deepest of these lakes, Lake Yoa at Ounianga Kebir, has now been demonstrated to have never dried out in the last 6000 years (Kröpelin *et al*., 2008) and therefore contains a unique, continuous, paleoenvironmental record of the mid-Holocene drying of the Sahara. On the other hand, the buffer against desiccation that is provided by fossil groundwater also slows down the lake's hydrological response to changes in rainfall and evaporation, potentially resulting in a muted or strongly non-linear relation between local paleohydrology and climate (Gasse, 2002 and Hoelzmann *et al*., 2004).

In this study we use fossil chironomid assemblages preserved in the Lake Yoa sediment record to quantitatively reconstruct water-chemistry (salinity) changes reflecting the lake's hydrological evolution over the past 6000 years. Salinity is a good indicator of lake water balance as influenced by local climate and hydrology (Engstrom and Nelson, 1991 and Fritz, 1996). It is also known to exert strong control on the species diversity and composition of aquatic algae and invertebrate communities (Hammer, 1986) both directly due to species-specific tolerance to osmotic stress (Marshall and Bailey, 2004, Hassell *et al*., 2006 and Sarma *et al*., 2006), and indirectly due to the role of salinity in the distribution of suitable substrates and food (Colburn, 1988, Williams, 1998, De Szalay and Resh, 2000 and Verschuren *et al*., 2000b). Prior to the 1990s, paleolimnological studies in true saltwater lakes were relatively uncommon, and saline-lake reconstructions using biological proxies (e.g., Paterson and Walker, 1974, Anadon *et al*., 1986 and Cohen and Nielsen, 1986; DeDeckker and Forester, 1988) were quite rare. Biological paleosalinity reconstructions have subsequently been recognized as highly informative, and are now carried out on all continents around the world (Smol and Cumming, 2000 and Heinrichs and Walker, 2006). Chironomidae (non-biting midges) are among the most reliable paleoenvironmental indicators in saline lakes (and saline lake phases in the history of a closed-basin lake) because unlike diatoms (e.g., Battarbee *et al*., 2005 and Ryves *et al*., 2006) their chitinous remains are not vulnerable to dissolution in a high-pH environment. Accordingly, paleolimnological studies have taken advantage of new chironomid-based salinity inference models to reconstruct climate (e.g., Heinrichs *et al*., 1997, Heinrichs *et al*., 2001, Verschuren *et al*., 2000a and Ryner *et al*., 2007) or sea-level change (e.g., Gandouin *et al*., 2007).

Applying the current chironomid-based salinity inference model for tropical African lakes (Eggermont *et al*., 2006) to the Saharan locality of Lake Yoa is, however, not a matter of course. One of the principal requirements for quantitative reconstructions using biological inference models is that the calibration data set must fully cover past faunal diversity and environmental conditions at the study site (Birks, 1998). The existing African chironomid calibration data set is derived from modern chironomid faunas in 67 lakes in East Africa (Kenya, Uganda, Ethiopia, Tanzania), eight lakes in West Africa (Cameroon), and one in North Africa (Chad) that cover a wide salinity range (15–68,400 µS/cm), but all except one are clearly within the Afrotropical biogeographical region. Given the possible mixture of Afrotropical and (southern) Palaearctic chironomid faunas in the fossil record of an aquatic ecosystem located in the Saharan transition zone between these two biogeographical realms (Dumont, 1979, Dumont, 1982 and Dumont and Verheye, 1984), we here assess several issues concerning the applicability of the African salinity inference models. First, we evaluate if the fossil chironomid fauna of Lake Yoa is sufficiently represented (i.e., has good modern analogues) in the present calibration data set for inference models to yield accurate reconstructions. Second, we evaluate whether expanding the African dataset with a (modest) number of local sites improves the precision of model outputs. Finally, we assess which transfer function produces the ecologically most meaningful reconstruction, using the fossil distributions of non-chironomid indicator taxa *Chaoborus* (Diptera), *Ephydra* (Diptera) and *Anisops* (Hemiptera) as a guide.

7.2 Regional setting

Lake Yoa (19.03° N, 20.31° E, 380 m above sea level) occupies a Pleistocene deflation basin in the desert oasis of Ounianga Kebir, situated halfway between the Tibesti and Ennedi mountains in northern Chad (Fig. 1). The prevailing sub-tropical desert climate shows distinct seasonal temperature variation (monthly mean temperatures of 26–42 °C during the day, 15–26 °C at night) but is arid year-round. Local rainfall is erratic (less than 21 mm of rainfall has fallen in the 14-year period prior to 1967) as regular summer monsoon rainfall from the south does not occur within ~300 km of the area, while dry northeasterly trade winds passing through the Tibesti–Ennedi corridor contribute to some of the highest evaporation rates measured worldwide (annual mean 6100 mm). The hypersaline Lake Yoa (4.3 km^2; 26 m deep; 68,000 μS/cm) was thermally stratified in January 1999, December 2003 and November 2004. Finely laminated profundal sediments strongly suggest permanent bottom anoxia, but at present we can not confirm that the lake is meromictic, i.e., that deep seasonal mixing never destratifies the entire water column. The lake is bounded to the south and west by sandstone cliffs, and to the north and east by dunes of medium to coarse quartz sand. Part of the groundwater feeding Lake Yoa is supplied by the Girki freshwater spring brook (250 μS/cm) that is sandwiched between these dunes. A second lake cluster is located at Ounianga Serir (18.56° N, 20.52° E), ~50 km to the east of Ounianga Kebir. The 8 lakes forming Ounianga Serir (Fig. 1) are mostly elongated, northeast to southwest oriented lakes which together occupy a surface area of ~15 km^2 and are separated from each other by dunes. The central, large hypersaline Lake Teli (156,900 μS/cm) works as an evaporative pump (George and Kröpelin, 2000 and Kröpelin, 2007b): high lake-surface evaporation is compensated both by local groundwater input and by a constant flow of water (and dissolved solids) drawn from adjacent lakes through the dunes towards Teli. This process has created a gradient of increasing salinity from the periphery (e.g., Lake Boku: 320 μS/cm) to the middle of the lake cluster (e.g., Lake Agouta: 2610 μS/cm). All lakes except Teli are covered to various extent by floating *Phragmites* (reed) mats. In addition Ounianga Serir includes several interdunal depressions filled with reed swamp but lacking open water.

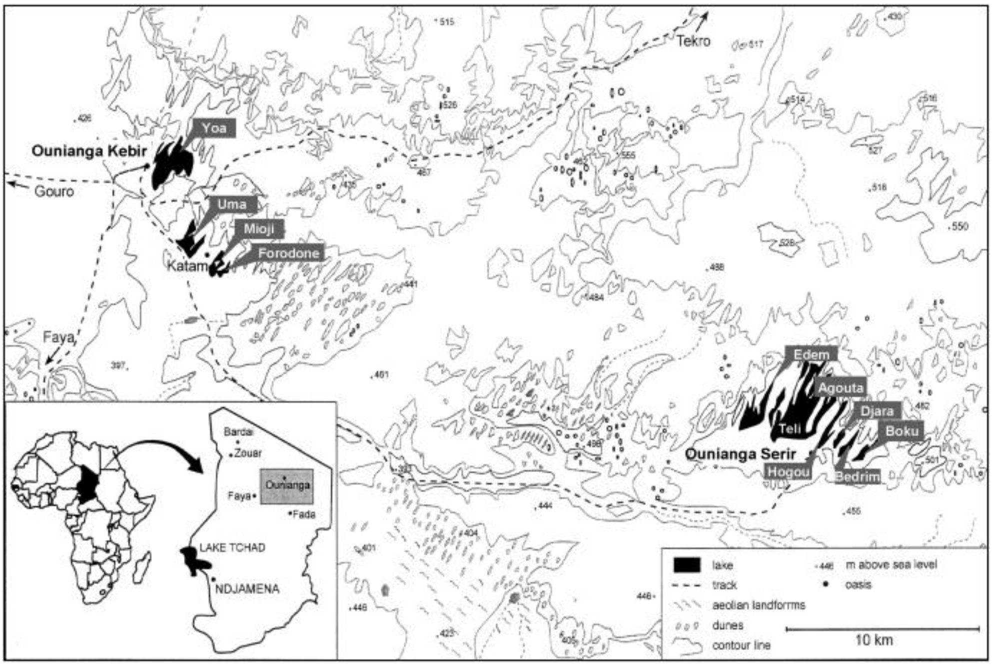

Figure 1: Map of the study region, showing the location of Lake Yoa at Ounianga Kebir, and the lake cluster at Ounianga Serir.

7.3 Materials and methods

7.3.1 Field methods, sediment composition and chronology

In 2003 and 2004, overlapping sediment cores (OUNIK03-2P, OUNIK03-3G, OUNIK04-1P) were retrieved from the deep northeastern sector of Lake Yoa (24.3 m water depth), using a single-drive piston corer (Wright, 1980) and a square-rod piston corer (Wright, 1967) operated with drive rods from an anchored platform. Core sections were extruded in the field into transparent PVC sheath, and packed in PVC water pipe cut lengthwise into two halves. The unconsolidated uppermost sediments were extruded in 0.5-cm-increments with a fixed-interval sectioning device (Verschuren, 1993), and packed in Whirl-Pak bags for transport. Overlapping core sections were cross-correlated using the fine sediment lamination as visual marker horizons. This produced a composite sediment sequence of 7.49 m total length labeled OUNIK03/04 (Kröpelin *et al*., 2008). Lake Yoa sediments are clayey to sandy muds with 5–20% organic matter, 5–25% carbonate, and 1–13% biogenic Si. Sediment chronology (Fig. 2) was established using the ^{137}Cs-inferred time marker of peak nuclear bomb testing in 1963–1964 and 17 AMS ^{14}C dates on charred grass, on fragments of *Typha* rhizome or on bulk organic matter. Paired ^{14}C dates on *Typha* rhizomes and bulk organic matter from the same core interval yielded similar results, indicating that most carbon uptake in the root system of these cattail stands is from the water. The age–depth model used in this paper is a 3rd-order polynomial regression of INTCAL04-calibrated ^{14}C ages (Reimer *et al*., 2004) vs cumulative dry weight downcore, after removal of three outliers and subtraction of the modern lake-carbon reservoir age (1467 ± 44 ^{14}C years) from all bulk organic and *Typha* rhizome ages. Given dating uncertainty resulting from analytical and age-modeling error (mean ± 40 ^{14}C years and ± 70 calendar years, respectively), all calendar ages given in the text are rounded to the nearest 100 years. The almost linear age–depth relationship (r^2 age vs depth = 0.982; r^2 age vs cum. dry wt = 0.985; $n = 14$) indicates a stable rate of sediment accumulation through time, therefore the absolute concentrations of fossil aquatic biota approximate their rate (flux) of offshore deposition.

We estimated the modern reservoir age from the mean ^{14}C age difference ($n = 3$) between two pairs of ^{14}C dates on terrestrial and aquatic organic matter, and between the uppermost ^{14}C date on bulk organic matter and its corresponding varve count (for details, see Kröpelin *et al*., 2008). Considering the strong hydrological evolution of Lake Yoa over the past 6000 years, the lake-reservoir age was almost certainly less than 1467 ± 44 ^{14}C years during the early part of the record, implying a possible underestimation of the true age of mid-Holocene events in our reconstruction. Lack of suitable terrestrial ^{14}C dating targets and varve-counting uncertainty in the lower core sections precludes constraint of the pre-modern lake reservoir age at this time.

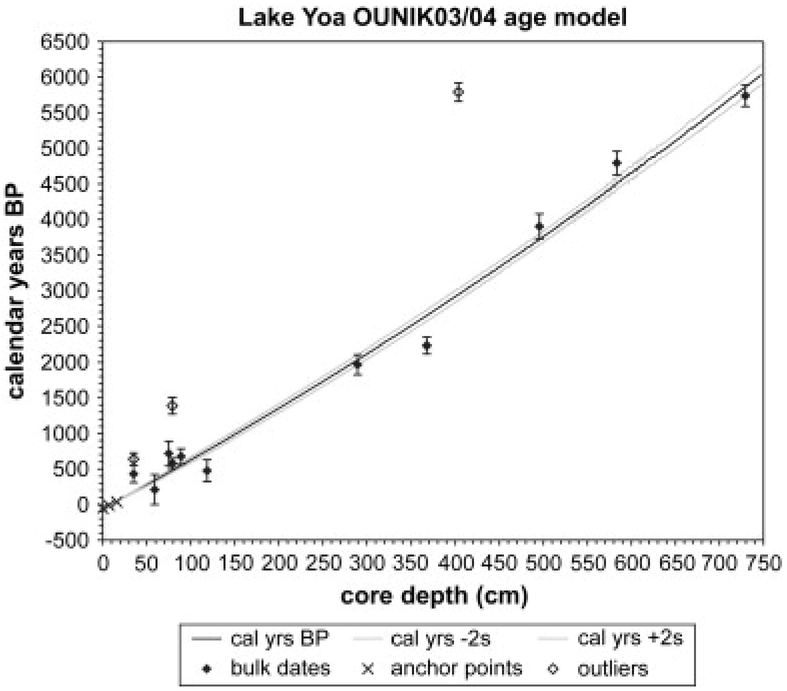

Figure 2: Calendar age–depth model for the composite OUNIK03/04 core from Lake Yoa.

7.3.2 Fossil invertebrate analysis

The aquatic larvae of the Chironomidae (Insecta: Diptera) are a dominant component of lake macrozoobenthos worldwide, and widely recognized as valuable paleoenvironmental indicators (Porinchu and MacDonald, 2003, Walker, 2001 and Walker, 2007). Our methodology for chironomid sample processing followed Walker (2001) and Verschuren and Eggermont (2007), with sediments being washed through a 150-µm sieve following deflocculation in warm 5–10% KOH. Analysis of fossil chironomid assemblages was carried out on 93 2-cm increments at 8-cm intervals (i.e., approximately one sample every 60 years), with one hiatus at 288–290 cm due to limited availability of material. Head capsules were picked from the residue at 30× and mounted in glycerine on microscope slides. Identification was done with a compound microscope at 100–400× by reference to identification guides for tropical Africa (Verschuren, 1997, Eggermont and Verschuren, 2004a, Eggermont and Verschuren, 2004b and Eggermont *et al*., 2005). Criteria for counting fragmentary fossils followed Walker (1987). Depending on fossil density and surface-sediment water content, between 3.5 and 19.2 g of wet mud was processed to yield the ~35–50 head capsules required for numerical analysis, given low taxonomic diversity (Shannon–Weaver index H') is <3.0 (Heiri and Lotter, 2001 and Quinlan and Smol, 2001).

Lake sediments also hold the remains of various other aquatic invertebrates with useful application in Quaternary paleoecology (Frey, 1964 and Frey, 1976). These include Trichoptera (e.g., Solem and Birks, 2000), Ceratopogonidae (biting midges; e.g., Walker *et al*., 1997 and Heinrichs *et al*., 2001), *Chaoborus* (phantom midges; e.g., Uutala, 1990, Uutala and Smol, 1996, Walker *et al*., 1997 and Heinrichs *et al*., 2001), Cladocera (water fleas; e.g., Frey, 1976, Frey, 1988 and Whiteside and Swindoll, 1988) and Ostracoda (seed shrimps; e.g., De Deckker and Forester, 1988, Griffiths *et al*., 2001, Holmes and Chivas, 2002 and Cohen *et al*., 2005). Apart from chironomids and ostracods, the use of these aquatic invertebrate remains as paleoenvironmental proxies in (sub-) tropical regions has been limited, despite their demonstrated potential (Mees *et al*., 1991, Verschuren *et al*., 2000b, Palacios-Fest *et al*., 2005 and Rumes *et al*., 2005). We analyzed non-chironomid invertebrate remains in the Lake Yoa core at 16-cm intervals (i.e., approximately one sample every 120 years) plus three additional levels. Identification was mostly done with a stereomicroscope at 30–130× by reference to Rumes *et al*. (2005) and primary literature mentioned therein. Other remains were picked from the residue and mounted in glycerine on microscope slides to be identified using a compound microscope at 100–400×.

Biostratigraphic plots were produced with TILIA version 2.0.b.4 (Grimm, 1993) and TGView version 2.0.2 (Grimm, 2004). Stratigraphically constrained sum-of-squares cluster analysis (CONISS; Grimm, 1987) applied to squared-root transformed species data allowed identification of core intervals with major changes in invertebrate communities. Stratigraphic zonation was further accomplished by optimal sum-of-squares zonation (Birks and Gordon, 1985), using the broken-stick model proposed by Bennett (1996) to estimate the number of statistically significant zones. This analysis was performed using ZONE version 1.2 (Juggins, 1991) and BSTICK version 1.0 (J.M. Line and H.J.B. Birks, unpublished software).

7.3.3 Quantitative salinity reconstruction

Salinity inferences were obtained in C2 version 1.3.4. (Juggins, 2003) using transfer functions based on weighted-averaging (WA), 2-component weighted-averaging partial-least-squares (WA-PLS(2)) and a weighted modern analogue technique (WMAT-4). In WA (Birks *et al.*, 1990), a taxon's optimum is the average value of all lakes in which the taxon occurs weighted by its percent abundance in each. It assumes that taxa display a unimodal response to the environmental variable of interest and are most abundant in lakes with values near their optimum. WA-PLS (ter Braak & Juggins, 1993) improves WA by using additional PLScomponents to take into account residual correlations among taxa (Fritz *et al*., 1991; Walker *et al*., 1997). In WMAT-4, the salinity inferred by a fossil assemblage is the weighted mean of the surface-water salinity of those four lakes in the calibration data set whose modern species assemblage is most similar to that particular fossil assemblage. We performed two series of reconstructions. The first was based on the existing inter-regional calibration dataset EL–WL (Eggermont *et al*., 2006) consisting of 76 lakes from East Africa (67), West Africa (8) and North Africa (1, Lake Yoa). In this study we used modified versions of the Eggermont *et al*. (2006) inference models, that incorporate all 96 taxa recorded in calibration lakes (i.e., also those taxa recorded in less than three lakes; cf. Birks, 1998), in order to allow *Cricotopus* type Ounianga Kebir to contribute to the Lake Yoa reconstruction. Depending on the transfer function, these trial models have a jack-knifed coefficient of determination between observed and predicted conductivity (r^2_{jack}) of 0.76–0.81, and a root-mean-squared error of prediction (RMSEP) of 0.37–0.40 $\log_{10}$ conductivity units (CU). In a second series of reconstructions we expanded the EL–WL calibration data set with surface-sediment assemblages from six regional Sahara lakes: the Girki freshwater spring brook at Ounianga Kebir (250 µS/cm) and five lakes at Ounianga Serir (Edem, Agouta, Hogou, Djara and Boku) with conductivity values between 320 and 2610 µS/cm; hypersaline Lake Teli (156,900 µS/cm) was not included as no chironomids were found there. This calibration dataset will be referred to as the EL–WL–S data set. The trial models derived from it have somewhat lower values for r^2_{jack} (0.73–0.77) and a correspondingly higher RMSEP (0.38–0.41 $\log_{10}$ CU).

The reliability of the chironomid-inferred salinity reconstructions were evaluated with three diagnostic statistics available in C2 version 1.3.4. (Juggins, 2003). The first diagnostic is the fraction of taxa in each fossil assemblage that are represented in the modern calibration set (Birks, 1998). Second, using MAT with squared chi-square distance as the dissimilarity coefficient, we assessed if a fossil assemblage had a good modern analogue assemblage in the modern calibration data set; the used cut-off dissimilarity value for a good modern analogue is the 10th percentile of the distribution of dissimilarities between calibration samples (Clarke *et al.*, 2006). Third, we calculated sample-specific errors (Birks, 1995) with 999 bootstrapping cycles.

7.4 Results

7.4.1 Taxonomy

A total of 17 chironomid taxa were identified, of which 15 are morphologically identical to taxa documented from lakes in tropical East or West Africa (Eggermont and Verschuren, 2004a, Eggermont and Verschuren, 2004b and Eggermont *et al.*, 2005). Two morphotypes, cf. *Stictochironomus* type Ounianga Kebir and *Chironomus* cf. *salinarius* have not previously been encountered in surveys of African subfossil chironomid larvae. Cf. *Stictochironomus* type Ounianga Kebir (Fig. 3c) resembles the morphotype nr *Stictochironomus* type Kayihara (Eggermont and Verschuren, 2004b) but its mentum has a trifid, not notched, median tooth with three equal apices, and the first lateral teeth are slightly smaller than the second laterals instead of being distinctly larger. The morphotype *Chironomus* cf. *salinarius* (Fig. 3a,b) resembles *Chironomus* near *imicola* (Kieffer) described from East Africa (Eggermont and Verschuren, 2004b) in having a mentum with the apex of the fourth laterals clearly below the line connecting the apices of the third and fifth laterals (mentum type II of Webb and Scholl (1985)), but differs from it in having a relatively larger central median tooth (never shorter than the first laterals), first and second laterals less fused (not over much of their length), and a pecten epipharynghis with ~15 equally-sized (not irregular) teeth. Comparison with reference material from The Netherlands (courtesy of H. Vallenduuk, Buro Vallenduuk, The

Netherlands; cf. larval descriptions in Vallenduuk *et al*., 1997) suggest that the Lake Yoa morphotype most closely resembles the Eurasian halophilic species *C. salinarius* Kieffer, which has not yet been recorded from Africa; the only visible difference is that *C. salinarius* mostly has mentum type I of Webb and Scholl (1985) whereas all Yoa specimens have a type II mentum. Hence, we use "conferatur" (*sensu* Eggermont and Verschuren, 2003a) in the name designation to mark this difference. Definitive species assignment will require collection of live material from Ounianga to analyze soft body parts and various labral elements not preserved on our fossil specimens.

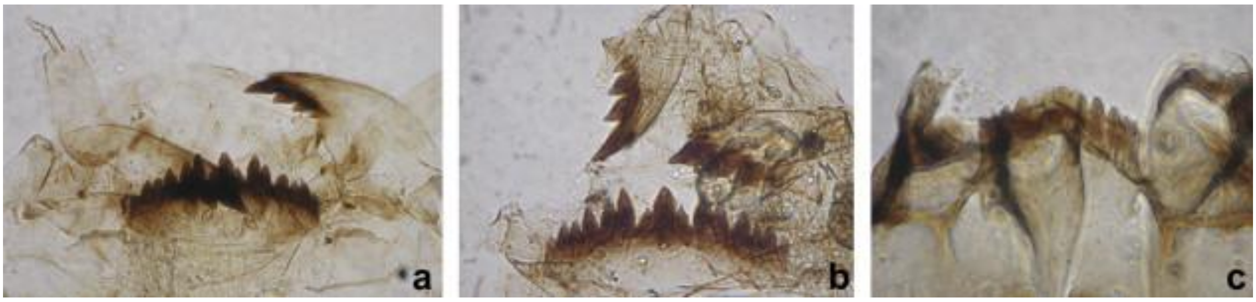

Figure 3: Sub-fossil remains of *Chironomus* cf. s*alinarius* (a, b), and cf. *Stictochironomus* type Ounianga Kebir (c).

Non-chironomid invertebrate remains from Lake Yoa could be assigned to six distinct fossil types. Five of these are chitinous exoskeletal fragments of aquatic insect larvae: the phantom midge *Chaoborus pallidipes/edulis* (Diptera: Chaoboridae), the brine fly *Ephydra* sp. (Diptera: Ephydridae), the waterboatman *Anisops* sp. (Hemiptera: Corixidae), and diverse mayfly (Ephemeroptera: Ephemeridae) and caddisfly (Trichoptera) larvae. *Anisops* (Hart *et al*., 1991, Lahr *et al*., 1999, Seaman *et al*., 1991, Teskey, 1984, Hammer, 1986 and Rumes *et al*., 2005) and *Ephydra* are both halophilic (Hart *et al*., 1991, Teskey, 1984, Hammer, 1986 and Rumes *et al*., 2005). As regards *Chaoborus*, all larval remains (mandibles with mandibular fan, maxillae and pharyngeal sphincters) match both *Chaoborus pallidipes* Theobald (Green and Young, 1976) and *Chaoborus edulis* Edwards (McGowan, 1976); distinction between these two taxa is ambiguous (Verbeke, 1958 and McGowan, 1976). The remaining invertebrate fossils were headshields, ephippia and carapaces of chydorid water fleas (Anomopoda Chydoridae), belonging to at least four genera (*Leydigia*, *Chydorus*, *Oxyurella* and *Alona*), but not analyzed in detail here.

7.4.2 Stratigraphy and zonation

Concentrations of chironomid head capsules in the Yoa record average 19.5 ± 5.5 head capsules/g dry sediment (hc/g), with the highest densities (>20 hc/g) recorded in the top sediments and between 620 and 475 cm (4900–3600 cal yr BP; Fig. 4). Abundances of *Chaoborus pallidipes/edulis*, Chydoridae, Corixidae and Ephydridae were sufficiently high to discern stratigraphic patterns that may reflect past water-balance changes. Remains of

Ephemeridae and Trichoptera were very scarce, and found only below 450 cm (before 3400 cal yr BP). CONISS identified six invertebrate assemblage zones based on all these groups plus the Chironomidae, and all zones were determined to be significant by the broken-stick model. This zonation also makes ecological sense (i.e., zones mark actual changes in the entire invertebrate community): besides the appearance/disappearance of one-two (dominant) taxa, the transition between zones is also marked by visible shifts (often 10–20% or more) in the relative abundances of the remaining taxa. The uppermost zone was additionally divided into two subzones based on distinct deep branching in the CONISS dendrogram (Fig. 4).

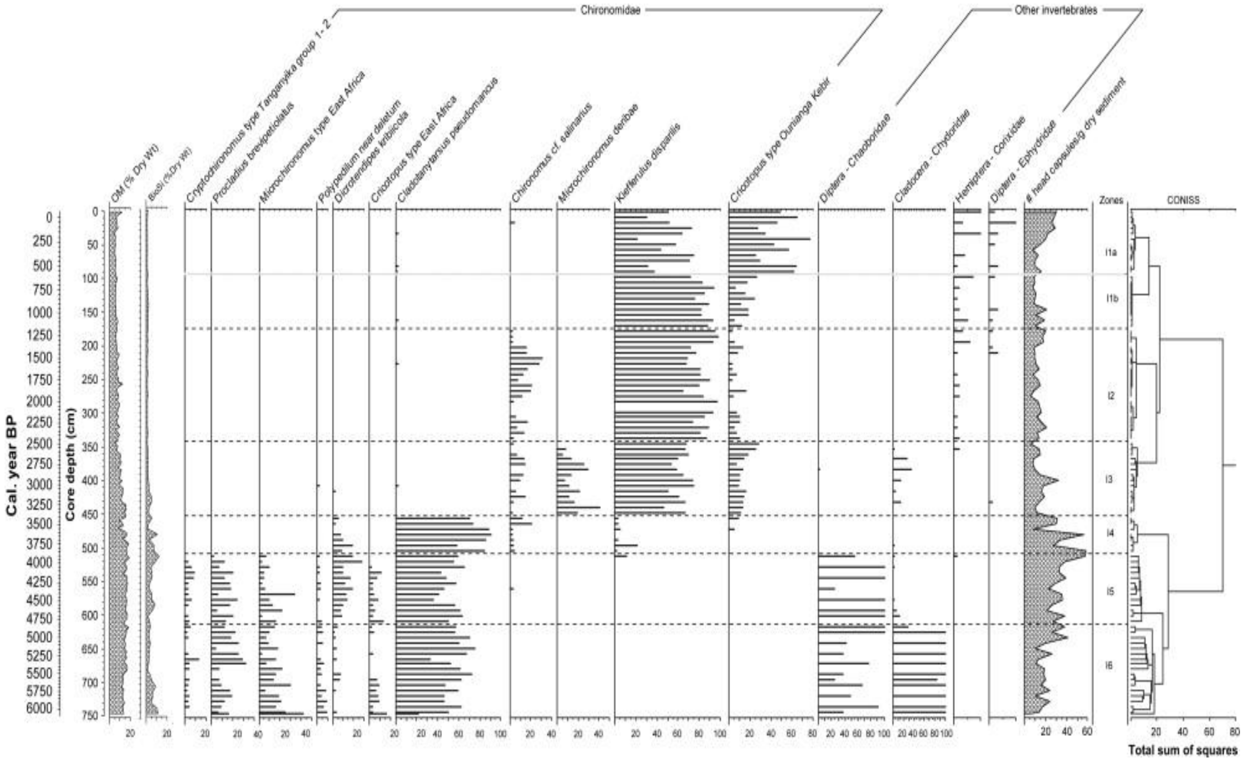

Figure 4: Stratigraphic distribution of aquatic invertebrate remains in composite core OUNIK03/04. Taxa are arranged from left to right according to their increasing weighted-average conductivity optimum; taxa with fossil abundance less than 0.1% of the total fossil abundance are not illustrated. Horizontal lines indicate invertebrate zone boundaries determined by CONISS and the broken-stick model.

7.4.2.1 Zone I6 (749–611 cm, 6100–4800 cal yr BP)

This zone is typified by high abundances of *Cladotanytarsus pseudomancus* (55 ± 13.3%) alongside fairly high numbers of *Procladius brevipetiolatus* (14.3 ± 9.6%) and *Microchironomus* type East Africa (15.4 ± 10.1%). *Cricotopus* type East Africa is distinctly present in the lower part of this zone (up to 15%) but occurs only sporadically in the upper part. *Cryptochironomus* type Tanganyika group 1–2, *Polypedilum* near *deletum* and *Dicrotendipes kribiicola* occur throughout, but together make up at most 20% of the chironomid fauna. Non-chironomid remains are dominated by *Chaoborus pallidipes/edulis* and a diverse chydorid assemblage (*Leydigia*, *Chydorus*, *Oxyurella*, *Alona*).

7.4.2.2 Zone I5 (611–507 cm, 4800–3900 cal yr BP)

Cladotanytarsus pseudomancus, *Procladius brevipetiolatus* and *Microchironomus* type East Africa occur in fairly similar abundances as in I6 (52.2 ± 9.1%, 13.5 ± 6.7% and 10.2 ± 9.1%, respectively), but the latter two decrease slightly near the top of this zone. *Cryptochironomus* type Tanganyika group 1–2 persists through I5 at values up to 10%, and also *Cricotopus* type East Africa is present throughout (5.6 ± 3.9%) except near its upper boundary. *Dicrotendipes kribiicola* shows a major increase compared to I6, with abundances of up to 28%. This zone is further characterized by a significant decrease in the Chydoridae (now only *Alona* and *Chydorus* occurring sporadically near the bottom and top), and high abundance of *Chaoborus pallidipes/edulis* mandibles.

7.4.2.3 Zone I4 (507–451 cm, 3900–3400 cal yr BP)

This zone is characterized by the complete disappearance of the freshwater taxa *Cryptochironomus* type Tanganyika group 1–2, *Procladius brevipetiolatus*, *Microchironomus* type East Africa and *Polypedilum* near *deletum*, and the first occurrences of *Cricotopus* type Ounianga Kebir, *Chironomus* cf. *salinarius* and *Kiefferulus disparilis*. *Dicrotendipes kribiicola* still occurs at values of 5–10% at the base of this zone, but in the upper part it becomes a minor component of the chironomid fauna. *Cladotanytarsus pseudomancus* persists as the dominant chironomid species (67.8 ± 28.2%). Other invertebrate remains are virtually absent, including *Chaoborus*; only two Cladocera specimens (*Alona* and *Chydorus*) were found, at 495 cm depth.

7.4.2.4 Zone I3 (451–341 cm, 3400–2500 cal yr BP)

The beginning of I3 is marked by significant change in the chironomid fauna: *Dicrotendipes kribiicola* and *Cladotanytarsus pseudomancus* disappear entirely (except for a brief recurrence at ca 3050 cal yr BP), leaving *Kiefferulus disparilis* as the dominant taxon (57.4 ± 18.5%). *Microchironomus deribae* appears for the first time (17.0 ± 10.0%), and *Cricotopus* type Ounianga Kebir shows an intermittent increase to ~30% (but with a mean of 13.0 ± 4.6%). *Chironomus* cf. *salinarius* is present throughout much of this zone, at fairly low abundances (6.8 ± 5.8%). The non-chironomid fauna in this zone is typified by the appearance of the salt-loving corixid *Anisops* near the top, and re-appearance of Chydoridae (*Alona cambouei*).

7.4.2.5 Zone I2 (341–173 cm, 2500–1200 cal yr BP)

This zone is characterized by the complete disappearance of *Microchironomus deribae*. *Kiefferulus disparilis* continues as the dominant chironomid (82.8 ± 10.1%), followed by a gradually expanding *Chironomus* cf. *salinarius* which peaks ca 1490 cal yr BP (and has an I2 mean of 11.7 ± 8.9%). *Cricotopus* type Ounianga Kebir falls back to a mean abundance of

5.4 ± 4.5%. This zone is further typified by the regular occurrence of *Anisops*, and in the upper part the first appearance of Ephydridae.

7.4.2.6 Subzone Ib (173–93 cm, 1200–600 cal yr BP)

The onset of Ib is marked by complete disappearance of *Chironomus* cf. *salinarius* and increasing numbers of *Cricotopus* type Ounianga Kebir (to a mean of 15.2 ± 7.1%). *Kiefferulus disparilis* still dominates the chironomid fauna (84.3 ± 7.2%), with abundances of up to 94%. Corixidae and Ephydridae are the other invertebrates typifying this subzone.

Subzone Ia (93–0 cm, 600 cal yr BP to present)

Most obvious in this subzone is the increasing importance of *Cricotopus* type Ounianga Kebir (47.9 ± 16.9%), becoming co-dominant with *Kiefferulus disparilis* (now 50.3 ± 18.0%). *Cladotanytarsus pseudomancus* also occurs sporadically at very low abundances (<3%), while Corixidae and Ephydridae remain common.

7.4.3 Salinity inferences and analogue comparisons

Fifteen of the 17 fossil chironomid taxa of Lake Yoa are represented in the African calibration data set EL–WL. The remaining two taxa (*Chironomus* cf. *salinarius* and cf. *Stictochironomus* type Ounianga Kebir) comprise only a small fraction of the fossil assemblages (mean of 3.9 ± 6.8% and 0.1 ± 0.6%, respectively). All samples also had good modern analogues in the EL–WL calibration dataset. However, for 31 samples below 450 cm depth (before 3400 cal yr BP), the expanded EL–WL–S calibration dataset contained even closer modern analogues (the distance to the closest analogue site decreased 9.3 ± 6.6% on average).

Past salinity variation in Lake Yoa as reconstructed by the various inference models is shown in Fig. 5 and Fig. 6. Sample-specific error for the EL–WL and EL–WL–S model outputs are basically identical (on average 0.47 $\log_{10}$ conductivity units (CU)). They are smaller in zones I6–I4 (WA: 0.42 ± 0.01 $\log_{10}$ CU; WA-PLS(2): 0.40 ± 0.02 $\log_{10}$ CU; WMAT-4: 0.44 ± 0.05 $\log_{10}$ CU) than in zones I3–I1 (WA: 0.45 ± 0.01 $\log_{10}$ CU; WA-PLS(2): 0.65 ± 0.18 $\log_{10}$ CU; WMAT-4: 0.45 ± 0.03 $\log_{10}$ CU). Reconstructions using the EL–WL–S calibration data set closely resemble those using EL–WL, but EL–WL–S model results are more similar to each other, especially the WA- and WMAT-4 output. Considering that the EL–WL–S data s*et al*so provides closer modern analogues for many I6–I4 samples, we mainly discuss model results based on the latter.

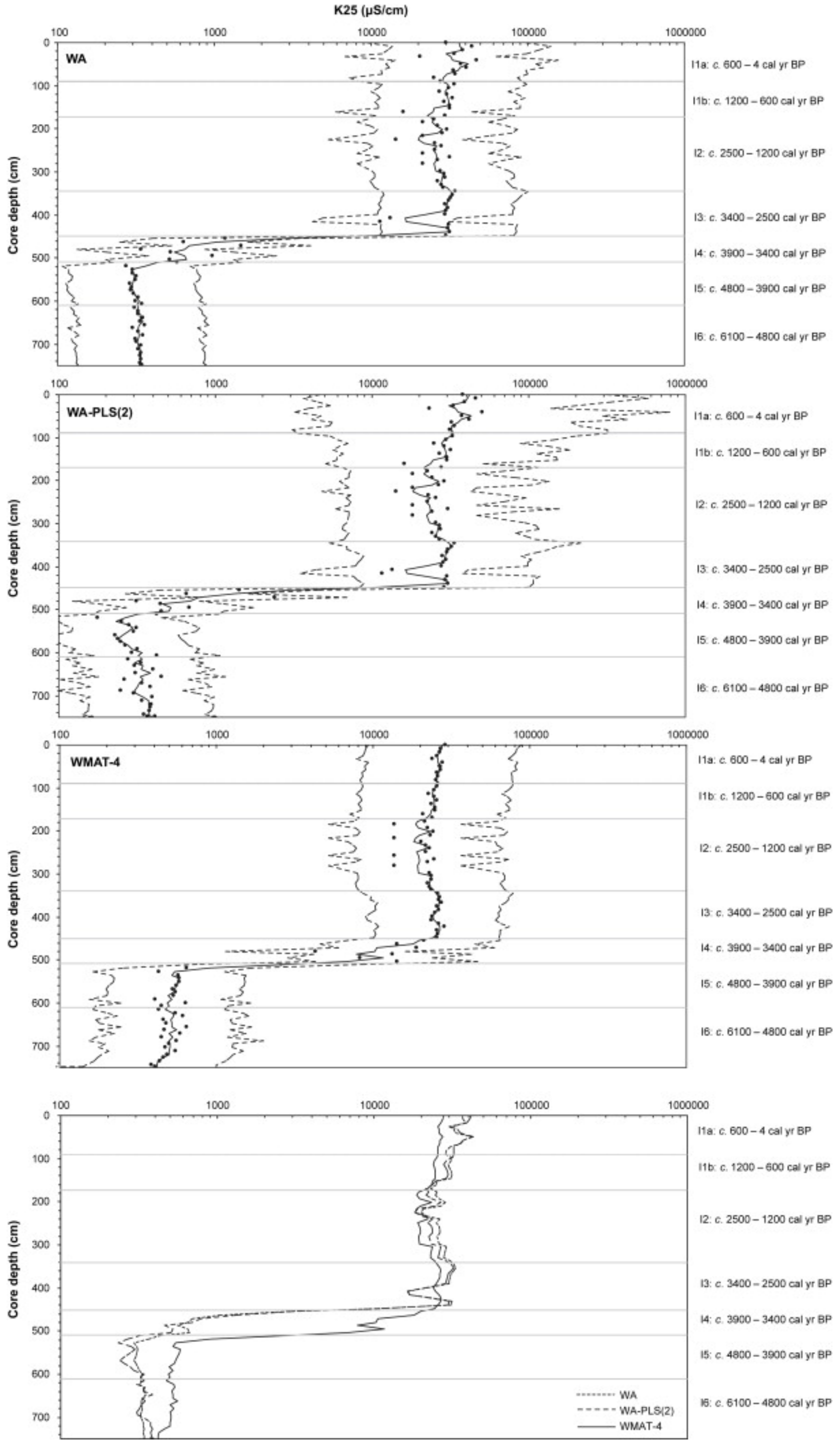

Figure 5: Chironomid-inferred salinity reconstruction for Lake Yoa using the EL–WL calibration data set (K25 = specific conductance at 25 °C). Shown are output of WA, WA-PLS(2), and WMAT-4 inference models. A 3-point moving average (full line) highlights the major trends in the data; uncertainty ranges (dotted line) are the sample-specific prediction errors.

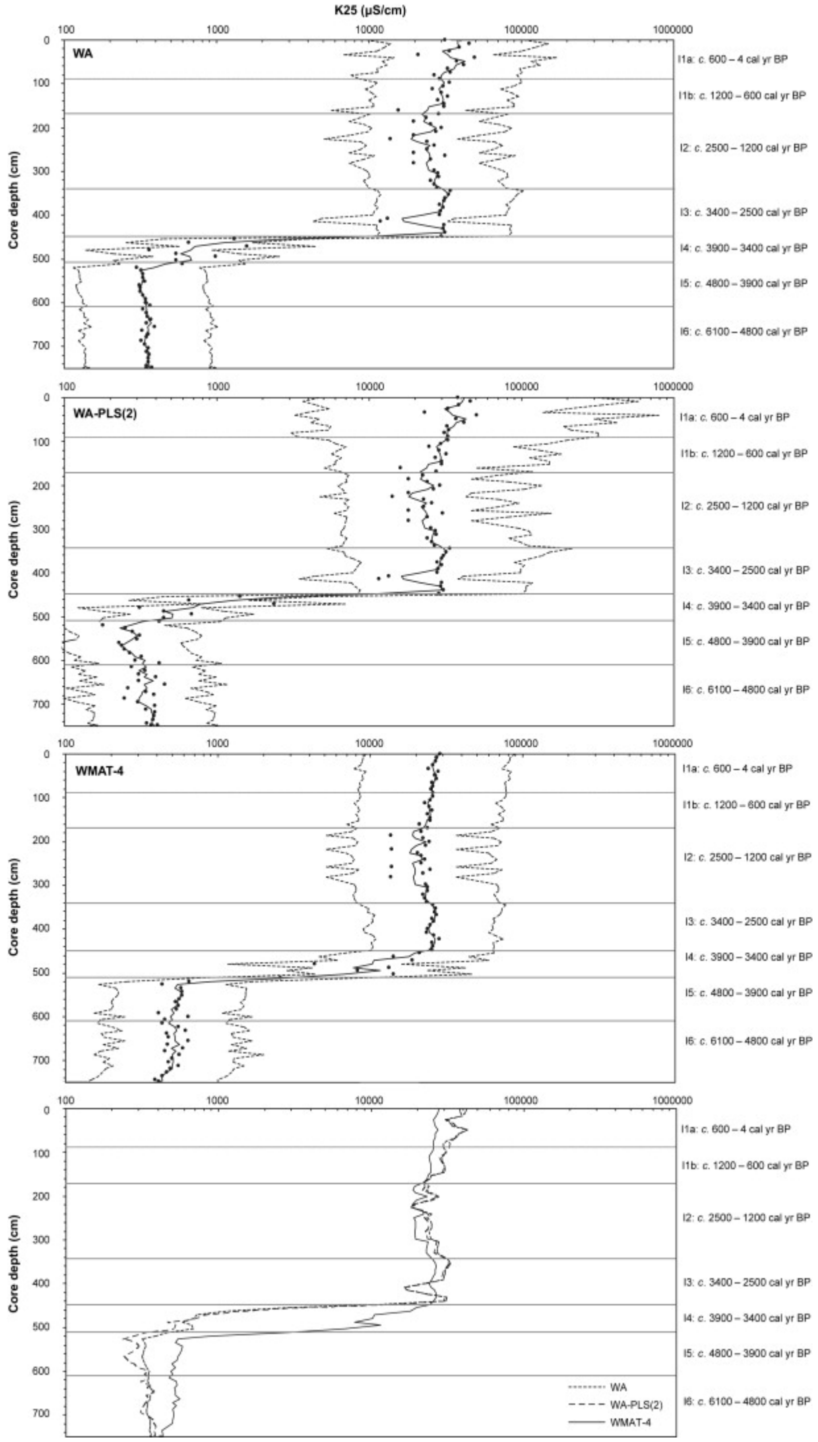

Figure 6: Chironomid-inferred salinity reconstruction for Lake Yoa using the EL–WL–S calibration data set (K25 = specific conductance at 25 °C). Shown are output of WA, WA-PLS(2), and WMAT-4 inference models. A 3-point moving average (full line) highlights the major trends in the data; uncertainty ranges (dotted line) are the sample-specific prediction errors.

The WA reconstruction can roughly be divided in five sections corresponding with one or more invertebrate assemblage zones. Section I6–I5 (6100–3900 cal yr BP) is characterized by near-continuous low inferred conductivity (~300–350 µS/cm), rising up to 600 µS/cm around 3900 cal yr BP. In I4 (3900–3400 cal yr BP) inferred conductivities increase markedly: they gently rise above 1000–1500 µS/cm around 3500 cal yr BP, and go steeply up to ~30,000 µS/cm around 3400 cal yr BP. In I3 (3400–2500 cal yr BP), inferred conductivities generally fluctuate between 29,000–35,000 µS/cm (on average 31,087 µS/cm), except for two intervals (at 415 and 407 cm depth) where values are distinctly lower (respectively 11,888 µS/cm and 13,209 µS/cm). In I2 (2500–1200 cal yr BP), inferred conductivities are on average ~4200 µS/cm lower than that in the previous section, and they dip in five intervals (at 281, 257, 217, 225 and 185 cm depth) where conductivities are below 19,800 µS/cm. In section I2–I1 (1160 cal yr BP to present), inferred conductivities gently rise again; they typically remain above 30,000–35,000 µS/cm (on average 33,766 µS/cm), and climb up to ~50,000 µS/cm. Lower conductivities (<21,000 µS/cm) are inferred at 161 and 33 cm depth.

Using the EL–WL dataset, WA model output generally follows the same trend. The reconstructions for zones I6–I5 and I4 are near-identical; inferred conductivities for zones I3, I2 and I1 are usually ~500–1000 µS/cm higher than when the EL–WL–S dataset is used.

The WA-PLS(2) reconstruction based on EL–WL–S is similar to the WA reconstruction, but the inferred values in I6–I5 are less uniform, and those in the other zones are ~4100–4600 µS/cm lower. The differences between EL–WL–S and EL–WL model output are similar to those for the WA-model, but discrepancies are more expressed (inferred values for I2 and I1 are respectively ~3000 and 4400 µS/cm higher when using the EL–WL data set).

The WMAT-4 reconstruction shows some conspicuous differences with the WA and WA-PLS(2) reconstructions. In zones I6–I5, WMAT-derived conductivities are on average ~100 µS higher than the corresponding WA and WA-PLS(2) values, and they already rise to 2000–3000 µS/cm at the top of I5 near 3900 cal yr BP, ~400 years earlier than in WA and WA-PLS. In I4, the difference between the weighted-averaging and WMAT-based model outputs is even more pronounced: inferred conductivity values have already crossed 3000 µS/cm at the bottom of this zone (3900 cal yr BP), they subsequently fluctuate between 1700 and 9000 µS/cm, and then rise up to ~25,000 µS/cm at 3400 cal yr BP marking the beginning of zone I3. In zone I3 there is no evidence for a temporary conductivity decrease near 3000 cal yr BP as is the case in reconstructions using WA and WA-PLS(2), but the zone-average value of WMAT-4 (26,667 µS/cm) is ~4000 µS/cm lower than those of WA and WA-PLS(2). In zone I2, WMAT-4 values are less scattered than those of WA and WA-PLS(2), but the average inferred conductivity (26,479 µS/cm) is comparable, and the same four intervals as mentioned before also produce markedly lower values (<15,800 µS/cm). In zone I1 the WMAT-4 reconstruction follows the same upward trend as the WA and WA-PLS reconstructions, but values are again less scattered; they average 28,396 µS/cm in subzone I1b (comparable to WA-based inferences) and 31,596 µS/cm in I1a (comparable to WA-PLS(2)-based inferences).

When using the EL–WL data set, WMAT-4 output closely resembles that described above, but the average inferred value in zones I6–I5 and I4 is respectively ~40 µS/cm and ~7700 µS/cm lower, whereas in zones I3–I1 it is ~3300 µS/cm higher.

7.5 Discussion

7.5.1 Representativeness of the chironomid calibration data set

All fossil assemblages in the Lake Yoa record have good modern analogues among reference lakes, suggesting that both the EL–WL and EL–WL–S calibration data sets encompass the full range of faunal diversity at the study site. Two taxa (*Chironomus* cf. *salinarius* and cf. *Stictochironomus* type Ounianga Kebir) are not represented. *Chironomus* cf. *salinarius* occurred in Lake Yoa between 3900 and 1200 cal yr BP alongside the well-known halophilic chironomids *Kiefferulus disparilis* and *Microchironomus deribae* (Verschuren, 1997) and the evidently halophilic hemipteran *Anisops* sp., suggesting that this taxon is also salt-loving or at least salt-tolerant. However, most African *Chironomus* have never been found in conductivities much in excess of ~2500 µS/cm (Eggermont *et al*., 2006). The only exception is the widely distributed *C. transvaalensis*, which can tolerate conductivities up to 8000 µS/cm (Lake Chilwa; McLachlan, 1974). However, line drawings of this species (McLachlan, 1969) show it to have a different dentition of the mentum. Thus *C.* cf. *salinarius* exemplifies the presence of a Palaearctic (~Eurasian) component in the Saharan chironomid fauna (Dejoux, 1974). Our morphotype closely resembles *C. salinarius*, the only Eurasian *Chironomus* commonly distributed in brackish and true saline lakes (>20,000 µS/cm; Vallenduuk *et al*., 1997), but this species has not yet been recorded from Africa. At least six other Palaearctic *Chironomus* species are known to tolerate salinities up to ~3000–5000 µS/cm (Vallenduuk *et al*., 1997). Of these, four (*C. aprilinus* syn. *halophilus*, *C. riparius*, *C. plumosus* and *C. piger*) have been reported from lagoons along the Mediterranean coast of North Africa (Ramdani *et al*., 2001), but none of these fully matches the morphology of our specimens. We therefore suspect the Lake Yoa *C.* cf. *salinarius* to be a local variant of the Palaearctic *C. salinarius*, or an African species with as-yet unknown larval morphology (and salinity tolerance).

The second taxon not included in the salinity inference models is cf. *Stictochironomus* type Ounianga Kebir. It was found only sporadically in subzone I1a (i.e., the last 600 years) alongside high numbers of the halophilic/halobiont *Kiefferulus disparilis*, *Anisops* sp. and Ephydridae, suggesting that this taxon is also salt-loving. Unfortunately there are no records of morphologically similar taxa in either the Palaearctic or Afrotropical region to confirm this. Even if we could attribute *Chironomus* cf. *salinarius* and cf. *Stictochironomus* type

Ounianga Kebir to known Palaearctic taxa, we currently lack the distribution data required to use them for quantitative salinity reconstruction.

Cricotopus type Ounianga Kebir, fairly common to abundant in Lake Yoa since 3400 cal yr BP, is another salt-tolerant or halobiont taxon in our data set with possibly non-African biogeographical affinity. None of the 19 known African *Cricotopus* species (Freeman, 1956) has to our knowledge ever been found in true salt lakes. On the other hand at least seven Palaearctic *Cricotopus* species are known to tolerate salinities up to ~2000–5000 µS/cm (Hirvenoja, 1973 and Langton and Visser, 2003), and among these *C. ornatus* is considered a true halobiont (Hirvenoja, 1973 and Walker *et al.*, 1995). Our morphotype matches descriptions of both *C. ornatus* (widespread in the Holarctic region and also recorded from Algeria; Hirvenoja, 1973) and *C. sylvestris* (widespread in Europe and the Middle East; Hirvenoja, 1973). *Cricotopus* type Ounianga Kebir is markedly different from *Cricotopus* type East Africa, which groups several freshwater species from sub-Saharan tropical Africa (Eggermont and Verschuren, 2004b and Eggermont *et al.*, 2005). The presence of *Cricotopus* type Ounianga in Lake Yoa surface sediments allowed us to include it in our salinity inference models, but more distribution records are required to better estimate this species' ecological parameters.

Dicrotendipes kribiicola is known as a stenotopic freshwater taxon, with a conductivity optimum of 189 µS/cm and reported range of 119–739 µS/cm (14 records; Eggermont *et al.*, 2006). Yet, this taxon inhabited Lake Yoa between 3900 and 3400 cal yr BP alongside the euryhaline *Cladotanytarsus pseudomancus* (most common in freshwater lakes but tolerating up to 5000–6000 µS/cm; Eggermont *et al.*, 2006) and the halophilic *Kiefferulus disparilis* and *Microchironomus deribae* (typical for meso- to polysaline soda lakes, but occasionally present in both freshwater and hypersaline lakes; Eggermont *et al.*, 2006). This suggests that either (1) *Dicrotendipes kribiicola* has a higher salinity optimum and broader tolerance range than currently estimated from available records; or (2) the taxon found at Lake Yoa is not *D. kribiicola* from East Africa (Eggermont and Verschuren, 2004b), but a morphologically very similar euryhaline species. The first hypothesis is difficult to test without extensive field collecting in semi-arid regions of northern Africa. Yet even in the present calibration data set, this species was most common in dilute waters below 200 µS/cm (particularly in lakes of tropical West Africa) and does not at all occur in the 16 calibration lakes between 800 and 2000 µS/cm. As for the second hypothesis, the genus *Dicrotendipes* is indeed known to include several salt-tolerant species (Heinrichs and Walker, 2006). As presently documented, *D. fusconotatus* is the most salt-tolerant *Dicrotendipes* species in Africa, known to survive conductivities up to and beyond 3000 µS/cm (Eggermont *et al.*, 2006). The mentum of this species has a clearly different dentition than *D. kribiicola* (Epler, 1988 and Eggermont and Verschuren, 2004b). Some *D. kribiicola* specimens in the Lake Yoa record have two equally-sized dorsal teeth on the mandible, which has never been unambiguously recorded on specimens in the EL–WL calibration data set (when an accessory dorsal tooth does occur, it is smaller than the dorsal tooth). Therefore, Lake Yoa specimens may belong to a different *Dicrotendipes* species, and thus its salinity optimum may be underestimated at present.

Overall we propose that the fossil Lake Yoa fauna is sufficiently well represented in the African calibration data set to allow paleosalinity reconstruction based on it.

7.5.2 Comparison of model outputs

Several studies (Walker *et al*., 1997, Lotter *et al*., 1999, Paterson *et al*., 2002 and Eggermont *et al*., 2006) showed that merging regional paleoenvironmental calibration data sets increases the likelihood of finding good modern analogues for fossil assemblages. In this study, expansion of the EL–WL calibration data set with local Sahara sites indeed improves analogue matching, but its actual influence on the salinity reconstructions appears to be fairly modest. In the saline portion of the reconstruction (zones I3–I1), where values based on the EL–WL–S data set are ~500–1000 µS/cm lower than those based on EL–WL, the discrepancy can be attributed to the somewhat lower modeled optimum of *Kiefferulus disparilis* (which usually represents >60% of those Yoa fossil assemblages) after adding the six Saharan reference lakes. This reduced optimum is due to the presence of this otherwise halophilic taxon in the surface sediments of Girki spring brook (250 µS/cm). Improved analogue matching for the freshwater portion of the reconstruction (zones I6–I4) can be explained by the fact that besides Yoa only freshwater Sahara lakes are included in EL–WL–S, of which Lake Boku (320 µS/cm) had high relative abundances of *Cladotanytarsus pseudomancus* (well above 50%) alongside small numbers of *Procladius brevipetiolatus* (6.3%) and *Cryptochironomus* type Tanganyika group 1–2 (2.1%), a species composition similar to that found in many zone I6–I4 core samples. Therefore, on the basis of chironomid community composition, Lake Boku, with its sandy littoral fringed with *Potamogeton* and *Phragmites*, can be considered the modern aquatic habitat most closely similar to the mid-Holocene Lake Yoa. Finally, whereas all chironomid taxa recorded in the ~6000–3900 cal yr BP freshwater phase of Lake Yoa are represented in the calibration data sets, two presumed halophilic species (*Chironomus* cf. *salinarius* and cf. *Stictochironomus* type Ounianga Kebir) are lacking from them. Hence, expanding the calibration data set did not result in better modern analogues for the inferred saline core assemblages. Even after expanding the data set, *Cricotopus* type Ounianga Kebir (making up 12% of the total fossil count) is still only represented by the modern Lake Yoa. Consequently the species' optimum and the derived reconstruction are biased towards the conductivity value of the modern lake.

Detailed features of a paleosalinity reconstruction (and thus the proxy climate signal) can depend strongly on which numerical technique (transfer function) is used to construct the inference model (Eggermont *et al*., 2006). In this study, WA and WA-PLS(2) model output are in agreement, having similar trends and inferred values. WMAT-4 model output, on the other hand, diverges from these during the transition from fresh to saline conditions (the episode covered by zone I4 including the top of I5): WMAT-4 conductivity already crosses the freshwater-saline boundary around 3900 cal yr BP whereas in the WA and WA-PLS(2) reconstructions it occurs around 3400 cal yr BP. This unquestionable discrepancy in timing reflects the sensitivity of each transfer function to the presence and/or relative abundance of chironomid taxa. Low inferred salinities (on average 830 µS/cm) for the period 3900–3400 cal yr BP inferred by WA and WA-PLS(2) mainly reflect the fact that the dominant (40–60% of the assemblage) and demonstrably salt-tolerant species *Cladotanytarsus pseudomancus* (Eggermont *et al.*, 2006) has a modest modeled salinity optimum of 447 µS/cm, due to its widespread distribution in fresh African lakes with sandy littoral substrates (Verschuren, 1997). Using weighted-averaging models this bias is not compensated by the presence of true halophilic taxa, since these add up to at most 20% of the assemblages. In WMAT-4, samples from the period 3900–3400 cal yr BP yield an average inferred value of 5790 µS/cm because the combined presence of *Kiefferulus disparilis* and *Cladotanytarsus pseudomancus* selects eu- and hypersaline lakes (such as Kikorongo and Nshenyi in Uganda, and Chitu in Ethiopia) as their closest modern analogues. Similarly, the large scatter of WA and WA-PLS(2) conductivity values in the saline lake phase results from different relative contributions of the three halophilic/halobiont taxa (*Microchironomus deribae*, *Kiefferulus disparilis* and *Cricotopus* type Ounianga Kebir) to each fossil assemblage. Less scatter in the WMAT-4 reconstruction is mainly related to the presence of *Cricotopus* type Ounianga Kebir in all saline-phase assemblages, which automatically selects Lake Yoa (the only calibration lake holding this species) as one of the four closest modern analogues.

7.5.3 Middle and Late Holocene evolution of Lake Yoa

7.5.3.1 Sequence and timing of salinity change as inferred from aquatic invertebrates

Considering model- and calibration-dependent limitations, absolute values of inferred conductivity should be treated with some caution. However, the main trend over the past 6000 years is fairly robust, with freshwater conditions (<500 µS/cm) being evident until ~ 4100 cal yr BP, a sharp increase to oligo- and mesosaline conditions (3000–9000 µS/cm) between 3900 and 3400 cal yr BP, and fairly stable eu- to hypersaline conditions (>25,000 µS/cm) from 3400 cal yr BP to the present. The stratigraphic distribution of non-chironomid invertebrates supports this quantitative reconstruction and helps to pin-point the exact timing of the fresh-to-saline transition in Lake Yoa. Between 6100 and 4800 cal yr BP, Lake Yoa's invertebrate fauna comprised a diverse chydorid (benthic water flea) community, the pelagic zooplankton predator *Chaoborus pallidipes/edulis*, and a species-rich chironomid fauna mainly consisting of steno- and eurytopic freshwater taxa, including *Polypedilum*. This suggests that until at least 4800 cal yr BP, Lake Yoa was a hydrologically open, deep and dilute (<500 µS/cm) freshwater environment with diversified nearshore habitat, including submerged macrophyte beds. A sharp reduction in chydorid remains around 4800 cal yr BP and distinct increase of a presumed salt-tolerant *Dicrotendipes* species (see Section 5.1) suggests that an increasingly more negative water balance resulted in measurable evaporative concentration. By 3900 cal yr BP, virtually all steno- and eurytopic freshwater chironomid taxa (*Cryptochironomus* type Tanganyika, *Procladius brevipetiolatus*, *Microchironomus* type East Africa, *Polypedilum* near *deletum*, *Cricotopus* type East Africa) disappeared, as well as *Chaoborus pallidipes/edulis* and the chydorid cladocerans. Only known salt-tolerant freshwater taxa (*Cladotanytarsus pseudomancus*) persisted, and known salt-loving taxa (*Kiefferulus disparilis*) appeared for the first time. This indicates that the important physiological threshold of 3000 µS/cm (Rawson and Moore, 1944 and Hammer, 1986) was crossed at that time, and not some 500 years later. We therefore favor the WMAT-4 reconstruction, which starts showing elevated salinity from ∼4100 cal yr BP and places the principal fresh-to-saline transition of Lake Yoa at 3900 cal yr BP, not 3400 cal yr BP as in the WA and WA-PLS(2) reconstructions. The transition to a true salt-lake ecosystem (>25,000 µS/cm) seems to have occurred rather abruptly around 3400 cal yr BP, when the remaining salt-tolerant freshwater taxa were exterminated and new salt-loving taxa appeared (*Microchironomus deribae*, *Cricotopus* type Ounianga Kebir) to complement the strongly expanding *Kiefferulus disparilis*. All chydorid fossils found in zone I3 could be attributed to *Alona cambouei* (see Sinev, 2001), a species known to inhabit saline waters (Frey, 1993). In this new, true salt-lake ecosystem, both primary productivity (recorded as % organic matter) and secondary productivity (represented by fossil chironomid abundance) of the aquatic ecosystem at Lake Yoa declined (Fig. 4). A fourth important ecological transition seems to have occurred around 2700 cal yr BP with the disappearance of the halophilic *Microchironomus deribae* and the immigration of the salt-loving hemipteran *Anisops*, which will later become the dominant macrozooplankton of Lake Yoa. The former is limited to salinities below ∼45,000 µS/cm (Eggermont *et al*., 2006), suggesting that this limit was crossed. Finally, the last ecological transition seems to have occurred around 1500 cal yr BP (AD 450), when *Chironomus* cf. *salinarius* disappeared together with strong expansion of *Cricotopus* type Ounianga Kebir and first appearances of brine flies, *Ephydra*. This testifies to a renewed trend of rising salinity (Fig. 6), and establishment of today's hypersaline habitat conditions (>60,000 µS/cm). Apparently, the large numbers (15–76%) of *Kiefferulus disparilis* (having a modeled salinity optimum of 11,089 µS/cm) are responsible for underestimation of the lake's true salinity from ∼2500 cal yr BP onwards. Overall, as confirmed by CONISS and the broken-stick model, we can state that the aquatic environment changed substantially over six successive time windows chaping the entire invertebrate community.

Given the probable but as yet unproven tolerance of the local *Dicrotendipes kribiicola* and *Chironomus* type Ounianga Kebir populations for elevated salinity (cf. Section 5.1), we need to consider whether the ‘disharmonious’ fossil assemblages (Gasse *et al*., 1997) comprising taxa with non-compatible ecological requirements may perhaps represent past living communities that were spatially or temporarily structured, and only formed mixed species assemblages as their remains became incorporated in the sediment record (as is often the case with diatoms: Fritz *et al*., 1991, Gasse *et al*., 1997 and Flower *et al*., 2006). Continuous fine lamination of the Lake Yoa sediment record indicates that the area of habitable lake bottom must always have been restricted to shallow nearshore environments above the oxycline, consequently that all remains of benthic invertebrates must have been transported to deeper/anoxic profundal regions from the better oxygenated littoral and sub-littoral environments where they had lived. Less saline conditions (i.e., potential habitat for freshwater taxa) do occur locally nearshore, but since fossil abundances remain fairly high in the upper (hypersaline) part of the sequence, the contribution of any freshwater taxa living nearshore to the total fossil assemblage extracted from a mid-lake profundal coring site is likely to be negligible. This mechanism does perhaps explain the erratic occurrence (reflecting low-density persistence?) of *Cladotanytarsus pseudomancus* throughout the section deposited since 3400 cal yr BP.

The possibility of seasonally structured chironomid communities should normally be discounted, as chironomid larval development is not fast enough (Toheski, 1995) to complete a generation in the hypothetical freshwater lens that could potentially have persisted for a few weeks or months during calm weather above a saline lower water column (as has been proposed for diatoms: Gasse *et al*., 1997). One possible exception is the fresh-to-saline transition period (3900–3400 μS/cm), when seasonal variation in epilimnetic salinity close to the physiological threshold may have created conditions for joint occurrence of freshwater and halophilic taxa. In this scenario, the fraction of the year offering favorable conditions to eurytopic freshwater taxa would have been decreasing as the fraction of year offering favorable conditions to halophilic taxa expanded. This may explain why, in zone I4, the last stand of *Cladotanytarsus pseudomancus* and *Dicrotendipes kribiicola* coincides with the first appearance of *Kiefferulus disparilis*. In the modern hypersaline Lake Yoa ecosystem, however, seasonal water-balance variation is minimal. Consequently we presume that *Chironomus* cf. *salinarius*, which occurred from 3900 to 1200 cal yr BP, is a true halophilic taxon.

Overall the stratigraphic distribution of non-chironomid groups supports the chironomid-based inference that over the past 6000 years Lake Yoa progressively evolved from freshwater to hypersaline conditions, rather than a sequence of fluctuations between less and more saline phases. One possible exception is the zone I3–I2 transition, where the decreasing abundance of *Cricotopus* type Ounianga Kebir yields chironomid inferences for the period 2500–1200 cal yr BP that are on average 2000–4000 μS/cm lower (depending on the numerical technique used) than before 2500 cal yr BP. Notably, the four distinct salinity minima in this period reconstructed by all models are due to complete absence of *Cricotopus* type Ounianga Kebir at 281, 257, 217 and 185 cm depth, while being fairly common in adjacent samples. In contrast, disappearance of chydorids and immigration of Ephydridae in zone I3 indicates that the period 2500–1200 cal yr BP was actually more saline than the period before. The temporary salinity maximum reached in zone I3 (3400–2500 cal yr BP) may be an artifact caused by the fact that the modeled optimum of *Microchironomus deribae* in both the EL–WL and EL–WL–S calibration data sets (16,016 μS/cm) is higher than that of *Kiefferulus disparilis* (11,088 μS/cm), although the latter species has a considerably higher salt tolerance (Verschuren, 1997 and Eggermont *et al*., 2006). Inclusion of more hypersaline lakes in our calibration data set would likely raise the optimum of *K. disparilis* and remove the temporary peak in reconstructed salinity associated with peak abundance of *M. deribae*.

7.5.3.2 Hydrological sensitivity of Lake Yoa to climate change

The now numerous available Holocene paleolake records from the arid and subarid belts of North Africa (for a recent synthesis see Hoelzmann *et al*., 2004) document a fairly consistent scheme of an early-Holocene moist and green Sahara followed by general aridification. However, pronounced differences in the apparent timing and amplitude of the hydrological change inferred from individual records point to both regional variability in climate change and site-specific influences of local topographic-hydrogeological factors on the evolution of water balance reconstructed from individual paleoenvironmental archives (Baumhauer, 1991 and Gasse, 2000). This complexity makes it difficult to substantiate the reality of apparent climatic fluctuation between moist and dry episodes observed in many records (Fleitmann *et al*., 2007; see, e.g., Fig. 7f), and complicates evaluation of the regional, possibly even continental, synchrony between those fluctuations (Gasse, 2002).

Pollen records of past vegetation change from the interior North African continent indicate terrestrial drying to have started between 7800 and 6800 cal yr BP in response to a fairly gradual decline in moisture balance not interrupted by abrupt climate events (Salzmann *et al*., 2002, Hoelzmann *et al*., 2004 and Kröpelin *et al*., 2008). These paleodata are consistent with the results of recent climate modeling studies showing a mostly gradual Holocene precipitation decline over the Sahara (Liu *et al*., 2007; Fig. 7b) in direct response to orbital insolation forcing of sub-tropical monsoonal dynamics (Kutzbach, 1980; Fig. 7a), and a rather weak biogeophysical feedback between climate and vegetation (Braconnot *et al*., 2007). Most lake-based paleohydrological records tend to show a more punctuated Holocene moisture-balance evolution, with sharp lake-level declines concentrated in the periods 6700–5500 and 4000–3600 cal yr BP accelerating the drying trend (Hoelzmann *et al*., 2004). A substantial number of records from semi-arid regions south of the Sahara additionally show a Late Holocene rebound to wetter conditions variously dated to between 4.3 and 3.0 kcal yr BP (Servant and Servant-Vildary, 1980, Mees *et al*., 1991, Chalié and Gasse, 2002 and Gasse, 2002; see Fig. 7f), and significant moisture-balance fluctuation in the last 1500 years (Holmes *et al*., 1997, Street-Perrott *et al*., 2000 and Hoelzmann *et al*., 2004).

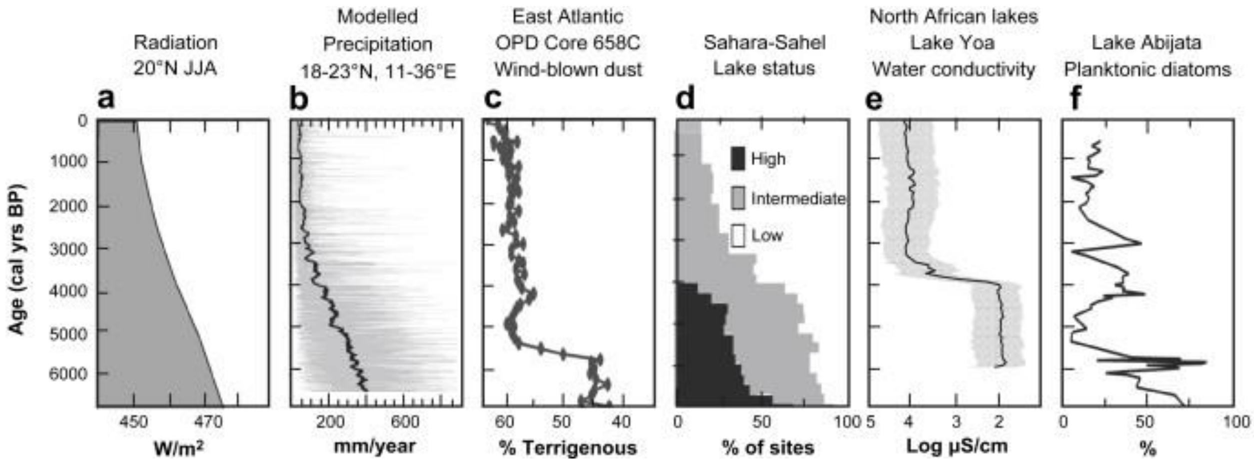

Figure 7: Comparison of climate forcing, modeling results and paleodata describing the aridification of the Sahara over the past 7000 years, modified after Liu *et al*. (2007). (a) Summer (June–August) insolation at 20° N (Berger and Loutre, 1991). (b) Simulated precipitation over the eastern Sahara (18–23° N, 11–34° E) in a synchronously coupled general circulation atmosphere-ocean-vegetation model (Liu *et al*., 2007): annual variability (thin grey line) and 100-year running average (thick black line). (c) Wind-blown desert dust in deep-sea sediments off northwestern Africa (deMenocal *et al*., 2000). (d) Cumulative lake status in the Sahara and Sahel (8–28° N, 20° W–40° E), from Liu *et al*. (2007) after (Hoelzmann *et al*., 1998) and (Hoelzmann *et al*., 2004). (e) Chironomid-inferred conductivity of Lake Yoa, Chad, using a WMAT-4 transfer function on the EL–WL–S calibration dataset; cf. Fig. 6c. (f) Percent planktonic diatoms at Lake Abiyata, Ethiopia.

The paleohydrological evolution of Lake Yoa based on our chironomid-based salinity reconstruction contrasts with paleodata in appearing to suggest a fairly stable moisture balance between 6000 and 3900 cal yr BP followed by a severe shift to strongly negative water balance between 3900 and 3400 cal yr BP that created conditions similar to those prevailing today. The question therefore arises whether the salinity history of Lake Yoa is a true reflection of climate-driven fluctuations in the regional water balance of the east-central Sahara.

All permanent lakes in the Sahara can only persist by virtue of significant groundwater inflows, even during the wettest episodes of the early Holocene (Pachur and Kröpelin, 1989). However, individual Saharan lakes differ greatly in the relative contributions of local rainfall (which is often negligible), surface runoff, (seasonal) river inputs, and groundwater to total water balance. Lakes with comparably large river input and limited groundwater support are more sensitive to climatic moisture-balance variation than lakes in small topographic depressions connected to large aquifers (Gasse *et al*., 1990, Baumhauer, 1991, Street-Perrott and Perrott, 1993 and Gasse, 2000). On the one extreme are ‘amplifier lakes’ with a very large drainage basin relative to the size of the lake and a well-developed hydrographic network. Here, rapid response to variation in rainfall and catchment-wide evapotranspiration can greatly accentuate relatively modest climate variability (Street, 1980). Unfortunately, in dry climatic regions such lakes are also more prone to desiccation, and truncation of their paleohydrological record (Verschuren, 1999). Lake Yoa is a prime example of the other extreme situation, in which near-complete dependence on groundwater input from a very large and deep aquifer (the Nubian Sandstone Aquifer) results in a decoupling of lake water balance from regional climate change at all but the longest time scales. Consequently the timing of the fresh-to-saline transition in Lake Yoa is strongly influenced by the progressive decrease of total water inputs, eventually crossing the minimum threshold needed to keep the lake hydrologically open (which had until then ensured removal of dissolved salts, via groundwater if not surface outflow). Still, broad coincidence of the Lake Yoa transition at ~ 4100–3400 cal yr BP with some paleohydrological evidence for accelerating aridification between 4000 and 3600 cal yr BP (Hoelzmann *et al*., 2004; Fig. 7) does suggest a direct climatic influence on the relative abruptness of the hydrological transition. Similarly we do not discount a climatic influence on the timing of other paleoecological transitions observed in the fossil invertebrate record over the past 6000 years. For example, the zone I3–I2 transition, marked by a species shift among halophilic chironomids and first appearance of the halobiont hemipteran *Anisops* sp., broadly coincides with establishment around 2700 cal yr BP of the modern hyperarid desert landscape (Kröpelin *et al*., 2008). The limited hydrological sensitivity of Lake Yoa to local climatic moisture-balance changes, due to massive input of fossil groundwater, considerably complicates the reconstruction of those changes on the basis of aquatic proxies. On the other hand, in allowing persistence of Lake Yoa throughout the hyper-arid desert climate prevailing today, this groundwater inflow is key to the preservation of a unique continuous paleoenvironmental archive of both the local aquatic and regional terrestrial ecosystem of the central Sahara.

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8

Regional diversity, ecology and palaeoecology of aquatic invertebrate communities in East African lakes General discussion

8.1 Diversity and environmental regulation of aquatic invertebrate communities

This study identified and considered a total of 139 aquatic invertebrate taxa from 62 western Uganda crater lakes, which are spread across the climatic and hydrological gradient between the sub-humid shoulder and semi-arid floor of the Rift Valley. Overall species richness and diversity were highest in lakes with relatively large areas of shallow water densely overgrown with aquatic macrophytes. These included both deep ($Z_{max} > 50$ m) and shallow ($Z_{max} < 20$ m) lakes with low turbidity. Most of these shallow lakes are situated within the boundaries of national parks (Kibale and Queen Elisabeth). In shallow lakes situated outside national parks, routine burning of secondary vegetation and intense subsistence agriculture inside gently sloping crater basins has contributed to their eutrophication (Kizito et al., 1993). Diversity in these lakes is relatively low, and similar to that in naturally eutrophic lakes.

Surface-water conductivity was one of the major factors determining the distribution and species richness of Cladocera, Ostracoda and various other aquatic invertebrates in Uganda lakes. Only a very limited number of taxa (12 taxa or 8.5% of the regional fauna) were encountered in true saline lakes (conductivity > 5000 µS/cm). Most western Uganda crater lakes are in the broad freshwater category, with conductivity ranging between 56 and 1450 µS/cm (Table 1, Chapter I). Over this range, aquatic invertebrate community structure was poorly correlated with salinity, but rather by pH and by the availability of a specific habitat or substrate (as in Williams et al. 1990; Verschuren *et al.*, 2000b; see also Fig. 1). In freshwater lakes, the diversity and abundance of Cladocera, Ostracoda, and to a lesser extent other aquatic invertebrates was positively correlated with the presence and diversity of aquatic macrophytes. Aquatic vegetation is thought to promote aquatic diversity by forming physical structures that creates multiple environmental gradients supplying unique niches to many types of organisms, and by serving as a refuge against predation (Jeppesen *et al*, 1997). Water plants may also provide additional food resources (periphyton, plant tissue, coarse particulate organic matter-(Declerck *et al.*, 2005). We also found a strong negative correlation between the Hill's N_2 diversity and species richness of cladoceran faunas and local pH (N_2: r= -0.67, $p < 0.001$; species richness: r=-0.66, $p < 0.001$).

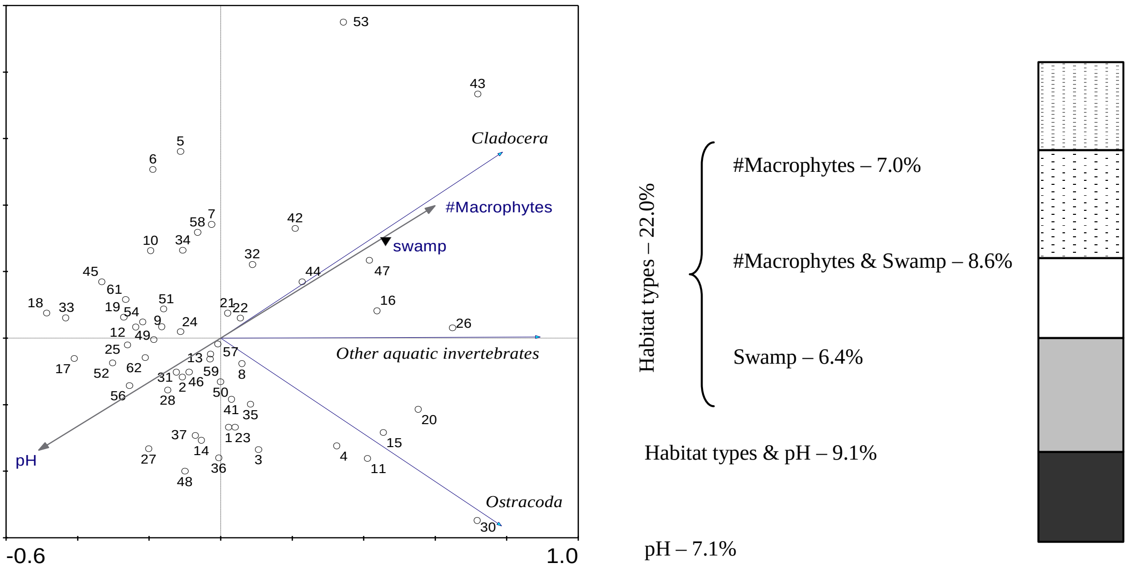

Figure 1: a) PCA ordination biplot on the centred and standardized species richness data from 56 freshwater lakes in western Uganda. It represents the associations between the species richness of Cladocera, Ostracoda and other aquatic invertebrates and the sampled freshwater lakes. Lakes are numbered according to Table 1 (Chapter II). The main explanatory variables (pH, #Macrophytes & swamp habitat) are projected as supplementary variables, and as such did not influence the ordinations. b) Results of variation partitioning, showing that pH and Habitat types explained 38.2% of the variance in species richness data

Lake productivity (trophic state), which in our dataset is determined by both basin morphometry (influencing mixing regime) and anthropogenic land use (determining nutrient loading), also appears to influence the aquatic invertebrate communities in a significant way. Although species richness has often been found to respond in a unimodal way to productivity (Mittelbach *et al.,* 2001; Declerck *et al*., 2005, 2007), our data suggested a more linear decreasing relationship. This may be because the trophic gradient we sampled is incomplete, as it does not include nutrient-poor rock pools or other very oligotrophic systems known to support few or no species (Dodson, 1987). Despite large variation in species richness between lakes, a gradual decrease in cladoceran and ostracod species richness from oligotrophic to hypertrophic lakes can be noted (Fig. 3). For the remaining group consisting of aquatic insects, Acari, molluscs and various other aquatic invertebrates, little difference in species richness was noted between oligo-, meso- and eutrophic Uganda lakes. However, within this group, a significant decrease in species richness does occur from eutrophic to hypertrophic lakes, which is probably related to the reduction (or even disappearance) of habitat provided by aquatic macrophytes. Indeed, in strongly eutrophied systems aquatic macrophytes become marginal or disappear because abundant phytoplankton hampers light penetration (Sand-Jensen & Borum, 1991). The species-poor communities in highly productive systems were not unique but tended to be a nested subset of the species-rich communities at the low end of the productivity gradient, which matches findings by Declerck *et al* (2007). It has been suggested that, in oligotrophic lakes, submerged vegetation is rare and species diversity poor due to nutrient limitation (Declerck *et al*., 2005). In our crater lake collection the presence of a gently sloping littoral area rather than nutrient availability was critical for the development of aquatic macrophytes in the least productive lakes.

A highly significant positive correlation was found between both cladoceran and overall species richness and the fraction of stable land cover (including both natural vegetation and forestry) inside the crater basin of lakes of intermediate depth (Z_{max} between 5m and 35m)(r_{clad}= 0.60, $p < 0.001$; r_{all}=0.61, $p < 0.001$). This is probably due to the reduction and disappearance of aquatic macrophyte habitat following eutrophication caused by catchment disturbance. Such a correlation is not found when limiting the dataset to either very shallow (Z_{max} < 5m) or deep lakes (Z_{max} > 50m). Inclusion of lakes up to 50m depth does not significantly alter the correlation. Several of the very shallow, polymictic lakes are naturally eutrophic or hypertrophic. Very deep lakes, on the other hand, are generally less sensitive to anthropogenic eutrophication (Szeroczyńska, 2002). We do not mean to imply that there is a simple causal relationship between land use and aquatic invertebrate species richness within the group of lakes of intermediate depth, as there are many other site-specific factors which will determine the relationship between anthropogenic land use and eutrophication, as well as between eutrophication and the distribution of the studied groups. However, intense land use is nevertheless a serious threat to aquatic invertebrate biodiversity in the study area.

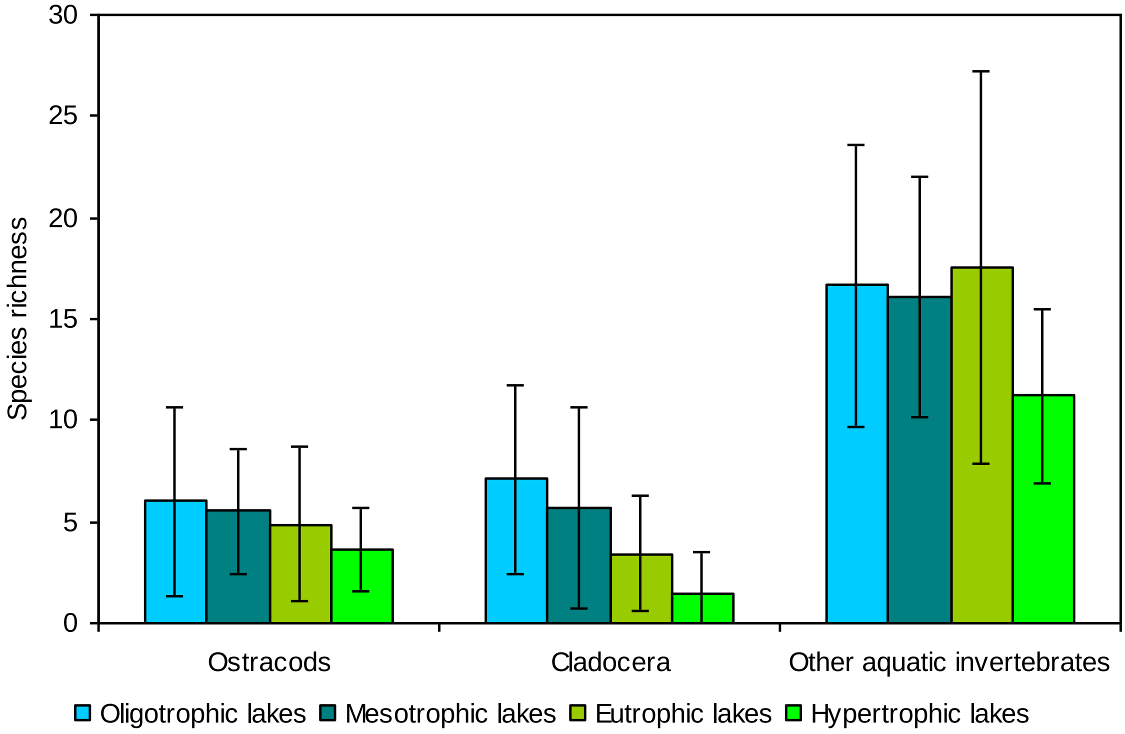

Figure 2: Relationship between average species richness and lake trophic state in 56 freshwater lakes in western Uganda

8.2 Diversity of ostracod communities – western Uganda and southern Kenya

Lake-sediment records of fossil ostracod assemblages have been used before to elucidate the environmental history of East African lakes (e.g. Richardson & Dussinger, 1986, Cohen & Nielsen, 1986), but palaeoecological interpretation has been hampered both by the failure to link the majority of fossil types to living species and a lack in quantitative ecological information for many taxa. Our study of present-day regional ostracod faunas in western Uganda and southern Kenya was intended to remedy this situation. Our analysis of the species composition of living ostracod communities in 62 lowland crater lakes of western Uganda yielded a total of 33 species from 26 genera. Ostracods were found in 57 freshwater lakes and their distribution was strongly influenced most strongly by the diversity of aquatic macrophyte habitat, salinity, and aquatic productivity. With the exception of a small swamp near Lake Wandakara, all of the sampled freshwater lakes are permanent, and seasonal hydrological fluctuations that do occur are relatively modest. In order to adequately interpret fossil assemblages deposited during climatically dry episodes when lakes were reduced to small or ephemeral systems, we also needed to obtain a picture of ostracod distribution in fresh waters experiencing very strong seasonal fluctuations. We therefore analyzed the species composition of living ostracod communities in 37 shallow lakes and ponds in southern Kenya. Despite a significantly smaller sampling effort (ostracods having been sampled as by-catch of a different project), a total of 32 species from 22 genera were found. In those systems, ostracod community composition was best explained by littoral vegetation cover, elevation (a proxy for mean annual air temperature) and surface-water temperature. Species richness estimators (Colwell & Coddington, 1994) indicated that total species richness is about 20% higher in the Kenyan than in the Ugandan study area. This is probably due to the larger environmental gradient covered in Kenya, which included ephemeral, semi-permanent and permanent pools as well as some highland lakes and man-made reservoirs. To illustrate this a PCA ordination was made of all sampled waters and 11 the biologically relevant environmental variables that were common to both datasets (Fig. 3). It should also be noted that several large-bodied ostracod species were restricted to temporary ponds lacking fish, a possible indication of the role of size-selective predation by fish and amphibians (See Chapter III). Targeted analysis of shallow, ephemeral and semi-permanent pools in western Uganda may yield a comparable number of large-bodied ostracod species, as indicated by the abundance of *Chrissia icosacanthus* in Wandakara swamp and the recovery of *Stenocypris curvirami* in the surface sediment of Lake Wankenzi, which is fringed by a swamp of papyrus, *Phragmites* and *Typha*.

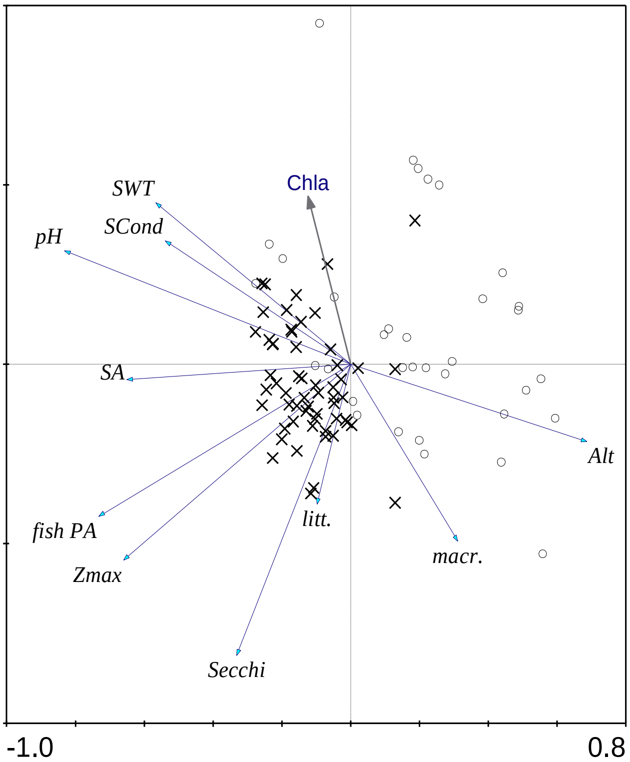

Figure 3: Principal components analysis (PCA) of 34 study sites in Kenya (circles), 57 study sites in Uganda (crosses) and 11 biologically relevant environmental variables (vectors); Chl a is included as a neutral variable. Environmental variables as defined in Chapter III

8.2.1 Palaeoecological implications of fossil assemblage compositions

8.2.1.1 Preservation of aquatic invertebrates in the surface sediments of tropical lakes

In order to accurately reconstruct past aquatic ecosystems it is essential to understand the relationship between living and fossil assemblages (Frey, 1986). The composition of fossil assemblages in lake sediments is influenced by various factors such as basin morphometry, transport-sedimentation processes, dissolution and fragmentation of remains, bioturbation, and temporal and spatial variations in local living communities (Korhola & Rautio, 2001). For the majority of aquatic organisms, lake depth and size (distance to shore) are the most important factors determining their representation in mid-lake sediments. Pelagic taxa dominate the fossil assemblages extracted from sediments from the centre of large lakes, whereas littoral taxa with low abundances in the live samples were rarely encountered in offshore sediments (see below). The fossil remains of the majority of aquatic invertebrate taxa are mostly deposited close to the original habitat, and relative depth (the steepness of bottom slope) is often a critical parameter determining the bottom area suitable for littoral taxa (Kattel *et al.*, 2007). In addition, some differences in the occurrence of species in living versus fossil assemblages result from the different time periods that are represented (Frey, 1988). Fossil assemblages are expected to integrate species composition from at least one whole year, whereas the living community was sampled at a discrete time of the year, in this study either the short (January-February) or long (July-September) dry season. In chapter 4 one of the objectives was to determine the extent to which the surface-sediment assemblages from the centre of the lake reflect the corresponding living aquatic invertebrate community. Relative abundance in fossil assemblages is easily determined and palaeoecological applications are often based on changes in relative abundances of particular species rather than on complete species turnover. In order to compare the living community with the fossil assemblages a relative abundance dataset was created combining data from different net samples, based on equal proportions of total littoral and total pelagic abundances. Creating this artificial per-lake relative abundance by combining the samples from the different habitats posed a problem, as even with similar sampling efforts the number of individuals collected at different sites within a lake could vary by several orders of magnitude. This is why we used presence-absence data, in chapters 1-3, which deal exclusively with the distribution of the living community.

8.2.1.2 Cladocera

In this study the presence, abundance and diversity of aquatic macrophyte habitat and pH were among the main structuring forces and explained similar amounts of the variation in both living cladoceran communities and the corresponding fossil assemblages of fresh Uganda crater lakes (Chapter V). As such, fossil cladoceran remains can be used to reconstruct changes in aquatic macrophyte development, as has been done in Europe (Jeppesen, 1998) and Australia (Thoms *et al.*, 1999). In Lake Yoa in the Sahara of northern Chad, the relatively abrupt mid-Holocene transition from a freshwater to saline lake environment was marked by a sharp reduction in fossil cladoceran remains (Eggermont *et al.*, 2008; Chapter VII). Within the set of Uganda freshwater lakes, a poor correlation was found between salinity and the composition of fossil cladoceran assemblages, suggesting limited potential to reconstruct more modest changes in past salinity. Major changes in cladoceran species richness are expected only when the salinity tolerance of resident aquatic macrophyte species are exceeded, with which many chydorid Cladocera are associated (Verschuren *et al.*, 2000b).

In fossil assemblages the ratio of planktonic Cladocera (mostly Daphniidae) to benthic Cladocera (mostly Chydoridae) is often determined by lake depth and size (Whiteside & Swindoll, 1988; Battarbee, 2000; Bigler *et al.*, 2006). In cold-temperate lakes where Daphniidae produce resting eggs in anticipation of winter each year, concentrations of fossil daphniid ephippia can be considered proportional to the size of the original living population at the time scale represented by fossil assemblages. This principle allows reconstruction of historical changes in fish predation (Verschuren & Marnell, 1997). Whether this is also the case in tropical lakes requires careful consideration. In the fluctuating dry-region lakes of eastern equatorial Africa, fish and zooplankton are affected by continuous habitat instability (Hickley *et al.*, 2002). Under such unstable environmental conditions, regular seasonal production of long-lived dormant stages is advantageous. Mergeay *et al.* (2004) hence used ephippia from a 200-year long sediment core to reconstruct historical changes in the *Daphnia* community of Lake Naivasha, a climate-sensitive Kenyan lake which has experienced a series of well-documented natural environmental changes. Few other palaeolimnological studies in tropical lakes have dealt with *Daphnia*. This is probably due to the general appreciation that *Daphnia* is uncommon in the wet tropics (Fernando *et al.,* 1987; Dumont, 1994). We also doubt whether *Daphnia* frequently produce dormant eggs when natural habitat stability is high, as is the case in most of the western Uganda crater lakes as well as in deep and stable north-temperate lakes. We recovered *Daphnia* ephippia from the surface sediments of only five out of 57 fresh Ugandan lakes, and always in low numbers. Analysis of the living fauna yielded five other lakes where *Daphnia* is present, again always in very low numbers (with the exception of a single sample from Lake Kyaninga). Thus, *Daphnia* is both relatively rare in the study lakes, and when present it produces few ephippia. *Daphnia barbata* was limited to the naturally eutrophic shallow Lake Kibengo. Also in Kenya this large-bodied *Daphnia* species preferentially occurs in eutrophic lakes where high turbidity hampers fish predation (Mergeay *et al.*, 2004, 2006). Conversely, we found the small-bodied *Daphnia laevis* typically in relatively clear water bodies where it may use submerged macrophyte beds as a predation refuge, as has been noted elsewhere (Hart, 1992, 2001; Mergeay *et al.*, 2006). Despite the relative paucity of *Daphnia* in western Ugandan crater lakes, there was a noticeable increase of planktonic Cladocera (*Daphnia, Ceriodaphnia, Moina*) remains in surface-sediment assemblages with core site depth, and its species composition was also influenced by the distance to shore (the littoral zone). A stratigraphic increase in littoral cladoceran remains with time may therefore not only reflect a historical increase in macrophyte habitat, but also a significant reduction in the distance between the core site and the littoral zone, as a result of a change in lake level.

8.2.1.3 Ostracoda

In both the living ostracod communities and corresponding mid-lake death assemblages from the Uganda crater lakes, a significant part of the variation in species composition between lakes was explained by the presence of sandy or muddy littoral substrates, mean annual temperature, and pH. In a study of the depth zonation of ostracod communities in Lake Turkana, Cohen (1986) noted that most ostracod taxa showed only weak and irregular associations with particular substrates, being found instead on a wide variety of bottom types. However, within the littoral zone he did find pronounced differences in the abundance of ostracod species between rocky bottoms and soft, vegetated mud bottoms. Several other authors have also noted the importance of substrate type for African ostracods (Tudorancea *et al.,* 1989, Holmes, 1998; Verschuren *et al.,* 2000b). This implies that the presence and abundance of specific ostracod species in a lake-sediment record will be influenced by the availability of suitable habitat. Outside tropical Africa also temperature is known to influence the occurrence (e.g. Delorme & Zoltai, 1984), growth rate, size and life span (e.g. Martens *et* *al.,* 1985) of individual ostracod species. However, the effect of temperature on the distribution of ostracod species in our Uganda study lakes is probably related to the difference between the large, warm, shallow and dilute lakes on the bottom of the Rift valley and the smaller, mostly deep, slightly concentrated lakes on the shoulder of the Rift valley, rather than being an effect of temperature itself. Ostracod assemblage diversity and abundance in surface sediments was very low in the slightly acidic (pH 6.5-7), dilute freshwater lakes. Diversity increased with increasing pH, and reached a maximum value in weakly alkaline lakes (pH 8-9). More alkaline lakes (pH 9-10) were either highly eutrophic (e.g. Lake Mirambi) or somewhat saline (e.g. Lake Ntambi) with relatively few ostracod species. Ostracod abundance however was nevertheless quite high in the slightly saline lakes Nambe and Kyanga. In fresh water, low-magnesium calcite is the first mineral to precipitate when evaporative concentration reaches the calcite branchpoint. As this is removed from the water column, concentrations of magnesium increase relative to calcium (Hardie & Euster, 1970; Ito *et al.,* 2003). Beyond this branchpoint, diversity tends to decrease but abundance further increases (De Deckker & Forester, 1988). Overall the patterns in our ostracod dataset resembled the model of De Deckker & Forester (1988), who noted that there is often a rise in both diversity and abundance with increasing salinity up to the calcite branchpoint. In our fossil dataset, the relationship between ostracods with conductivity was less obvious due to the low ostracod diversity in hypertrophic lakes (independent of their conductivity) and the absence of ostracods in truly saline lakes. However, in our data of the living communities Ca, Mg, the Mg/Ca ratio and salinity did structure ostracod distribution, as is the case in temperate regions (Bunbury & Gajewski, 2005; Viehberg, 2006). In North America, Mg/Ca ratios >1 of lake water are known to support the highest species richness (Smith, 1993; Bunbury & Gajewski, 2005). These environmental parameters did not significantly explain part of the variance in the fossil assemblages, which indicates that there are significant differences between the fossil and live ostracod assemblages.

Despite temporal and spatial integration of fossil remains in the sediment, most ostracod species were less widely distributed among lakes based on mid-lake fossil assemblages than based on samples of the living communities. Average ostracod species richness was 5.4 and 3.3 for live and fossil assemblages, respectively. This impoverished fossil fauna may result from a combination of low pH and calcite undersaturation of bottom waters, leading to shell dissolution upon death (Colman, 1990). Mourgiart & Carbonel (1994) found only a very limited number of species below 7.5 m water depth in Lake Titicaca, and noted total dissolution of dead ostracod valves below 14 m. Delorme (1990) suggested a pH value of 8.3 as the threshold for shell dissolution. In Uganda we recorded a bottom pH lower than 8.3 in all but three freshwater lakes (Chapter II), which would suggest generally bad preservation conditions. There are, however, several indications that preservation conditions were not the critical factor in determining fossil ostracod assemblages. Firstly, neither fossil ostracod species richness nor the fraction of species that was present in the living community but not in the fossil assemblage was correlated with bottom pH or Ca. Secondly, fossils of pelagic

Oncocypris species were more widely distributed than live sampling suggested; whereas large-bodied taxa such as *Chrissia icosacanthus*, *Acocypris platybasis* and *Stenocypris major* were mostly lacking in the fossil assemblages. As such, our data suggest that transportation/sedimentation processes rather than dissolution of the valves determined assemblage composition. Finally, both core site depth and minimum distance to the littoral zone were found to structure the fossil ostracod assemblage. This important influence of lake morphometric factors implies that fossil ostracod assemblages can be used as a proxy for changes in lake depth and size through time. For example, Ryner *et al.* (2007; Chapter VI) related low ostracod fossil densities to phases of high lake levels in Lake Emakat inside Empakaai Crater (northern Tanzania).

8.2.1.4 Aquatic insects

Fossil skeletal remains of aquatic insect larvae were by far the most ubiquitous type of remains encountered in the studied crater lakes. These included taxa from the littoral benthic habitat (e.g. mayflies, Ephemeroptera), the offshore benthic habitat (e.g. the chironomids *Chironomus formosipennis* and *Procladius brevipetiolatus*), the pelagic habitat (e.g. the phantom midge *Chaoborus*) and even the lotic habitat (e.g., Simuliidae). Several groups of halobiont Diptera dominated both the living community and mid-lake death assemblages of the saline lakes: Stratiomyidae, *Culex* sp., *Ephydrella* type and cf. *Culicoides*. Fossil assemblages dominated by these taxa can thus be interpreted to reflect poly- to hypersaline conditions, as has been done already in Holocene records from Sudan (Mees *et al.*, 1991) and Chad (Eggermont *et al.*, 2008; Chapter VII). The quasi-omnipresent species-rich chironomids are among the best studied groups of aquatic invertebrates, and they have previously been shown to be good proxies for quantitative reconstruction of past salinity (Eggermont *et al.*, 2006) and temperature change (Eggermont *et al*., 2009) in African lakes. In Lake Katinda and Wandakara, the chironomid fauna seems to have responded mainly to changes in lake level and land use, for which currently no chironomid-based inference models exist. In the Lake Katinda record, there are indications that the sublittoral benthic chironomids responded to changes in land use long before the truly littoral invertebrate community responded. This may be due to the fact that aquatic invertebrates in the littoral zone are not likely to respond to changes associated with soil erosion and increasing productivity until these changes become great enough to affect the littoral habitat itself (Whiteside, 1969; Hofmann, 1987; Frey, 1988). Lotic Simuliidae were recovered from two lakes with significant surface inflow. In one of theses lakes, Lake Mbajo, a living Simuliidae was recovered near the inflowing stream. Although quite rare, their remains could be used to trace the history of the riverine influence in lakes (cfr. Rück et al, 1998). Fossil mandibles of the Chaoboridae have frequently been used to reconstruct past status of fisheries in North America (e.g. Uutala & Smol, 1996), based on the differences between various species' daily vertical migration behaviour, and hence their ability to co-exist with planktivorous fish. In our study lakes the proportion of *Chaoborus* in the total fossil invertebrate assemblage (excluding chironomids) is higher in productive lakes than in oligotrophic lakes, which may indicate that the reduced visibility associated with high algal biomass improves their capacity to co-exist with zooplanktivorous fish (Wissel et al., 2003). This pelagic predator benefits from the presence of a hypolimnetic refugium to escape vertebrate predation (Rine & Kesler, 2001; Rumes, 2005). In Chapter V we therefore used *Chaoborus* to trace lake-level changes during the part of lake history when there are no independent indicators of anthropogenic disturbance.

Caddisfly (Trichoptera) larvae are aquatic, and sclerites from their head capsule and thorax as well as fragments of their cases can be abundant in some lake sediments (Elias, 2001). Trichopteran remains are most often deposited in shallow water, in the outer part of the reed belt where both emergent and submerged vegetation occurs (Bennike & Wiberg-Larsen, 2002). Exploratory analysis of the overall abundance of trichopteran remains in our data indicated a negative correlation with lake productivity (Chl *a*: r= -0.31, P< 0.05). The fact that no correlation was found with their specific near-shore habitat is likely due to their limited transport before burial, so that the chance of recovering trichopteran remains at the mid-lake core sites was determined by the distance to the littoral zone rather than by their abundance in the littoral zone.

Mayfly (Ephemeroptera) remains of the families Baetidae, Caenidae and Ephemeridae were frequently encountered in the surface sediments. In the surface sediment data set, the relative abundance of Caenidae was positively correlated with Secchi depth (r= 0.34, P< 0.05). Only in oligotrophic lakes, the relative abundance of Caenidae was significantly negatively correlated with lake size (Dmin: r= -0.43, P< 0.05). Overall, the abundance of ephemeropteran remains decreased with increasing lake trophic state (Fig. 4).

Odonata and Hemiptera were only rarely recorded in the surface sediments although they were very common in the live samples. This indicates that only a small fraction of their remains has been transported from the littoral zone to the offshore core sites. Indeed, remains of littoral aquatic insects are known to be most common in littoral lake sediments with high content of organic detritus (Elias, 2001).

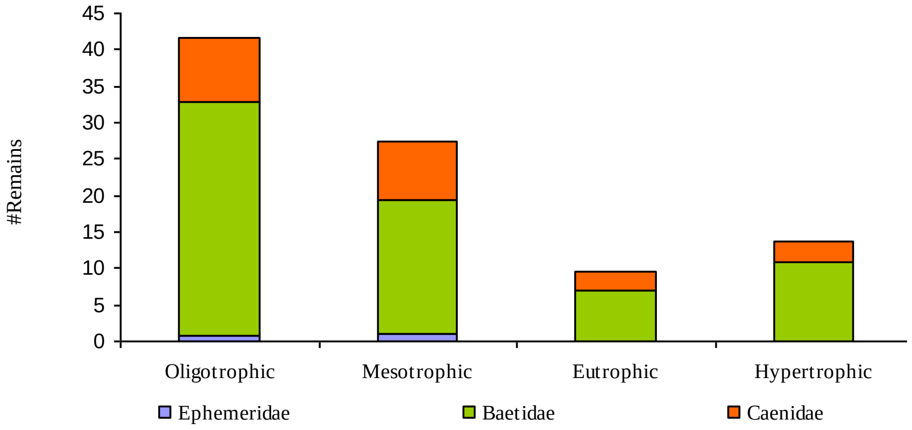

Figure 4: Relationship between average number of Ephermeroptera remains per gram dry weight and lake trophic state in 56 study sites in western Uganda.

8.2.1.5 Other aquatic invertebrates

Quantitative studies focusing on mollusc remains in lake sediments require large volumes of sediment recovered from near-shore locations (Miller & Tevesz, 2001). In our off-shore surface sediment samples, mollusc remains were very scarce despite their abundant presence in the living littoral fauna of many study lakes. Additional screening of near-shore sediments from three study sites (Kyaninga, Mbajo and Bugwagi) revealed numerous gastropod remains (Rumes, unpublished data). This suggests that also molluscs tend to be buried close to their shallow-water habitat and are not frequently transported for offshore. Therefore, in our study of the sediment records of Lake Katinda and Lake Wandakara we considered mollusc remains in these mid-lake cores to reflect the presence of suitable littoral habitat in close proximity to the core site, indicative of very low lake level.

Thus far, fossil statoblasts of freshwater Bryozoa have been used to reconstruct water-level fluctuations or the relative importance of open-water conditions, the extent of macrophyte or littoral zone development, disturbances in the littoral zone, lake trophic state, and temperature/climate (reviewed in Francis, 2001). We recovered a total of 477 statoblasts belonging to two genera (*Plumatella* and *Lophopedella*) from surface-sediment samples of 41 lakes; these comprised on average 2% of all identified aquatic invertebrate fossils. Identification to the species level based on statoblast characteristics is feasible, but so far identification keys are only available for the freshwater Bryozoa of North America (e.g. Ricciardi & Reiswig, 1994; Wood, 2001). In our data statoblasts were slightly more abundant in oligo- and mesotrophic lakes compared to eutrophic lakes, and they were either absent or present in very low densities in hypertrophic lakes. Crisman *et al.* (1986) found a positive correlation between statoblast accumulation rate and macrophyte cover. In our study, we only have data on the presence of various types of aquatic macrophytes, not on their extent. Hence, the relationship between statoblast accumulation rate and macrophyte cover could not be examined. Statoblasts were quite rare in the records of both Lake Wandakara (present in 3 out of 54 intervals) and Lake Katinda (present in 20 out of 111 intervals).

Oribatid mites are mainly associated with aquatic vegetation or washed or blown in from terrestrial vegetation and litter close to the lake (Solhøy, 2001). Species assemblages found in lake sediments tend to be a mixture of aquatic, wetland and terrestrial species (Erickson, 1988; Solhøy & Solhøy, 2000). Their use in palaeolimnology remains limited due to scant knowledge of their taxonomy and ecological preferences in most parts of the world (Solhøy & Solhøy, 2000). In our study, oribatid mites were recovered from both living communities and fossil assemblages in the majority of lakes. Pterogasterina appear indicative of elevated conductivities, although this group was also recovered from a number of freshwater lakes. As we did not differentiate between terrestrial and aquatic taxa, oribatids were not included in the discussion of the sediment cores from Lake Katinda and Lake Wandakara, although in general their abundance was similar to that of other littoral taxa associated with aquatic macrophytes (Fig 5). This is similar to the results of a palaeoecological study on Lake Kråkenes (western Norway), where despite a greater diversity of wetland and terrestrial species, the fossil oribatid assemblage was dominated by true aquatic species associated with aquatic macrophyte vegetation (Solhøy & Solhøy, 2000).

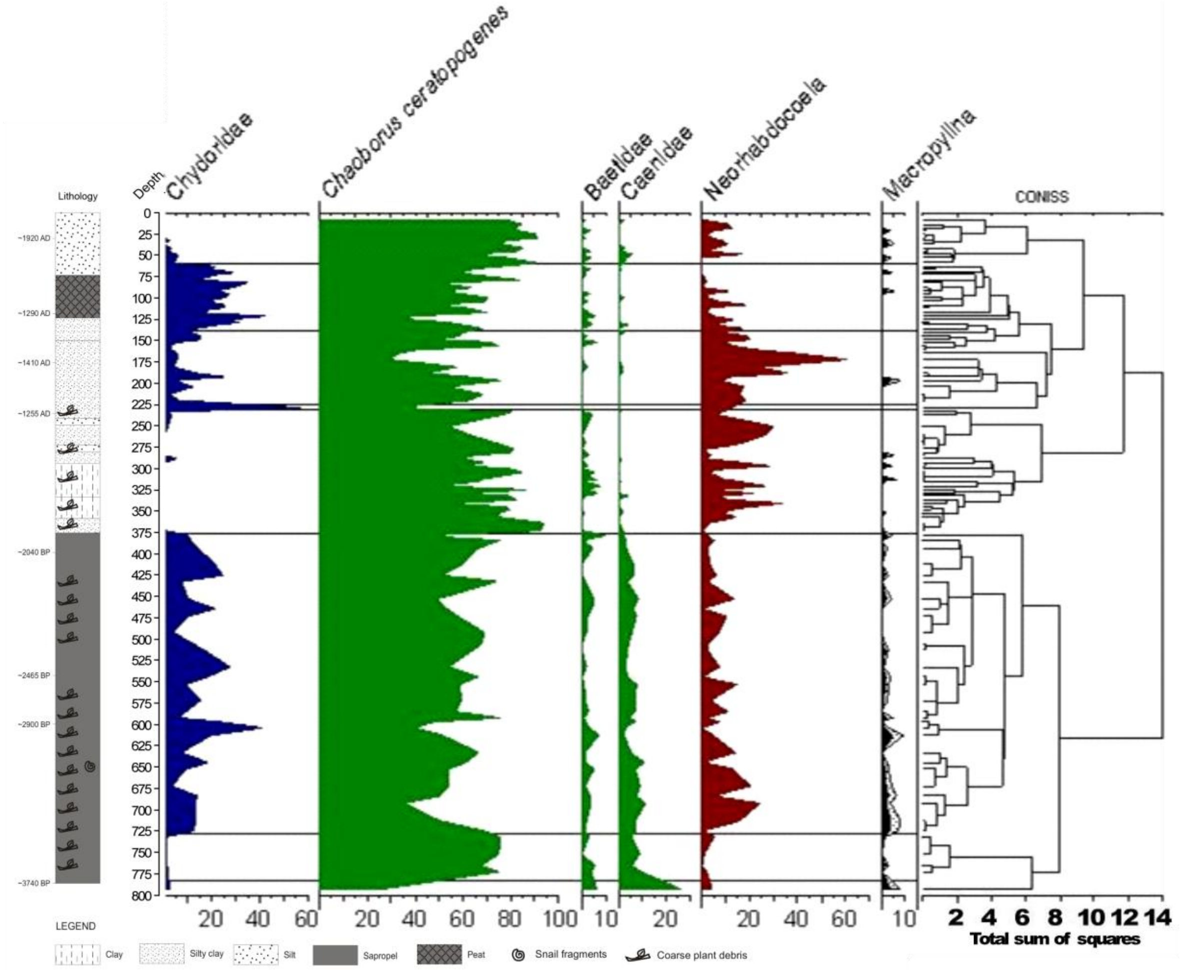

Figure 5: Stratigraphic distribution of Chydoridae, *Chaoborus ceratopogenes,* Baetidae, Caenidae, Neorhabdocoela and Macropylina in Lake Katinda, zonation as determined by BSTICK and CONISS (for the whole aquatic invertebrate assemblage, see Chapter V).

Testate amoebae are unicellular animals with a discrete shell or test enclosing the cytoplasm. These tests are readily preserved and abundant in peat and lake sediments (Warner, 1990a). Because our fossil analysis was limited to remains > 150 µm, we probably recovered only a subset of the local species (size-range of testate amoebae: 10-400 µm; Beyens & Meisterfeld, 2001). These included representatives of four genera, of which *Arcella* numerically dominated both living and fossil assemblages. In the surface-sediment samples, testate amoebae were indicative of relatively dilute freshwater conditions and *Arcella discoides* was associated with diverse aquatic vegetation in both living and fossil assemblages. In the record of Lake Katinda, high densities of *Arcella* tests were associated with a period of low lake levels and extensive macrophyte development. Hardly any *Arcella* tests were recovered during the period of intensive anthropogenic activity (~2000-500 cal.yrs BP), which we assume probably increased lake productivity. This matches earlier findings that densities of testate amoebae are considerably lower in eutrophic lakes than in oligotrophic ones (Schönborn, 1962). Densities of *Arcella* were considerably lower (~5 times) in the surface sediments of eutrophic and hypertrophic lakes than in the sediments of oligo- and mesotrophic lakes. It remains unclear, why there is a switch from *Arcella* to *Centropyxis* in the record of Lake Wandakara during the last 500 years as no clear relationship between *Centropyxis* abundance and specific environmental parameters could be deduced from the surface sediments.

Flatworms of the order Neorhabdocoela (Platyhelminthes: Turbellaria) produce thick- walled resting eggs or oocytes for propagation and for surviving unfavourable conditions (Heitkamp, 1988). These are highly resistant to decomposition, vary in size (60-200 µm), shape and ornamentation, which allows identification to species and type level (Haas, 1996). In our analysis of the surface sediments, there was a significant negative correlation between numbers of Neorhabdocoela and lake size (Dmin: $r= -0.27$, $P< 0.05$). Haas (1996) predicted that Neorhabdocoela were likely to be good indicators for lake productivity, lake level, and even water temperatures during long-lasting climatic trends. In the records of Lake Katinda and Lake Wandakara, increased abundances of Neorhabdocoela egg cocoons were associated with periods of higher lake trophic state and lower lake levels, as deduced from the analysis of fossil chironomid and other aquatic invertebrate assemblages (illustrated for Lake Katinda: Fig 5).

8.2.1.6 Fish

Analyses of mitochondrial DNA indicate that populations of haplochromine cichlid fishes have persisted in relative genetic isolation in some of the larger crater lakes in western Uganda for about 50 000 generations (years) (Sato *et al*., 2003). Direct observations (e.g. the presence of juvenile fish in the living samples or observation during the sampling) and indirect observations (e.g. conversations with local fishermen, game wardens etc.) confirmed the presence of fish in virtually all studied freshwater lakes, with generally higher abundances in eutrophic and hypertrophic lakes. The latter was also reflected in the increasing number of fish remains (scales, teeth and bones) per gram sediment along the trophic gradient ($r=0.31$, $p<0.05$). In contrast to Davidson *et al.* (2003), no negative correlation was found between the density of fish remains and the distance to the shore, instead a trend was found of increasing densities of fish remains with increasing distance to the shore, although this trend was not significant. In the palaeoecological studies of Lake Katinda and Lake Wandakara (Chapter V), the presence of fish was confirmed from the start of the records, ~3700 and ~2000 cal. years BP, respectively. In both lakes, the abundance of fish remains increased drastically after the onset of anthropogenic activity in the crater basin, which may be the result of eutrophication, the introduction of new species, or a combination of both.

8.3 The late-Holocene history of environmental change in western Uganda

8.3.1 ~3800 to ~2150 cal. yr BP

Studies on sediment archives from East Africa's great lakes indicate that the area experienced a transition from a wet early Holocene to a more arid late Holocene by 5500-5200 cal. yr BP (Gasse, 2000; Russell *et al.*, 2003). At 4000 cal. year BP, Lake Edward experienced a major drought event (Russell & Johnson, 2005) also tentatively recorded in our Lake Katinda record at ~3800 cal. yr BP. Littoral taxa dominated the aquatic invertebrate community and there is a pronounced peak in inorganic matter content of the sediment. In Lake Katinda, lake levels increased and stayed relatively high between ~3800 and ~2800 cal. yr BP. Pelagic *Chaoborus* and benthic mud-dwelling chironomids dominated the aquatic invertebrate assemblages. We interpreted a pronounced peak in littoral chydorids, the occurrence of a number of rare littoral chironomid species, and a slight increase in carbonate content at ~2800 cal. yr BP as a temporary drop in lake level, which appears synchronous with inferred drought at Lake Edward (Russell & Johnson, 2005). Between ~2800 and 2150 cal. yr BP, core sedimentology, chironomid and other aquatic invertebrate indicators were once again typical of relatively high lake levels, and overall faunal composition was similar to that between ~3800 and ~2800 cal. yr BP.

8.3.2 ~2150 to ~1000 cal. yr BP

In Lake Katinda, circa ~2150 cal. yr BP, the abundance of *Cladotanytarsus pseudomancus*, a chironomid species associated with coarse sandy substrate, started to increase considerably, while abundances of mud-dwelling *Procladius brevipetiolatus* and *Tanypus* near *guttatpennis* decreased. During this gradual increase of *Cladotanytarsus*, core sedimentology and the proportion of pelagic *Chaoborus* to littoral insects remained fairly stable up to ~2000 cal. yr BP, which suggested that lake level did not vary dramatically. At ~2000 cal. yr BP, a pronounced change in sediment composition was accompanied by a decrease in *Chaoborus* and an increase in most littoral insect taxa, indicating a second lowstand episode, again apparently synchronous with a major drought recorded at Lake Edward ~2000 cal. yr BP (Russell & Johnson, 2005). Starting ~1900 cal. yr BP the sedimentology and fossil aquatic invertebrate assemblage indicated increased erosion and reduced transparency resulting in shrinking aquatic macrophyte habitat and an impoverished littoral fauna. Although the changes in benthic chironomids indicated anthropogenic erosion starting ~2150 cal. yr BP, littoral insect taxa only responded after the regional drought at ~2000 cal. yr BP. This regional aridity, which is also evidenced at the start of the Lake Wandakara record, may have caused the human population in the Lake Katinda area to congregate near the surviving water supplies, thus increasing human pressure on the lake. Aquatic invertebrates in the littoral zone probably only responded to changes associated with increasing productivity when these changes became great enough to affect the littoral habitat itself (Whiteside, 1969; see above) i.e. increased turbidity which negatively impacted aquatic macrophyte habitat.

In both lakes a gradual transgression reaching high lake levels until ~1000 cal. yr BP was marked by a decrease in littoral taxa. Vegetation records from Lake Kasenda, starting from 1250 BP, suggest that a well-developed medium-altitude humid forest and overall humid conditions prevailed in the area around Lake Wandakara until 1100 BP (Ssemmanda *et al.*, 2005).

8.3.3 ~1000 to ~250 cal. yr BP

Between 1100 BP and 1000 BP the moist semi-dedicious forest contracted and was largely replaced by grassland, suggesting increased aridity (Ssemmanda *et al.*, 2005). In the records of Lake Wandakara and Lake Katinda, a decrease in lake level at ~1000-800 cal. yr BP is indicated by increasing chydorid abundance and a falling back of *Chaoborus*. In both lakes, there was also a small increase in ostracod abundance; and in Lake Wandakara, snail fragments were noted in the sediment record. Evidence for a widespread arid phase at ~ AD 1000-1200 is found in other records from western Uganda (e.g. Ssemmanda *et al.*, 2005; Russell *et al.*, 2007) as well as from other East African lakes (Stager *et al.*, 2005; Russell & Johnson, 2005). This drought coincided with the onset of human impact in the crater basin of Lake Wandakara (Russell *et al*., 2009) causing major changes in the chironomid faunal assemblage (i.e. a shift towards species thriving on coarse sediments). There is ample palaeoecological and sedimentary evidence of increasing human impact from ~1000 cal. yr BP in the area around Lake Wandakara, including studies from nearby Kabata Swamp (Robertshaw & Taylor, 2000) and Lake Kasenda (Ssemmanda *et al*., 2005). In Lake Wandakara, chironomid species associated with littoral macrophytes further decreased and *Chaoborus* thrived when lake levels rose from ~800 to ~600 cal. yr BP. In Lake Wandakara, *Chaoborus* abundance seemed to mostly reflect past lake-level fluctuation. In this lake, low lake levels, reflecting arid phases, were recorded from ~600 to ~500 cal. yr BP and ~300 to ~250 cal. yr BP. Hypersaline Lake Kitagata, which was not impacted by human activities, also provided indications of aridity during the 1500s and 1600s (Russell et al. 2007). In Lake Katinda, magnetic susceptibility (a proxy for anthropogenic soil erosion) also gradually decreased in this period, which indicates a reduction in anthropogenic land use in the crater basin.

8.3.4 ~1750 to 2000 AD

From ~1750 to ~1850 AD, aridity was widespread throughout equatorial East Africa (Verschuren *et al.*, 2000a, Bessems *et al.*, 2008), and large nucleated settlements in western Uganda were abandoned in favour of pastoralism (Taylor *et al*., 2000). In Lake Katinda this period is marked by a peaty sediment horizon, an abundance of littoral taxa and a partial recovery of taxa which had strongly decreased or disappeared at the onset of anthropogenic impact in the crater basin. No such peat layer was found at Lake Katinda for the drought at ~AD 1000, even though isotopic and diatom data from Lake Kasenda suggest that the event at ~AD 1000 was more severe than that at AD 1750 (Ryves *et al.,* in press). In Lake Wandakara, littoral taxa dominated the aquatic fauna at ~1750 AD, resulting in a temporary higher diversity, followed by a zone with very low fossil densities. It has been suggested that this zone of very low fossil densities represents an instantaneous deposit at the end of a prolonged dry period. Alternatively, high abundances of Ostracoda and the presence of a number of rare littoral taxa (*Ecnomus,* Odonata) in combination with low *Chaoborus* and Chydoridae abundances suggest that this massive unit was deposited during a lake low stand which led to somewhat elevated conductivities (Chapter V). Both alternatives explain the elevated values for inorganic matter, and the dominance of littoral ostracods and diatoms (Bessems, 2007; Ryves *et al.,* in press). Increased humidity starting ~1850 led to the return of increasingly diverse moist semi-dedicuous forest in the vicinity of Lake Wandakara (Ssemmanda *et al*., 2005). The increase in lake levels is characterized by an increase in the pelagic *Chaoborus* and benthic chironomids to the detriment of littoral insect taxa. The latter still maintain a significant presence, indicating the presence of a well-developed littoral zone with aquatic macrophytes. Significant anthropogenic impact is noticeable, from ~1920 AD at Lake Katinda and from ~1960 AD in Lake Wandakara, by an increase in magnetic susceptibility and of taxa associated with higher lake trophic state or coarse, sandy sediments. In pollen data from Lake Wandakara, Ssemmanda *et* al (2005) also found clear evidence of increasing human impact at the start of the second half of the 20th century, with agriculture replacing forest.

8.3.5 Coherence of the palaeoecological records of Lake Katinda and Lake Wandakara

In many cases, Lake Katinda and Lake Wandakara show a common response to major regional events, particularly droughts at ~2000 BP, ~1000 – 800 BP and ~AD 1750-1850, and to the wetter period during the latter half of the 1800s. Even though the two lakes are of similar depth, the proportion of littoral taxa to pelagic taxa is much higher in Lake Wandakara than in Lake Katinda due to the difference in lake size (Lake Wandakara is ten times smaller than Lake Katinda) and the shorter distance from the core site to the littoral zone in Lake Wandakara. Catchment processes affecting erosion in the crater basin and, as a result, limnological processes were likely to be more important at Lake Katinda where the ratio of catchment area:lake area is ~5, than at Lake Wandakara where this ratio is ~3. In addition, our analysis revealed that there were clear regional differences in the history of anthropogenic impact. In Lake Wandakara, variations in littoral remains, which reflected changes in the extent of the littoral habitat as well as lake level, were far more pronounced than in Lake Katinda. Due to the offshore location of the core site in Lake Katinda, our record from that lake more accurately reflected whole-lake changes rather than changes in littoral habitat. Despite such basin-specific factors influencing the sensitivity of each lake to climate variability and human impact, and thus the strength of signatures recorded by proxies, in both lakes a pronounced change in the mid-20th century can be attributed to the effects of intensifying human activity on aquatic productivity. As for all palaeoecological studies, a multi-proxy and multi-site approach remains was necessary to distil a coherent story, and to separate local from regional drivers.

8.3.6 The aquatic invertebrate assemblage and past salinity changes

Historical salinity changes in Lake Katinda and Lake Wandakara were fairly modest. Much clearer indications of how changes in salinity affect aquatic invertebrate community composition were found in a reconstruction of the mid- and late-Holocene desiccation of the Sahara (Eggermont et al., 2008; Chapter VII). Long-term changes in the zoobenthos and zooplankton communities of Lake Yoa (Ounianga region, northeastern Chad) were reconstructed to document the hydrological evolution of this groundwater-fed aquatic ecosystem (Eggermont *et al.*, 2008). Major shifts in the aquatic invertebrate community signalled successive phases in the change from a dilute freshwater lake to today's hypersaline lake. The fossil distributions of various aquatic invertebrate taxa, whose ecological tolerances were determined from literature records and our study in western Uganda, could be used to assess the reliability of quantitative salinity inferences based on fossil chironomid assemblages. In contrast, in the sediment record of Lake Emakat, Empakaai Crater (northern Tanzania), low fossil densities prevented an independent assessment of the chironomid inferred salinity change at the start of the Holocene, using assemblages of other aquatic invertebrates (Ryner *et al*., 2007; Chapter VI).

8.4 Future research and dissemination of results

Biodiversity and ecology

Our analysis of regional ostracod diversity in western Uganda would benefit from a survey of the ostracod fauna in temporary aquatic habitats, swamps and man-made reservoirs. This would also allow for a more complete comparison of the ostracod fauna of western Uganda and southern Kenya.

The large collection of living samples taken from a large number of aquatic habitats with documented environmental variables could be exploited more thoroughly in order to address some of the gaps in current knowledge of freshwater biodiversity and ecology (cfr. Bailan *et al.*, 2008). For example, aquatic Oribatida have been collected alive from over 40 crater lakes. Identification of these specimens to species level will shed light on the distribution of this group in the afrotropical region, from which only seven oribatid species are known (Schatz & Behan-Pelltier, 2008).

Palaeoecology and methodology

It would be very interesting to more thoroughly study the effect of post-mortem transport and sedimentation on the fossil composition of various aquatic invertebrate assemblages using surface sediments from a number of transects spanning various distances to shore. For some groups, we were unable to statistically determine their palaeoecological indicator value. For bryozoan statoblasts, for example, this was due to lack of a quantitative estimate of macrophyte extent (see earlier).

Environmental change

Ideally, our reconstruction from Lake Katinda should be expanded with an analysis of various other aquatic and terrestrial proxies such as pollen, diatoms and fossil algal pigments. Pollen analysis could be very useful in providing independent evidence of anthropogenic activities in the area, while diatoms and pigments could be used to confirm changes in lake trophic state (Battarbee *et al.*, 2001, Leavitt & Hodgson, 2001). Synchronicity of the changes in terrestrial vegetation between Lake Kasenda (Ssemmanda *et al.*, 2005) and Lake Katinda would indicate the regional nature of such changes. Diatom-based transfer functions for quantitative reconstruction of total phosphorus (TP) or total nitrogen (TN) have been developed and applied in many regions (Lotter *et al.*, 1998; Rippey & Anderson, 1996; Gasse, 2000), but for tropical Africa these do not yet exist. The development of such inference models in our study region may prove to be quite a challenge, however, because diatoms often comprise only a minor component of phytoplankton communities in these wind-sheltered crater lakes (C. Cockuyt, unpublished data).

Reconstruction of the long-term environmental history of crater lakes currently situated within the boundaries of national parks could further reveal whether these lakes are truly pristine or have undergone past anthropogenic impacts. If they prove to be truly pristine, then their environmental history has been completely determined by climatic changes. If, on the other hand, they have been subjected to past anthropogenic influence, then they would represent an excellent opportunity to study long-term ecosystem recovery.

Dissemination of results

We gathered a significant amount of information on the distribution of several groups of aquatic invertebrates in these small crater lakes in western Uganda and of ostracods in temporary pools and lakes in southern Kenya. To facilitate usage and analysis of the data collected during this study, data will be made accessible through the internet via the Global Biodiversity Information Facility (GBIF). A series of meetings with local stakeholders in Uganda and Kenya is scheduled for early 2010. At these meetings, relevant limnological data shall be made available to national and local management authorities. The research chapters in this thesis are intended for publication in the relevant scientific literature.

General conclusion

As anthropogenic land disturbance continues to increase worldwide, aquatic scientists are faced with the challenge of determining how human activities influence the structure and function of aquatic ecosystems and the potential for restoration of impacted waters (Sutherland *et al*., 2002). Submerged macrophytes have a significant impact on the trophic structure, dynamics and water clarity of shallow lakes (Scheffer *et al*., 1993). Lakes with a high abundance of submerged macrophytes are characterized by transparent waters, abundant piscivorous fish, a diverse waterfowl community and overall high biodiversity. Indeed, in our dataset, diversity of aquatic invertebrates was highest in lakes with abundant aquatic macrophytes. The presence and abundance of aquatic macrophytes was related to basin morphometry and the intensity of anthropogenic land use. Eutrophication due to anthropogenically enhanced nutrient inputs is a serious problem for many lakes. Enhanced nutrient influx may result in an initial increase in macrophyte coverage and associated aquatic invertebrate fauna, but excessive fertilization will eventually lead to dramatic plant decline (Jeppesen, 1998). The effect of anthropogenic eutrophication appears to be fairly modest in the deep, meromictic lakes in our study area (Plisnier *et al.*, in prep.), but it drastically altered aquatic ecosystem functioning in a number of shallow lakes. This has led to an impoverished aquatic invertebrate fauna and diminished ecosystem services. Our results indicate that it is advisable to avoid agricultural activities within the (steep) crater basins of shallow lakes.

Our rapid biological screening (RBS) of the fossil assemblages of various relatively large (> 150 µm) aquatic invertebrate taxa added significant value to chironomid-based reconstructions. Chironomid analysis can be used for a quantitative reconstruction of lake salinity and, in our study of lakes Katinda and Wandakara, the chironomid fauna also responded quickly to habitat changes brought about by human impact. RBS allows us to extend the salinity range beyond the upper tolerance range of chironomids, and studied groups also respond sensitively to changes in lake level and human impact. Increasing the taxonomic resolution of the studied groups and inclusion of smaller remains may increase the accuracy and sensitivity of the RBS, but analyses would also consume more time.

Our analyses indicate that aquatic biota in western Ugandan lakes have been subject to strong natural fluctuations in environmental parameters in the course of the last 4000 years. Human impact starting ~2150 and ~900 years ago, for Lake Katinda and Lake Wandakara respectively, changed the composition of the aquatic invertebrate fauna. Although the aquatic invertebrate fauna partly recovered when humans vacated the area of Lake Katinda for over 150 years, in both lakes the effects of natural environmental change on the aquatic biota, though significant, were subordinate to those of changes in anthropogenic land use.

Rising population pressure and the effects of anthropogenic climate change are expected to have a significant impact on these crater lakes. Sustainable land use management practices can limit the negative impact of increased land use for agricultural use, while the protection of a number of specific locations with high biodiversity within national parks can protect regional biodiversity and increase the chances of ecosystem recovery through re-colonization.

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Appendix

List of publications of the author

A1 publications

Eggermont H., D. Verschuren, M. Fagot, **B. Rumes**, B. Van Bocxlaer & S. Kröpelin, 2008. Aquatic community response in a groundwater-fed desert lake to Holocene desiccation of the Sahara. *Quaternary science reviews* 27(25-26): 2411-2425. (Thesis chapter)

Kropelin S., D. Verschuren, A.M. Lezine, H. Eggermont, C. Cocquyt, P. Francus, J.-P. Cazet, M. Fagot, **B. Rumes**, J. M. Russell, F. Darius, D. J. Conley, M. Schuster, H. von Suchodoletz & D. R. Engstrom, 2008. Climate-driven ecosystem succession in the Sahara: The past 6000 years. Science 320(5877): 765-768.

Ryner M., F. Gasse, **B. Rumes** & D. Verschuren, 2007. Climatic and hydrological instability in semi-arid equatorial East Africa during the late Glacial to Holocene transition: A multi-proxy reconstruction of aquatic ecosystem response in northern Tanzania. *Palaeogeography, palaeoclimatology, palaeoecology* 248(3-4): 440-458. (Thesis chapter)

Rumes B., H. Eggermont & D. Verschuren, 2005. Representation of aquatic invertebrate communities in subfossil death assemblages sampled along a salinity gradient of western Uganda crater lakes. *Hydrobiologia* 542: 297-314.

Vandekerckhove T.T.M., S. Watteyne, W. Bonne, D. Vanacker, S. Devaere, **B. Rumes**, J.P. Maelfait, M. Gillis, J.G. Swings, H.R. Braig & J. Mertens, 2003. Evolutionary trends in feminization and intersexuality in woodlice (Crustacea, Isopoda) infected with *Wolbachia pipientis* (alpha-Proteobacteria). *Belgian journal of zoology* 133(1): 61-69.

A1 publications submitted/in preparation

Audenaert L., C. Cocquyt, **B. Rumes**, H. Eggermont, V. Baetens & D. Verschuren. Response of tropical African lake ecosystems to natural and anthropogenic habitat change: a 200-year paleoecological study contrasting pristine and disturbed crater lakes in western Uganda.

Rumes, B., H. Eggermont & D. Verschuren. Environmental regulation of the distribution and faunal richness of Cladocera in western Uganda crater lakes. (Thesis chapter)

Rumes, B., K. Martens & D. Verschuren. Environmental regulation of ostracod (Crustacea: Ostracoda) communities in western Uganda crater lakes. (Thesis chapter)

Rumes, B., K. Martens & D. Verschuren. Ostracod (Ostracoda, Crustacea) communities in shallow Kenyan lakes and ponds. (Thesis chapter)

Rumes, B., H. Eggermont & D. Verschuren. Ecological and taphonomic controls on the composition of fossil aquatic invertebrate assemblages across a wide environmental gradient of East African lakes. (Thesis chapter)

Rumes, B., I. Bessems, G. Kabihogo,.H. Eggermont & D. Verschuren. 5 A four thousand year history of crater lakes in western Uganda: response of the aquatic invertebrate fauna to climatic and anthropogenic impacts. (Thesis chapter)

Plisnier P.D., D. Verschuren, **B. Rumes**, C. Cocquyt, H. Eggermont, J. M. Russell, H. Hughes & L. André, in prep. Trophic levels and mixing of Ugandan crater lakes.

C. Cocquyt, P. Plisnier, V. Gelorini, **B. Rumes** & D. Verschuren. Observations on the limnology and phytoplankton community of crater Lake Kyaninga (Uganda), with special attention to its diatom flora. Submitted to Systematics and Geography of Plants.

Cover picture - front
Sampling at Lake Kikorongo (2008, photograph by Pierre-Denis Plisnier)

Cover pictures - rear
From left to right: *Pleuroxus* cf. *varidentatus* Frey, *Gomphocythere expansa* (Sars), *Dicrotendipes septemmaculatus* (Becker), *Chaoborus (Sayomyia) ceratopogenes* Theobald (photographs by Bob Rumes)