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

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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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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; 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; 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

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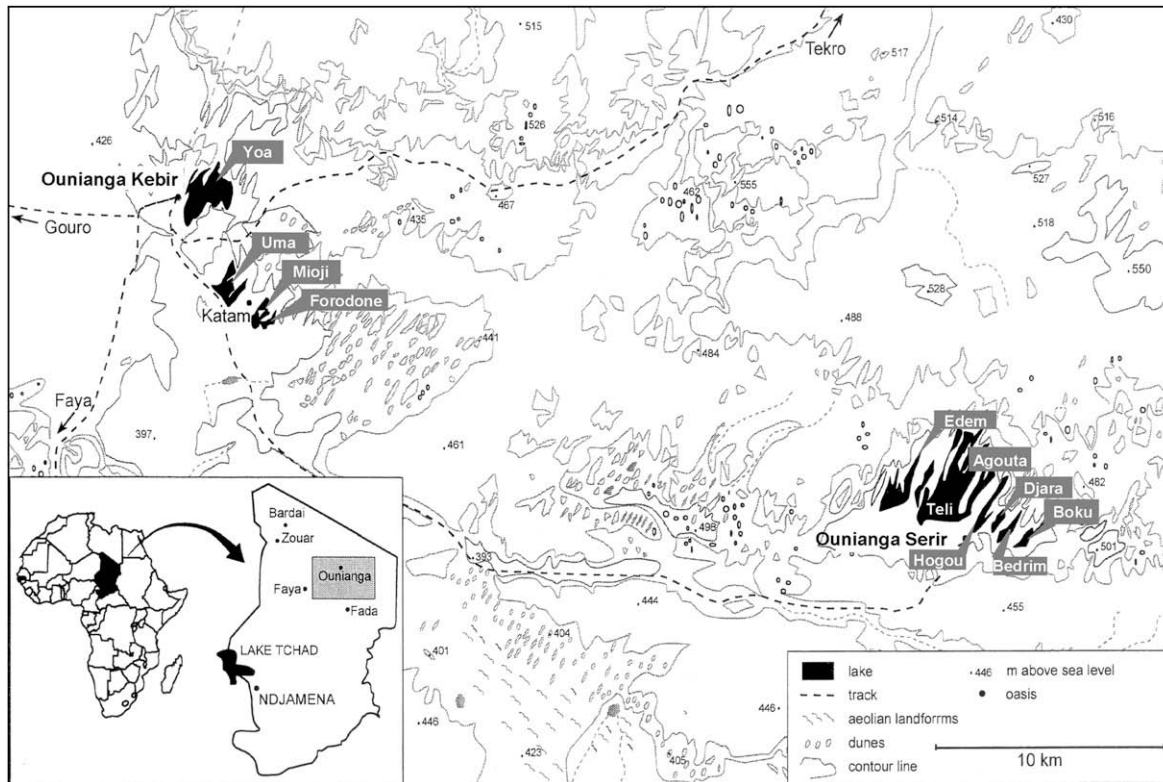E-mail address: hilde.eggermont@ugent.be (H. Eggermont).

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

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; 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; 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; 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; 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; Cohen and Nielsen, 1986; DeDeckker and Forester, 1988) were quite rare. Biological paleo-salinity reconstructions have subsequently been recognized as highly informative, and are now carried out on all continents around the world (Smol and Cumming, 2000; 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; 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, 2001; Verschuren et al., 2000a; 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 biogeo-graphical realms (Dumont, 1979, 1982; 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.

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 km², 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 km² 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; 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.

3. Materials and methods

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.
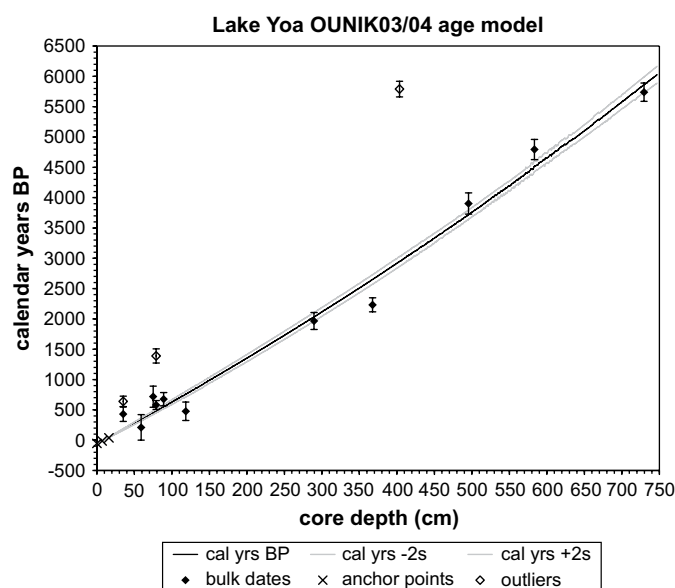

Fig. 2. Calendar age–depth model for the composite OUNIK03/04 core from Lake Yoa.

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.

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, 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,b; 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; Quinlan and Smol, 2001).

Fig. 3. Sub-fossil remains of *Chironomus* cf. *salinarius* (a, b), and cf. *Stictochironomus* type Ounianga Kebir (c).

Lake sediments also hold the remains of various other aquatic invertebrates with useful application in Quaternary paleoecology (Frey, 1964, 1976). These include Trichoptera (e.g., Solem and Birks, 2000), Ceratopogonidae (biting midges; e.g., Walker et al., 1997; Heinrichs et al., 2001), *Chaoborus* (phantom midges; e.g., Uutala, 1990; Uutala and Smol, 1996; Walker et al., 1997; Heinrichs et al., 2001), Cladocera (water fleas; e.g., Frey, 1976, 1988; Whiteside and Swindoll, 1988) and Ostracoda (seed shrimps; e.g., De Deckker and Forester, 1988; Griffiths et al., 2001; Holmes and Chivas, 2002; 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; 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).

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 and WA-PLS, the influence of individual taxa on inferred salinity is inversely proportional to the width of their salinity tolerance as determined by their modern distribution in a set of reference lakes (the calibration data set), as well as their percent abundance in the fossil assemblage. 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.

4. Results

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,b; 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.

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; Rumes et al., 2005) and *Ephydra* are both halophilic (Hart et al., 1991; Teskey, 1984; Hammer, 1986; 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; 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.

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).

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

This zone is typified by high abundances of *Cladotanytarsus pseudomancus* ($55 \pm 13.3\%$) alongside fairly high numbers of *Procladius brevipetiolatus* ($14.3 \pm 9.6\%$) and *Microchironomus* type East Africa ($15.4 \pm 10.1\%$). *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*).

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 ($52.2 \pm 9.1\%$, $13.5 \pm 6.7\%$ and $10.2 \pm 9.1\%$, 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 ($5.6 \pm 3.9\%$) 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.

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 ($67.8 \pm 28.2\%$). Other invertebrate remains are virtually absent, including *Chaoborus*; only two Cladocera specimens (*Alona* and *Chydorus*) were found, at 495 cm depth.

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 ($57.4 \pm 18.5\%$). *Microchironomus deribae* appears for the first time ($17.0 \pm 10.0\%$), and *Cricotopus* type Ounianga Kebir shows an intermittent increase to ∼30% (but with a mean of $13.0 \pm 4.6\%$). *Chironomus* cf. *salinarius* is present throughout much of this zone, at fairly low abundances ($6.8 \pm 5.8\%$). 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*).

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 ($82.8 \pm 10.1\%$), followed by a gradually expanding *Chironomus* cf. *salinarius* which peaks ca 1490 cal yr BP (and has an I2 mean of $11.7 \pm 8.9\%$). *Cricotopus* type Ounianga Kebir falls back to a mean abundance of $5.4 \pm 4.5\%$. This zone is further typified by the regular occurrence of *Anisops*, and in the upper part the first appearance of Ephydridae.

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 $15.2 \pm 7.1\%$). *Kiefferulus disparilis* still dominates the chironomid fauna ($84.3 \pm 7.2\%$), with abundances of up to 94%. Corixidae and Ephydridae are the other invertebrates typifying this subzone.

4.2.7. 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 ($47.9 \pm 16.9\%$), becoming co-dominant with *Kiefferulus disparilis* (now $50.3 \pm 18.0\%$). *Cladotanytarsus pseudomancus* also occurs sporadically at very low abundances (<3%), while Corixidae and Ephydridae remain common.
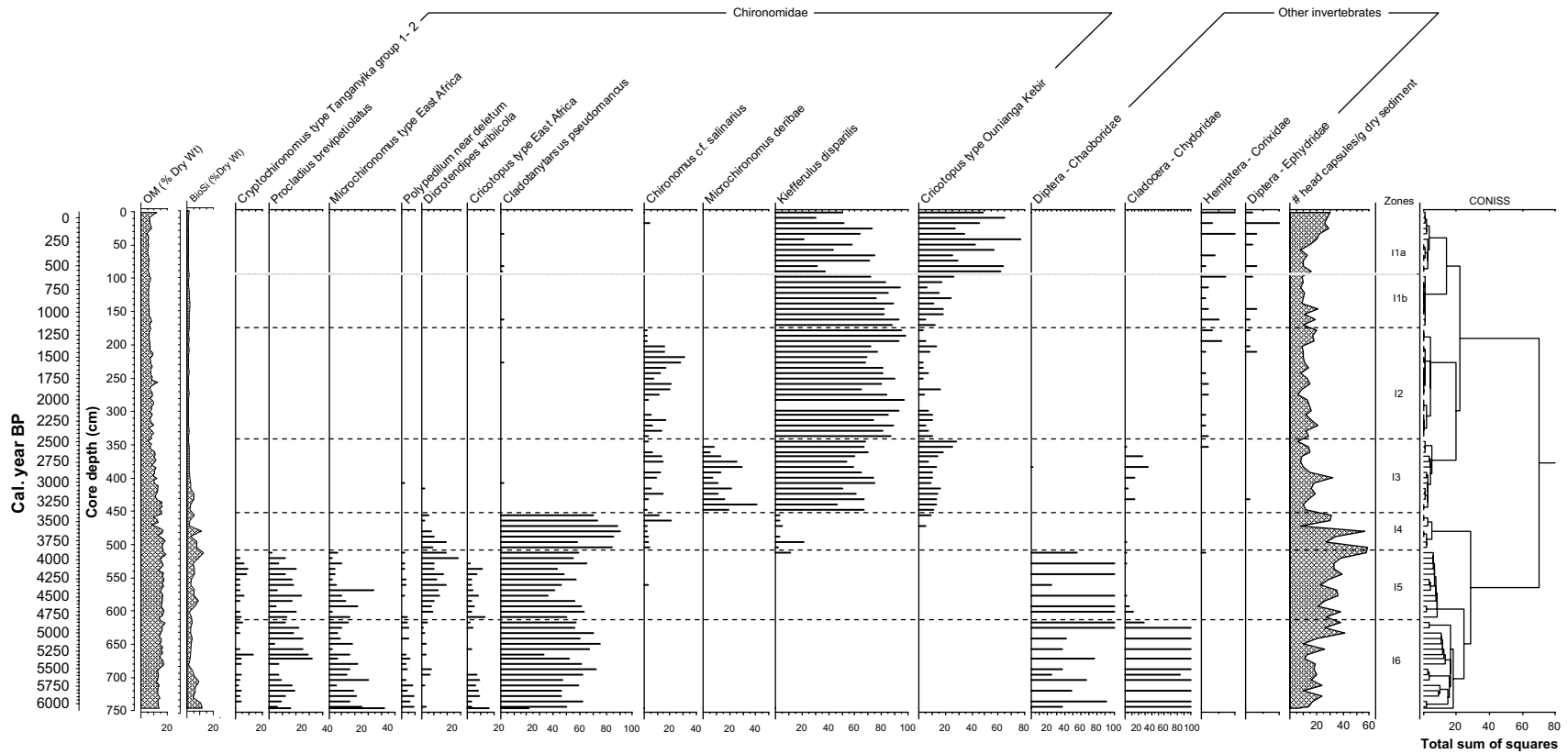
Fig. 4. Stratigraphic distribution of aquatic invertebrate remains in composite core OUNIK03/04. Taxa are arranged from left to right according to their increasing weighted-average conductivity optimum; taxa with fossil abundance less than 0.1% of the total fossil abundance are not illustrated. Horizontal lines indicate invertebrate zone boundaries determined by CONISS and the broken-stick model.

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 $3.9 \pm 6.8\%$ and $0.1 \pm 0.6\%$, 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 $9.3 \pm 6.6\%$ on average).

Past salinity variation in Lake Yoa as reconstructed by the various inference models is shown in Figs. 5 and 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: $0.42 \pm 0.01 \log_{10}$ CU; WA-PLS(2): $0.40 \pm 0.02 \log_{10}$ CU; WMAT-4: $0.44 \pm 0.05 \log_{10}$ CU) than in zones I3–I1 (WA: $0.45 \pm 0.01 \log_{10}$ CU; WA-PLS(2): $0.65 \pm 0.18 \log_{10}$ CU; WMAT-4: $0.45 \pm 0.03 \log_{10}$ 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 set also provides closer modern analogues for many I6–I4 samples, we mainly discuss model results based on the latter.

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 $\sim 30,000$ 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 $\sim 50,000$ 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 $\sim 25,000$ 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.

5. Discussion

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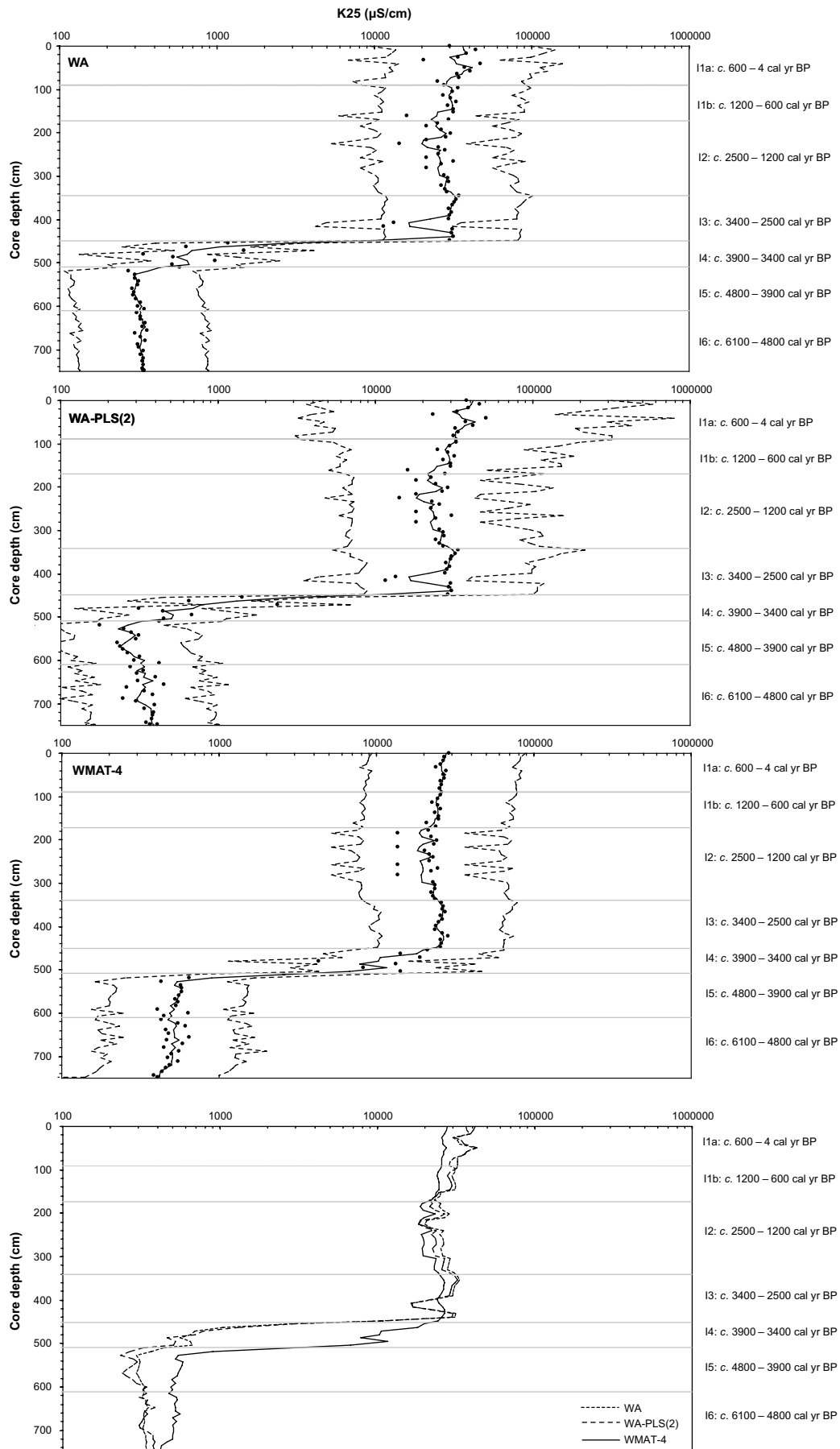
Fig. 5. Chironomid-inferred salinity reconstruction for Lake Yoa using the EL–WL calibration data set (K25 = specific conductance at 25 °C). Shown are output of WA, WA-PLS(2), and WMAT-4 inference models. A 3-point moving average (full line) highlights the major trends in the data; uncertainty ranges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

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; Langton and Visser, 2003), and among these *C. ornatus* is considered a true halobiont (Hirvenoja, 1973; 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; 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; 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.

5.2. Comparison of model outputs

Several studies (Walker et al., 1997; Lotter et al., 1999; Paterson et al., 2002; 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.
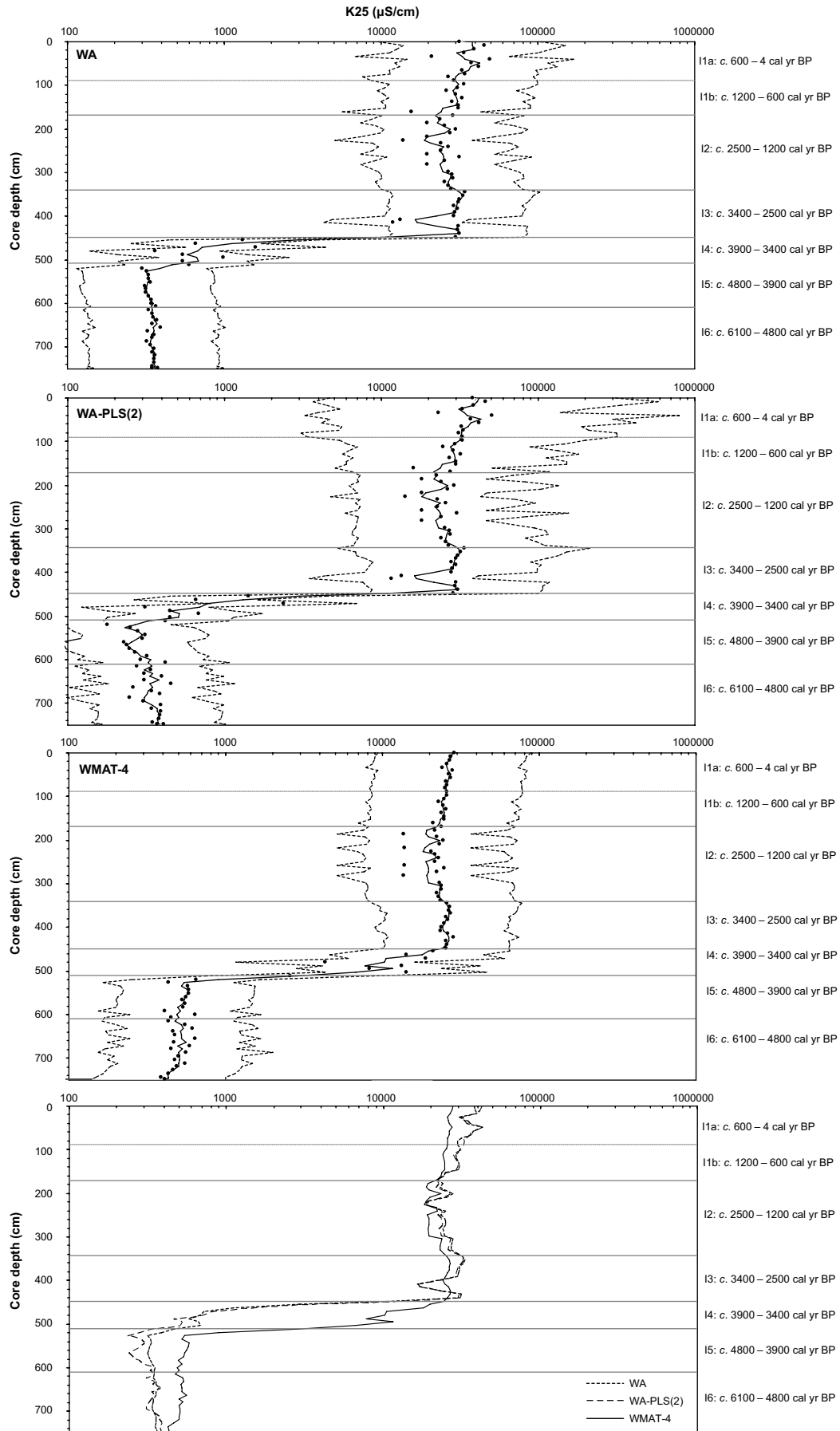
Fig. 6. Chironomid-inferred salinity reconstruction for Lake Yoa using the EL–WL–S calibration data set (K25 = specific conductance at 25 °C). Shown are output of WA, WA-PLS(2), and WMAT-4 inference models. A 3-point moving average (full line) highlights the major trends in the data; uncertainty ranges (dotted line) are the sample-specific prediction errors.

5.3. Middle and Late Holocene evolution of Lake Yoa

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; 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 known to tolerate salinities up to ~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 temporally 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; 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
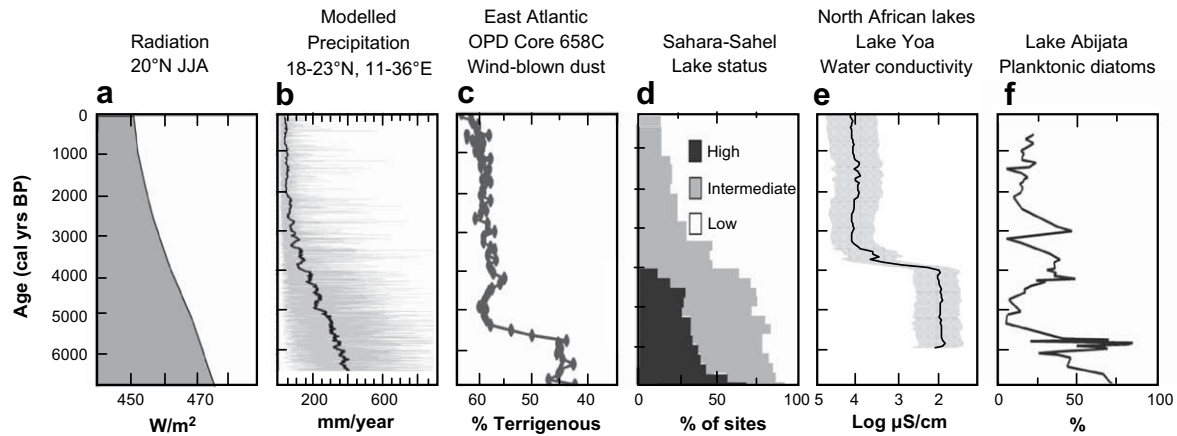
Fig. 7. Comparison of climate forcing, modeling results and paleodata describing the aridification of the Sahara over the past 7000 years, modified after Liu et al. (2007). (a) Summer (June–August) insolation at 20° N (Berger and Loutre, 1991). (b) Simulated precipitation over the eastern Sahara (18–23° 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, 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 (Chalié and Gasse, 2002).

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; 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*.

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; 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; 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; Gasse, 2002; see Fig. 7f), and significant moisture-balance fluctuation in the last 1500 years (Holmes et al., 1997; Street-Perrott et al., 2000; Hoelzmann et al., 2004).

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; 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.

Acknowledgments

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