Quantitative reconstruction of past salinity variations in African lakes: assessment of chironomid-based inference models (Insecta: Diptera) in space and time

Dirk Verschuren, Brian F. Cumming, and Kathleen R. Laird

Abstract: Faunal records of 20 common midge species (Diptera: Chironomidae) in 32 African surface waters with salinities ranging from 20 to 41 000 $\mu S \cdot cm^{-1}$ were used to develop inference models for quantitative reconstruction of past salinity variations from larval chironomid fossils preserved in lake sediments. Weighted-averaging regression and calibration models using presence–absence data (P/A) and presence–absence data with tolerance down-weighting (P/A_{tol}) produced bootstrapped coefficients of determination (r^2) of 0.78 and 0.81, respectively, and root mean squared errors (RMSE) of prediction of 0.42 and 0.39 log conductivity units. Historical conductivity data from African lakes are scarce. Therefore, model performance was tested in time by comparing chironomid-inferred conductivity estimates with the corresponding diatom-inferred estimates in sediment records of two fluctuating lakes in the Rift Valley of Kenya. A hybrid procedure in which presence–absence calibration models were applied to abundance-weighted fossil data yielded significantly higher correlation between chironomid- and diatom-inferred time series (Lake Oloidien AD 1880–1991, r^2 = 0.76–0.78; Crescent Island Crater AD 900–1993, r^2 = 0.56–0.61) than by applying the same models to presence–absence fossil data (r^2 = 0.47–0.56 and 0.26–0.42, respectively). Overall, model performance confirms that Chironomidae are valuable bioindicators for natural and man-made changes in the water balance of African lakes.

Résumé : Nous avons combiné les données de la répartition de 20 espèces de moucherons (Diptères: Chironomidae) dans 32 lacs africains aux salinités mésurant entre 20 $\mu S \cdot cm^{-1}$ et 41 000 $\mu S \cdot cm^{-1}$ avec des données chimiques de ces lacs et développé des modèles de déduction pour la reconstruction de variations de salinité à partir d'assemblages de chironomides fossiles préservés dans les sédiments lacustres. Les modèles de régression et d'étalonnage à pondération de moyenne utilisant des donneés présence–absence (P/A) ou présence–absence avec minorisation des tolérances (P/A_{tol}) produisaient des coefficients de détermination (r^2) de 0,78 et 0,81 et des erreurs quadratique moyenne bootstrap (RMSE) de 0,42 et 0,39. De mesures historiques de salinité provenant des lacs Africains étant assez rare, les testes de performance de ces modèles dans le domaine temporel ont été fait aussi par comparer les estimations de salinité passées déduites des chironomides avec celles déduites des diatomées dans les enregistrements paléolimnologiques de deux lacs fluctuants dans la Vallée du Rift au Kenya. Un procédé hybride applicant les modèles d'étalonnage présence–absence aux données fossiles d'abondances ponderées a réalisé des corrélations (Lake Oloidien AD 1880–1991, r^2 = 0,76–0,78; Crescent Island Crater AD 900–1993, r^2 = 0,56–0,61) supérieures aux celles obtenus par applicant les mêmes modèles aux données fossiles présence–absence. La performance de ces modèles confirme le potentiel des Chironomides fossiles en tant qu'indicateurs aux changements climatiques et anthropogènes de la hydrologie des lacs africains.

Introduction

Sediments accumulating on the bottom of fluctuating lakes are a major source of information on past climate change in subhumid and semiarid regions worldwide. Long-term variation in the regional balance of rainfall and evaporation (i.e., effective moisture integrated over the drainage basin) drives changes in lake level and water chemistry, which in turn influence sedimentation, oxygenation, nutrient cycling, and the osmotic stress to which aquatic biota are exposed. If limnological conditions permit undisturbed sediment accumulation over a sufficiently long period of time despite climate-driven lake-level changes (Dearing 1997; Verschuren 1999), lake-system response to climate change is incorporated in

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the sediment record as a datable sequence of characteristic sedimentological, geochemical, and biological signatures. This allows the sediment record to be used as a natural archive from which the history of past climate change can be reconstructed (Smol et al. 1991).

Accurate, quantitative reconstruction of climate history from lake-sediment records requires calibration of the relationships between the various sedimentary climate indicators and climate-driven changes in water balance. For biological climate indicators (e.g., diatoms, chrysophytes, ostracods, and chironomids), this most often involves the development of transfer functions (Birks et al. 1990), which mathematically describe the modern distribution of individual species across a representative collection of lakes in relation to select environmental variables that reflect a lake's hydrological status (e.g., depth or salinity). Over the past decade, these numerical methods have evolved to include robust procedures for error estimation and are now an established research tool in biological paleolimnology (Birks 1998). Nevertheless, statistical inference of past climate always carries significant uncertainty, even when the link between a particular climate indicator and climate has been validated through comparison with instrumental climate or lake-monitoring data (e.g., Laird et al. 1996). This is because linkages between aquatic community structure (more specifically, its preserved fossil counterpart) and climate-driven changes in water balance are often complex and characterized by threshold effects (Smol and Cumming 2000). Much effort is currently directed at generating multiple time series of (quasi-) independent climate-indicator data from physical, biological, and geochemical sources in the same lake-sediment record on the premise that an integrated evaluation of these multiple lines of evidence should allow a more coherent and trustworthy reconstruction of past climate.

Fossil diatoms are among the biological indicators most widely used in climate reconstruction (Stoermer and Smol 1999), and in Africa they are currently the best-studied biological indicators for climate-driven changes in lake water balance (Fritz et al. 1999). Fossil midge larvae (Diptera: Chironomidae), in contrast, had until recently been little exploited as a biomonitoring tool for past environmental change in Africa (Walker 1995), although they are well-established indicators of late Quaternary climate change in north-temperate regions (e.g., Levesque et al. 1993; Brooks et al. 1997; Brooks and Birks 2000). As in diatoms, chironomid species distribution in tropical aquatic ecosystems is strongly influenced by salinity (Pinder 1995), both directly due to variable tolerance to the osmotic stress caused by high and (or) fluctuating salinity (Bayly 1972) and indirectly due to the role of salinity in the distribution of suitable substrates and food (Williams 1984). The dominant influence of salinity on chironomid faunal composition in African lakes is amply documented by regional surveys (e.g., Tudorancea et al. 1989) and field studies of shallow lakes going through multiyear cycles of lake-level decline and recovery (McLachlan 1979; Vareschi and Vareschi 1984). Paleolimnological sensitivity studies (Verschuren et al. 1999*a*, 2000*a*) likewise demonstrated rapid restructuring of chironomid faunas in response to climate-driven changes in lake depth, salinity, or mixing regime. African Chironomidae are already being used in paleoenvironmental reconstructions (Mees et al. 1991; Verschuren et al. 1999*b*, 2002), but mainly through a qualitative, indicator-species approach. Quantitative chironomid paleoecology in Africa is hampered by inadequate knowledge of species' habitat preferences and environmental tolerances. This situation could be improved through standardized collection of linked faunal and environmental data from a suitably large number of African lakes, but political and logistic factors render rapid completion of such a reference data set unlikely.

In the context of lake-based climate reconstruction in East Africa (Verschuren et al. 2000*b*), we developed quantitative conductivity-inference models based on published presence–absence (P/A) data of 20 common species of Chironomidae in 32 African surface waters. In this paper, we assess the performance of these models in space and time by (*i*) examining associated statistical parameters; (*ii*) comparing chironomid-inferred conductivity estimates with instrumental conductivity data spanning the past 70 years; and (*iii*) comparing chironomid- and diatom-inferred conductivity estimates in the sediment records of two lakes in Kenya that cover 200 and 1100 years of environmental history. Performance assessment in time, in particular, is critical to determine the real potential and applicability of a biological inference model in paleoenvironmental reconstruction.

Methods

Chironomid calibration data set

We compiled data on the modern distribution of African Chironomidae in relation to salinity from 37 published species lists (1–13 species; mean = 3.8) from 32 African surface waters (29 lakes, two reservoirs, and one slow-flowing river), ranging from 20 to 41 000 $\mu S \cdot cm^{-1}$ (Table 1). Many of the surveyed lakes are large to very large, reflecting a historical research bias for lakes with socio-economic significance (Hare and Carter 1987). Most shallow African lakes are hydrologically closed (Livingstone and Melack 1984) or river-fed amplifier systems (Street-Perrott and Roberts 1983) characterized by significant long-term variation in depth, surface area, and water chemistry. When chemistry data from the time of collection were not available, we used the mean of historical conductivity values when variation was low (Opi, 15–25 $\mu S \cdot cm^{-1}$; Upemba, 145–255 $\mu S \cdot cm^{-1}$; George, 165–207 $\mu S \cdot cm^{-1}$; Baringo, 460–530 $\mu S \cdot cm^{-1}$; Langano, 1643–1728 $\mu S \cdot cm^{-1}$; Chitu, 40 000 – 40 810 $\mu S \cdot cm^{-1}$). In lakes with significant conductivity variation (Oloidien, 472–2900 $\mu S \cdot cm^{-1}$; Chilwa, 300–12 000 $\mu S \cdot cm^{-1}$; Nakuru, 11 000 – 160 000 $\mu S \cdot cm^{-1}$), collections without linked conductivity data were excluded, and collections from periods of distinctly different conductivity were treated separately. We also excluded faunal surveys based on light trapping of adult midges because such collections cannot be linked with certainty to a specific aquatic larval habitat.

Diatom calibration data set and conductivity-inference model

The African diatom calibration data set consists of 274 modern diatom floras and linked water-chemistry data from 164 African surface waters ranging from 40 to ~100 000 $\mu S \cdot cm^{-1}$ (Gasse et al. 1995). This data set was created by combining regional data sets from Northwest Africa,

Table 1. Geographical and conductivity data on 32 surface waters in tropical Africa with studied collections of chironomid larvae.

No.	Name	Type	Latitude	Longitude	Area (ha)	Conductivity (μS·cm^{-1})
1	Opi	Fluvial	06°45′N	07°29′E	2	20
2	Chari	River	12°03′N	15°00′E	na	60
3	Kariba	Rreservoir	17°00′S	28°00′E	525 000	75
4	Victoria	Tectonic	01°00′S	33°00′E	6 880 000	98
5	Chad South	Tectonic	12°55′N	14°15′E	950 000	108
6	George	Tectonic	00°00′N	30°13′E	25 000	186
7	Upemba	Tectonic	08°40′S	26°20′E	53 000	200
8	Koka	Reservoir	08°23′N	39°04′E	1 5 000	224
9	Naivasha	Tectonic	00°45′S	36°20′E	17 100	308
10	Ziway	Tectonic	08°00′N	38°50′E	43 400	350
11	Chilwa	Tectonic	15°20′S	35°40′E	70 000	250; 2 500[a]
12	Baringo	Tectonic	00°37′N	36°05′E	13 000	495
13	Chad North	Tectonic	13°35′N	13°40′E	950 000	525
14	Tanganyika	Tectonic	06°00′S	29°30′E	3 290 000	606
15	Oloidien	Tectonic	00°47′S	36°16′E	574	620
16	Albert	Tectonic	01°40′N	31°00′E	559 000	730
17	Abaya	Tectonic	06°20′N	37°50′E	116 200	800
18	Awasa	Tectonic	07°03′N	38°24′E	8 800	868
19	Edward	Tectonic	00°20′S	29°35′E	215 000	925
20	Chamo	Tectonic	05°50′N	37°34′E	55 100	1 078
21	Kivu	Tectonic	02°00′S	29°07′E	237 000	1 240
22	Langano	Tectonic	07°36′N	38°45′E	23 000	1 686
23	Djiboulboul	Interdunal	13°45′N	14°30′E	Fragmented	2 600
24	Sonachi	Maar crater	00°47′S	36°16′E	14	3 000
25	Aranguadi	Maar crater	00°45′N	39°00′E	54	5 100
26	Kilotes	Maar crater	00°45′N	39°00′E	77	6 300
27	Nakuru	Tectonic	00°22′S	36°05′E	4 200	11 000 – 28 000[b]
28	Abijata	Tectonic	07°36′N	38°36′E	20 500	15 120
29	Shala	Tectonic	07°28′N	38°31′E	40 900	22 470
30	Bogoria	Tectonic	00°16′N	36°09′E	3 300	35 700
31	Elementeita	Tectonic	00°27′S	36°05′E	1 800	38 000
32	Chitu	Maar crater	07°24′N	38°25′E	80	40 405

Note: Lake surface-area values are approximate, since many lakes fluctuate considerably between years. Conductivity values are those linked directly to the chironomid collections; in saline lakes, known historical ranges are often significantly larger. Primary references for the collections and linked water-chemistry data are given in Verschuren (1997). na, not applicable.

[a] $n = 2$.

[b] $n = 5$.

East Africa, and Niger and includes both live and recently buried diatom assemblages from various inland aquatic environments, including lakes, swamps, bogs, and springs. Diatom-based conductivity estimates were calculated with a weighted-averaging regression and calibration model that with inverse deshrinking, has a jackknifed coefficient of determination (r^2) of 0.81 and a root mean squared error (RMSE) of prediction of 0.39 log conductivity units.

Chironomid-based conductivity-inference models

The chironomid-based conductivity-inference models are derived from P/A data of 20 species (= taxa) at 37 different values (= sites) of surface-water conductivity. Conductivity values were log-transformed before model development to compensate for their skewed distribution towards low conductivity values. The mean and standard deviation of each species' reported conductivity range were used as estimates of its conductivity optimum and tolerance, respectively. Consequently, species with narrow tolerances in the model are either species with narrow preferences or species reported from few sites. Two species with only one confirmed occurrence each (*Psectrocladius viridescens* and *Chironomus alluaudi*) were retained for model calibration because of their high abundances in the fossil data sets available for model testing. Using the computer program WACALIB v. 3.5 (Line et al. 1994), we developed two types of models: one based on estimated conductivity optima (P/A models) and one based on estimates of both optima and tolerances (P/A$_{\mathrm{tol}}$ models). In the latter, *Psectrocladius viridescens* and *Chironomus alluaudi* are effectively removed from calculations because WACALIB 3.5 awards species with single occurrences in the calibration data set a default tolerance range that is several orders of magnitude larger than that of other species. In both P/A and P/A$_{\mathrm{tol}}$ models, an inverse deshrinking step was used to rescale the conductivity estimates (Line et al. 1994). Conductivity inference from fossil assemblages was done (*i*) directly on fossil percent-abundance data and (*ii*) after transforming fossil percent-abundance data to P/A data. We refer to the former as hybrid model applications, because the P/A and P/A_{tol} models are calibrated using modern P/A data, but then each species in a fossil assemblage is given a weight proportional to its percent abundance. These applications should be considered as exploratory, as no sample-specific error estimates can be generated from data expressed on two different scales.

Assessment of model performance in space and time

We evaluated the capacity of our inference models to predict the modern conductivity of reference lakes from their r^2 and RMSE values and from the distribution of residuals. For this analysis, we used conductivity estimates generated through bootstrapping (Line et al. 1994) to avoid a possibly misleading inflation of the predictive ability of transfer functions that occurs when the same samples and lakes are used for model development and evaluation (Birks et al. 1990). We assessed model performance in a temporal context through comparisons of the conductivity estimates based on fossil chironomids with historical conductivity measurements and with conductivity estimates based on fossil diatoms. For these analyses, we used sediment-core data from Lake Oloidien (Verschuren et al. 1999*b*) and Crescent Island Crater (Verschuren et al. 2000*b*) and a compilation of historical water-chemistry data from these lakes (Verschuren 1996). The fossil and historical data are linked through core chronologies based on ^{210}Pb dating and anchored in a sequence of marker horizons reflecting historical events (Verschuren 1999). The fossil data from Lake Oloidien comprise 23 paired chironomid and diatom assemblages extracted at 4-cm intervals from core NO91.1-S, which covers the last ~200 years; the historical period (1883–1991) is covered by 18 paired samples. The fossil data set totals 3023.5 specimens (15–312.5 per sample, mean = 131.5), of which 99.2% is identified to species with reference to Verschuren (1997) and the primary literature mentioned therein. Twenty-seven species were found; the subset of 14 species that are represented in our calibration data set accounts for 96.9% (range 91.2%–100% per sample) of the fossil inventory. Crescent Island Crater fossil data comprise 149 paired chironomid and diatom assemblages extracted at 4-cm intervals in the upper 602 cm of core NC93.2-L, which covers the last ~1100 years; the historical period (1883–1993) is covered by 30 samples. This fossil data set totals 9264.5 specimens (4.5–188 per sample, mean = 62.2), of which 99.8% is identified to species. Twenty-five species were found; the 13 species represented in the calibration data set account for 97.5% (range 87.3%–100%) of the fossil inventory. Our comparison of conductivity-inference models used all 23 paired chironomid and diatom assemblages from Lake Oloidien and 130 paired assemblages from Crescent Island Crater. In the latter record, 20 intervals from near the surface and between 192- and 264-cm depth were combined two-by-two to obtain a chironomid fossil count of at least 20 specimens; nine samples from thick monospecific diatom mats (Verschuren et al. 2000*b*) were omitted because they likely represent short-term sedimentation events.

Results

Chironomid calibration data set

The species in the calibration data set were present at 1–15 sites (mean = 7.1). The estimated conductivity optimum of most species is below 1000 μS·cm^{-1}, and tolerances typically span an order of magnitude (Fig. 1). Only three taxa, *Microchironomus deribae*, *Kiefferulus disparilis*, and *Tanytarsus minutipalpis*, have optima above 5000 μS·cm^{-1} and can be considered halobiontic. *Cladotanytarsus pseudomancus* is euryhaline, occurring throughout the freshwater range and in saline waters up to 21 000 μS·cm^{-1}. Weighted-averaging inference models based on these P/A data possess high coefficients of determination (r^2_{boot} = 0.78–0.81) and fairly low RMSEs of prediction (0.39–0.42 log conductivity units; Fig. 2). However, uneven distribution of the prediction error along the conductivity gradient (i.e., systematic variation in the difference between observed and inferred values) show that both the P/A and P/A_{tol} models are rather insensitive to conductivity variation within a broad range of fresh waters. Transition from fresh to saline waters appears characterized by wholesale species replacement around 3000 μS·cm^{-1}.

Lake Oloidien fossil record

We previously found good agreement between conductivity estimates inferred from fossil diatom assemblages and independent historical data (Verschuren et al. 1999*b*). Briefly, maximum inferred values of 12 700 – 13 600 μS·cm^{-1} (Figs. 3*a*–3*b*) during the mid-19th century agree with early reports from Maasai herdsmen that Lake Oloidien was not suited to water their cattle. Given the model-specific prediction error of 0.39 log conductivity units (Gasse et al. 1995), minimum inferred values of 300–350 μS·cm^{-1} during the early 20th century high stand, when Lake Oloidien was confluent with the main basin of Lake Naivasha, agree well with a measured value of 472 μS·cm^{-1} from Lake Oloidien in 1930 and values of 320–431 μS·cm^{-1} from Lake Naivasha in 1929–1931. Diatom-inferred values of 540–890 μS·cm^{-1} during recent decades also agree with measured values of 620–1040 μS·cm^{-1} for the period 1973–1984. Decreasing values of inferred conductivity to 540 μS·cm^{-1} at the sediment surface suggest that recently buried fossil assemblages do not yet reflect the renewed rise of lake-water conductivity during the late 1980s (to ~1200 μS·cm^{-1} in 1991, when the core was collected). No instrumental conductivity data are available from during or shortly after the low stand of 1946–1957, so it is uncertain whether the diatom-inferred high of 6500 μS·cm^{-1} towards the end of that low stand was in fact reached. Strong reductions in most freshwater invertebrates at that time, among the Chironomidae as well as other groups (Verschuren et al. 1999*b*), suggest that conductivity did exceed 3000 μS·cm^{-1}, a common physiological limit for aquatic invertebrates (Hammer 1986).

During the past 200 years, the chironomid community of Lake Oloidien experienced several distinct shifts (Fig. 4). Assemblages from before ~1890 are characterized by the presence of halobiontic species such as *Microchironomus deribae* and *Kiefferulus disparilis* and peak abundance of the euryhaline *Cladotanytarsus pseudomancus*. A silty clay horizon at the bottom of the core, representing intermittent lake desiccation before ~1840, is dominated by the halobionts, in

Fig. 1. Range and average documented conductivity of 20 common Chironomidae in African lakes (thin lines and step, with number of records), with means and standard deviations of log-transformed values (thick lines and solid circles) as used in the inference models.

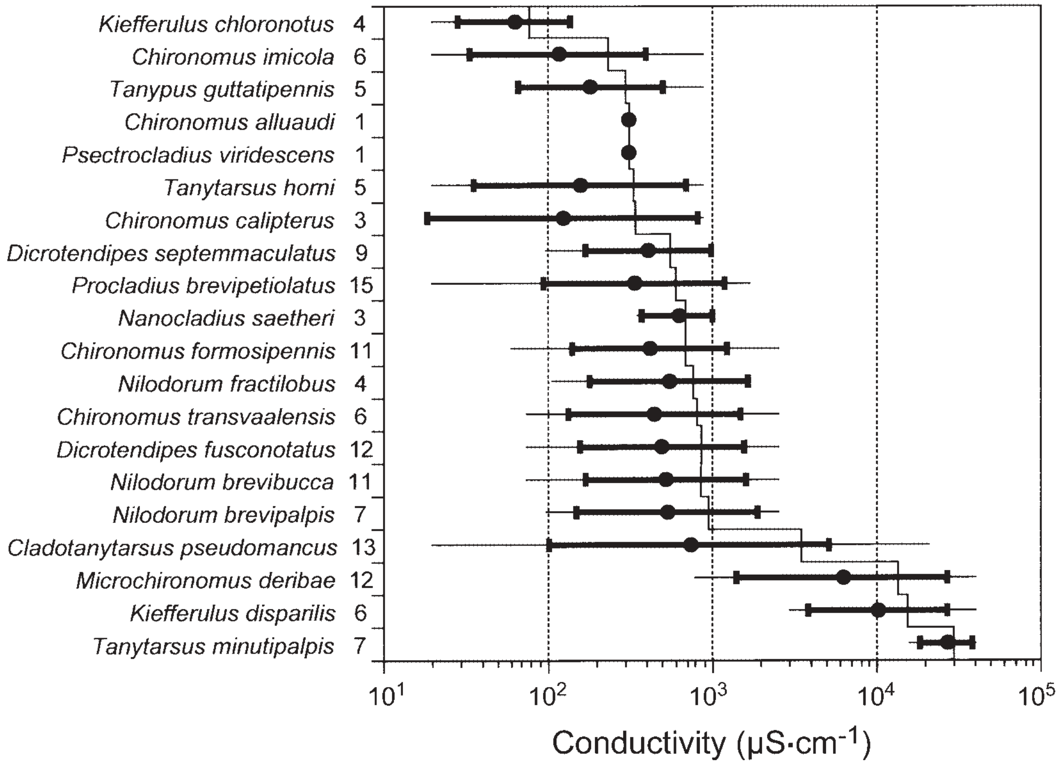
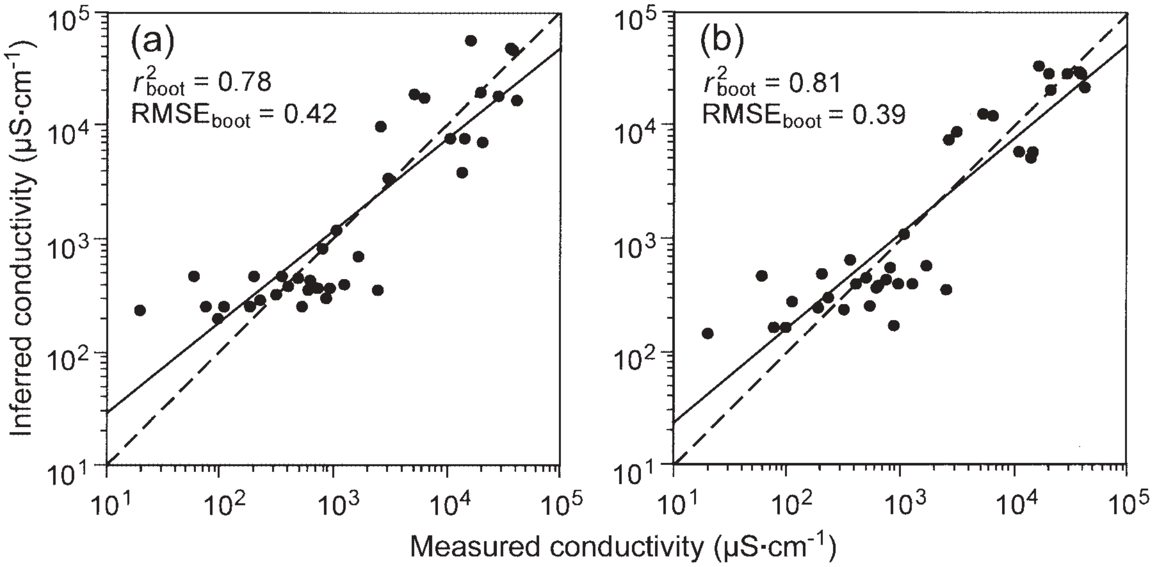


Fig. 2. Chironomid-inferred versus observed conductivity in modern African lakes (n = 37) based on presence–absence calibration models without (*a*: P/A) and with (*b*: P/A$_{tol}$) species down-weighing proportional to their tolerance, using inverse deshrinking and bootstrapping. Solid line, linear regression; broken line, equality between observed and predicted values.



particular *Tanytarsus minutipalpis*. In contrast, assemblages dated between 1890 and 1940 are characteristic of freshwater conditions, with peak abundances of *Tanytarsus horni* and *Dicrotendipes septemmaculatus*. Between ~1940 and 1970, these are displaced again by more salt-loving and salt-tolerant species. Chironomid assemblages in the top 20 cm of the core reflect the return of freshwater conditions after ~1970.

Chironomid-inferred conductivity estimates for Lake Oloidien (Figs. 3*c*–3*f*) are within the prediction error of available instrumental data, except that surface-sediment assemblages also fail to reflect the renewed rise of lake-water conductivity during the late 1980s. Conductivity values of 475 and 345 μS·cm^{-1} inferred for ~1930 using the simple P/A and P/A$_{tol}$ models match the measured range of 320–472 μS·cm^{-1}, and values of 400–845 μS·cm^{-1} for ~1970–

Fig. 3. Chironomid-inferred reconstructions of past conductivity variations in Lake Oloidien (Kenya) compared with diatom-inferred conductivity estimates and historical measurements. (*a*) Lake-level change over the past ~200 years (solid and stippled lines) relative to the elevation of the sill separating Lake Oloidien from Lake Naivasha (broken line; Verschuren 1999). (*b*) Diatom-inferred conductivity reconstruction using the inference model of Gasse et al. (1995), compared with historical measurements (diamonds). (*c–f*) Chironomid-inferred conductivity reconstructions using presence–absence calibration models without (*c*, *e*: P/A) and with (*d*, *f*: P/A_{tol}) tolerance down-weighing applied to fossil presence–absence data (*c*, *d*: simple P/A and P/A_{tol}) and fossil percent-abundance data (*e*, *f*: hybrid P/A and P/A_{tol}).

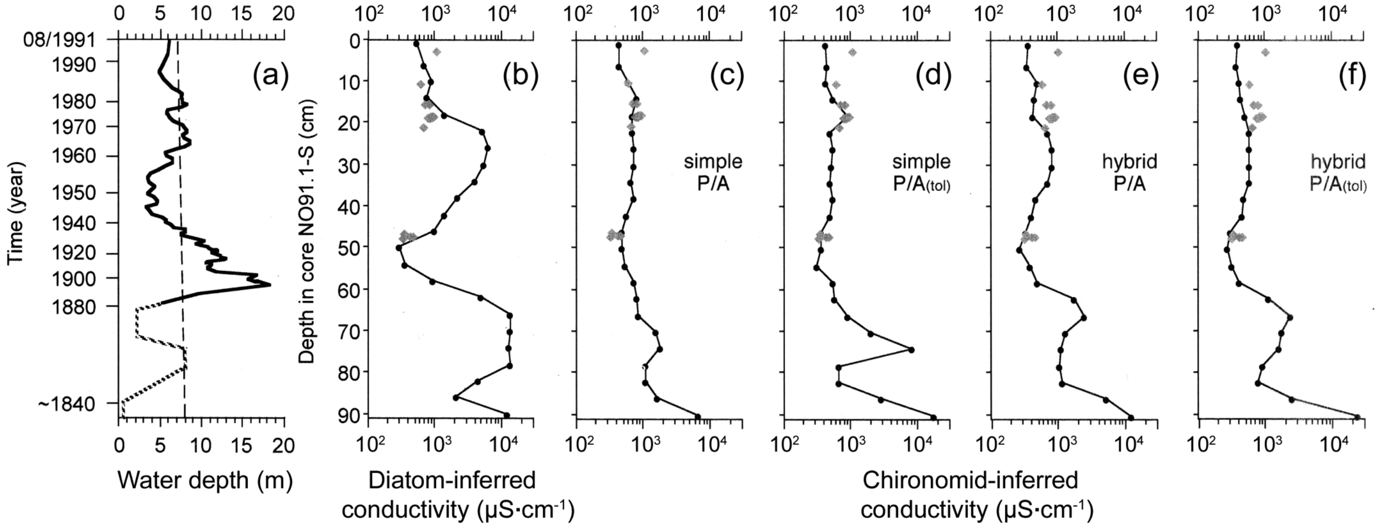
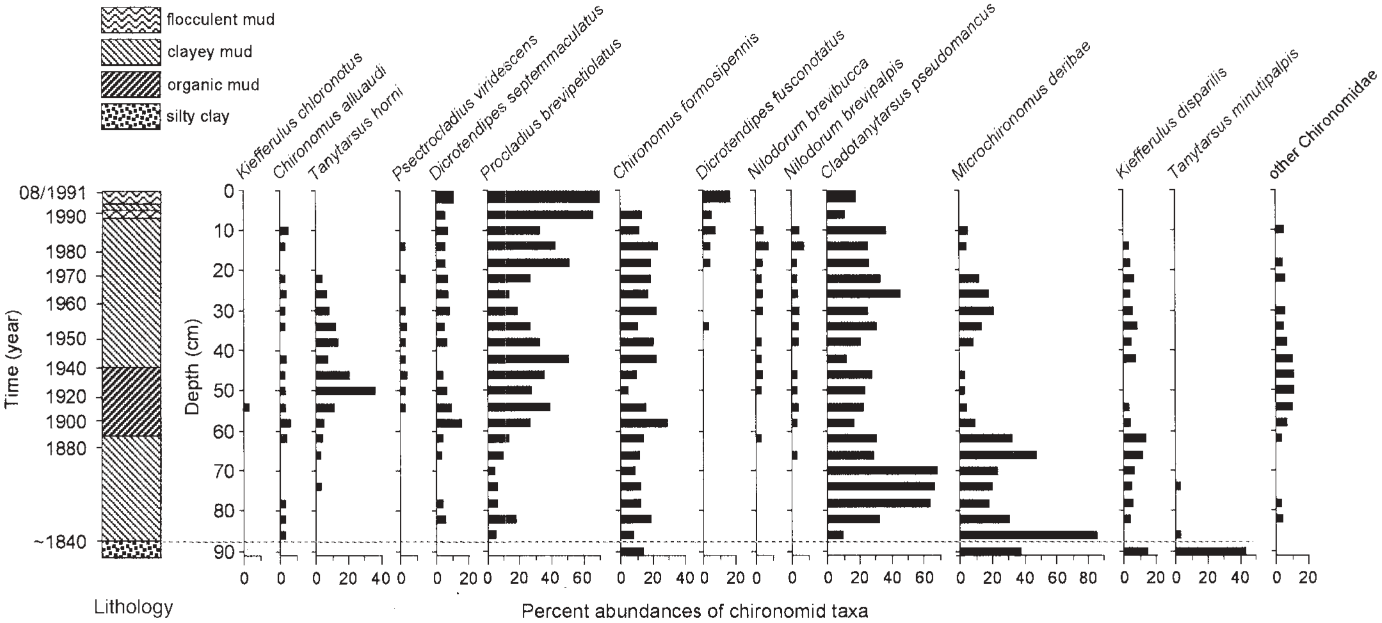
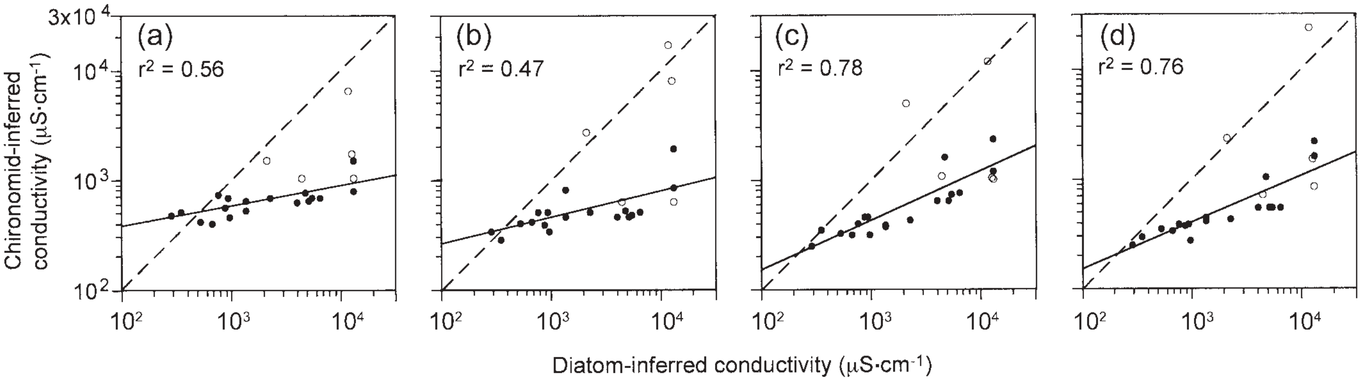


Fig. 4. Lithology of core NO91.1-S from Lake Oloidien (Kenya) and down-core distribution of fossil larval Chironomidae. Species are arranged from left to right in order of increasing salinity optima.



1985 overlap with the measured range of 620–1040 µS·cm^{-1}. Using the hybrid P/A and P/A_{tol} models, inferred values of 320 and 285 µS·cm^{-1} for 1930 match the measured range, but values of 380–650 µS·cm^{-1} for the period 1970–1985 fall below it. Strikingly, chironomid-inferred estimates of peak conductivity during episodes of low lake level fall consistently below the corresponding diatom-inferred estimates, no matter which model is used. They range from 515 to 780 µS·cm^{-1} for the mid-20th century lowstand, when diatom-inferred peak conductivity is 6500 µS·cm^{-1}, and from 1750 to 8200 µS·cm^{-1} during the mid-19th century, when diatom-inferred conductivity is 12 700 – 13 600 µS·cm^{-1}. An exception is the pre-1840 desiccation phase, when dominance of halobiontic species is translated into conductivity estimates ranging between 6700 and 23 500 µS·cm^{-1} compared with ~13 000 µS·cm^{-1} inferred from diatoms. Correlation between chironomid- and diatom-inferred conductivities (Figs. 5*a*–5*d*) is good for the section representing the historical period (r^2 = 0.47–0.78, n = 18, $p < 0.01$ in all cases), but more modest when pre-1880 samples are included (r^2 =

Fig. 5. Correlations between chironomid-inferred and diatom-inferred conductivity for the historical part of the Lake Oloidien record (1880–1991; $n = 18$) using (*a*, *b*) simple and (*c*, *d*) hybrid presence–absence models without (*a*, *c*: P/A) and with (*b*, *d*: P/A_{tol}) tolerance down-weighing. Solid line, linear regression; broken line, equality of model solutions. Inferences for the prehistorical portion of the record were added as passive data points (open circles; $n = 5$).



0.33–0.48, $n = 23$, $p = 0.007 - 0.035$). Samples from the ~1840–1850 phase of lake filling deviate most strongly from the general relationship.

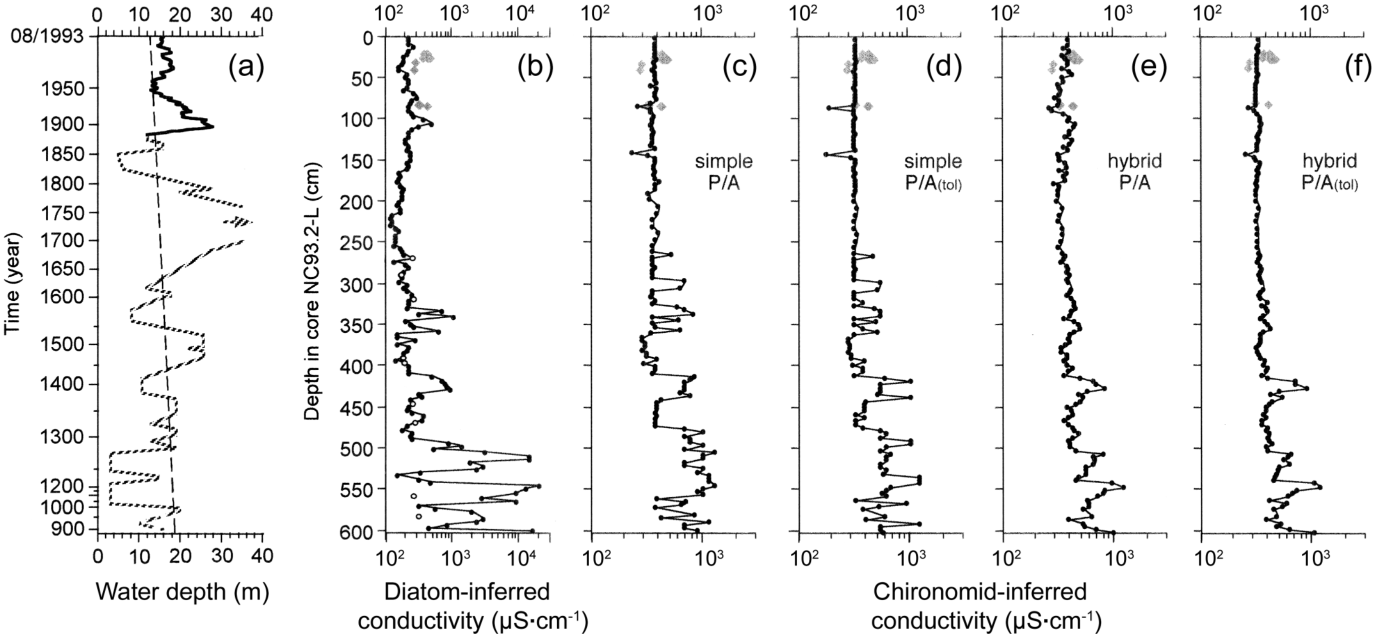
Crescent Island Crater fossil record

Crescent Island Crater is normally confluent with the main basin of Lake Naivasha, which is hydrologically open because it loses dissolved salts to the ground water (Gaudet and Melack 1981). Consequently, Crescent Island Crater has remained fresh during historical times, and local conductivity (1929–1980: 280–491 $\mu S \cdot cm^{-1}$, $n = 19$) has not been significantly different from that of Lake Naivasha (1929–1990: 233–499 $\mu S \cdot cm^{-1}$, $n = 42$). Diatom-inferred conductivity estimates (Fig. 6*b*) for the upper 120 cm of core NC93.2-L are consistent with these data, ranging between 166 and 313 $\mu S \cdot cm^{-1}$ (except for an excursion to ~500 $\mu S \cdot cm^{-1}$ at 100–110 cm, dated to ~1900). However, over the past 1100 years the level of Crescent Island Crater has repeatedly dropped below the sill separating it from Lake Naivasha, namely during the Medieval Climatic Optimum (~AD 1000–1270) and on three occasions during the Little Ice Age (~AD 1380–1420, 1560–1620, and 1810–1850; Verschuren et al. 2000*b*). Diatom-based reconstruction of water-chemistry changes (Fig. 6*b*) suggests hydrologic closure of the crater and strong evaporative concentration during such arid episodes, with conductivity rising up to 20 000 $\mu S \cdot cm^{-1}$ during the Medieval Climatic Optimum. However, during the most recent severe low stand (~AD 1810–1850), Crescent Island Crater appears to have remained fresh, presumably because the preceding 150-year period of broad confluence with Lake Naivasha had removed its accumulated burden of dissolved salts.

This eventful history of Crescent Island Crater over the past 1100 years is also reflected in the evolution of its chironomid fauna. Three freshwater species (*Procladius brevipetiolatus*, *Dicrotendipes septemmaculatus*, *Chironomus formosipennis*) and the salt-tolerant species *Cladotanytarsus pseudomancus* occur throughout the core profile, but their abundances fluctuate in well-defined decade-scale patterns of ups and downs. For example, during the episode of highest inferred lake level (~AD 1650–1800; Fig. 6*a*), *Dicrotendipes septemmaculatus* expanded to 60%–70% of the fossil assemblage at the expense of the three others. During episodes of lowest inferred lake level (e.g., ~AD 1000–1270), the salt-tolerant *Cladotanytarsus pseudomancus* expanded to 70%–80%. At other times, the abundance changes were more complex, but overall the occurrence of *Dicrotendipes septemmaculatus* and *Cladotanytarsus pseudomancus* in this fossil record is consistent with their modern ecology and with a local paleolimnological study of their habitat preferences (Verschuren et al. 2000*a*). The fossil occurrence of the halobiontic species *Microchironomus deribae* and *Kiefferulus disparilis* (Fig. 7) is largely restricted to the lower third of the core, during inferred lowstand episodes when diatoms indicate lake conductivity was well above the tolerance limit of typical freshwater taxa (Figs. 6*a*–6*b*). The pulsed disappearance of these halobionts after AD 1270 mirrors the expansion of the freshwater species *Psectrocladius viridescens*, which reached 60% abundance during the early 20th century. Other freshwater species such as *Tanytarsus horni* and *Nilodorum brevibucca* occurred in Crescent Island Crater only at certain times in the past.

In Crescent Island Crater, chironomid-inferred conductivity estimates for the last 120 years agree with the available instrumental data, averaging 300–400 $\mu S \cdot cm^{-1}$ depending on the model used. Characteristically, output from simple P/A and P/A_{tol} models (Figs. 6*c*–6*d*) displays a limited number of different conductivity values, equalling the number of species combinations in the fossil record. The effect is most pronounced in P/A_{tol} model output, because *Chironomus alluaudi* and *Psectrocladius viridescens* have negligible influence on model calculations (because of their single occurrence in the calibration data set), effectively reducing species diversity and the number of possible species combinations. For example, in the simple P/A_{tol} model, a value of 330 $\mu S \cdot cm^{-1}$ is generated whenever samples only contain *Dicrotendipes septemmaculatus*, *Procladius brevipetiolatus*, *Chironomus formosipennis*, and *Cladotanytarsus pseudomancus*, besides *Chironomus alluaudi* and *Psectrocladius viridescens*. Isolated minima of 184 and 198 $\mu S \cdot cm^{-1}$ at depths of 140 and 84 cm reflect the two occurrences of *Kiefferulus chloronotus*, which in the calibration data set is limited to the most dilute lakes (<108 $\mu S \cdot cm^{-1}$). Output from the hybrid model applications (Figs. 6*e*–6*f*) displays significantly more detail, including a discernable signal of lowest conduc-

Fig. 6. Chironomid-inferred reconstructions of past conductivity in Crescent Island Crater (Kenya) compared with diatom-inferred estimates and historical measurements. (*a*) Lake-level change over the past ~1100 years (solid and stippled line) relative to the elevation of the sill separating Crescent Island Crater from Lake Naivasha (broken line; Verschuren 2001). (*b*) Diatom-inferred conductivity reconstruction using the inference model of Gasse et al. (1995), compared with historical measurements (diamonds). (*c*–*f*) Chironomid-inferred conductivity reconstructions using presence–absence calibration models without (*c*, *e*: P/A) and with (*d*, *f*: P/A$_{tol}$) tolerance down-weighing applied to fossil presence–absence data (*a*, *b*: simple P/A and P/A$_{tol}$) and fossil percent–abundance data (*c*, *d*: hybrid P/A and P/A$_{tol}$).



tivity values coinciding with peak lake level during AD 1650–1780 (180- to 280-cm depth). This signal is slightly more pronounced in hybrid P/A model output than in hybrid P/A$_{tol}$, because in the latter the influence of the highly salt-tolerant *Cladotanytarsus pseudomancus* on model calculations is muted.

Chironomid- and diatom-inferred conductivity estimates for Crescent Island Crater are significantly correlated (r^2 = 0.26–0.61, n = 130, $p < 0.01$ in all cases), with hybrid model applications yielding the best correlations (Fig. 8). As in Lake Oloidien, peak chironomid-inferred conductivity values tend to be lower than the corresponding diatom-inferred estimates. During the Medieval Climatic Optimum, chironomid-inferred conductivity remains mostly below 1500 $\mu S \cdot cm^{-1}$ (Figs. 6*c*–6*f*), whereas diatom-inferred conductivity reaches up to 20 000 $\mu S \cdot cm^{-1}$. Similarly, during the lowstand of AD 1560–1600, diatoms infer a distinct peak of ~1000 $\mu S \cdot cm^{-1}$, whereas chironomid-inferred conductivity barely differs from background freshwater values of 300–400 $\mu S \cdot cm^{-1}$ except in the simple P/A model (Fig. 6).

Discussion

The coefficients of determination (bootstrapped r^2 = 0.78–0.81) and RMSEs of prediction (0.39–0.42 log conductivity units) of the hybrid P/A and P/A$_{tol}$ conductivity-inference models are comparable to those of a model based on Chironomidae from western Canada (bootstrapped r^2 = 0.72, RMSE = 0.52; Walker et al. 1995) and models based on African diatoms (jackknifed r^2 = 0.80–0.81, RMSE = 0.39–0.44; Gasse et al. 1995). Tandem application of diatom- and chironomid-based inference models on the same sediment records can greatly increase trust in the validity of reconstructed paleoenvironmental change and may help identify situations where diatom-based inferences are unreliable because of poor diatom preservation (Barker et al. 1990). Strong correlation between chironomid- and diatom-inferred conductivity estimates in both test records, when applying the hybrid P/A and P/A$_{tol}$ models, strengthens reconstructions of lake history with regard to the timing and relative magnitude of past environmental change. Still, our analyses also revealed apparent weaknesses in the current chironomid-based models as compared with diatom-based models. These are (*i*) statistical weakness related to the use of presence–absence and hybrid models, rather than models using abundance weighting in both the calibration and fossil data sets; (*ii*) uneven distribution of residuals between inferred and observed conductivities; and (*iii*) underestimation of the inferred amplitude of past conductivity variation.

Use of presence–absence and hybrid models

The simple P/A and P/A$_{tol}$ models, in which presence–absence data were used both in model calibration and its application to the fossil record, did reproduce historical conductivity values and some of the stronger conductivity excursions in the diatom-based reconstructions, but overall their correlation with either the lake-level or diatom-based reconstructions is unimpressive. By using presence–absence fossil data, salinity change is inferred only when the species composition of the fossil assemblage changes. These models are unresponsive to even strong fluctuations in the relative abundance of freshwater and salt-loving species; only the

Fig. 7. Lithology of core NC93.2-L from Crescent Island Crater (Kenya) and down-core distribution of fossil larval Chironomidae. Species are arranged left to right in order of increasing conductivity optima.

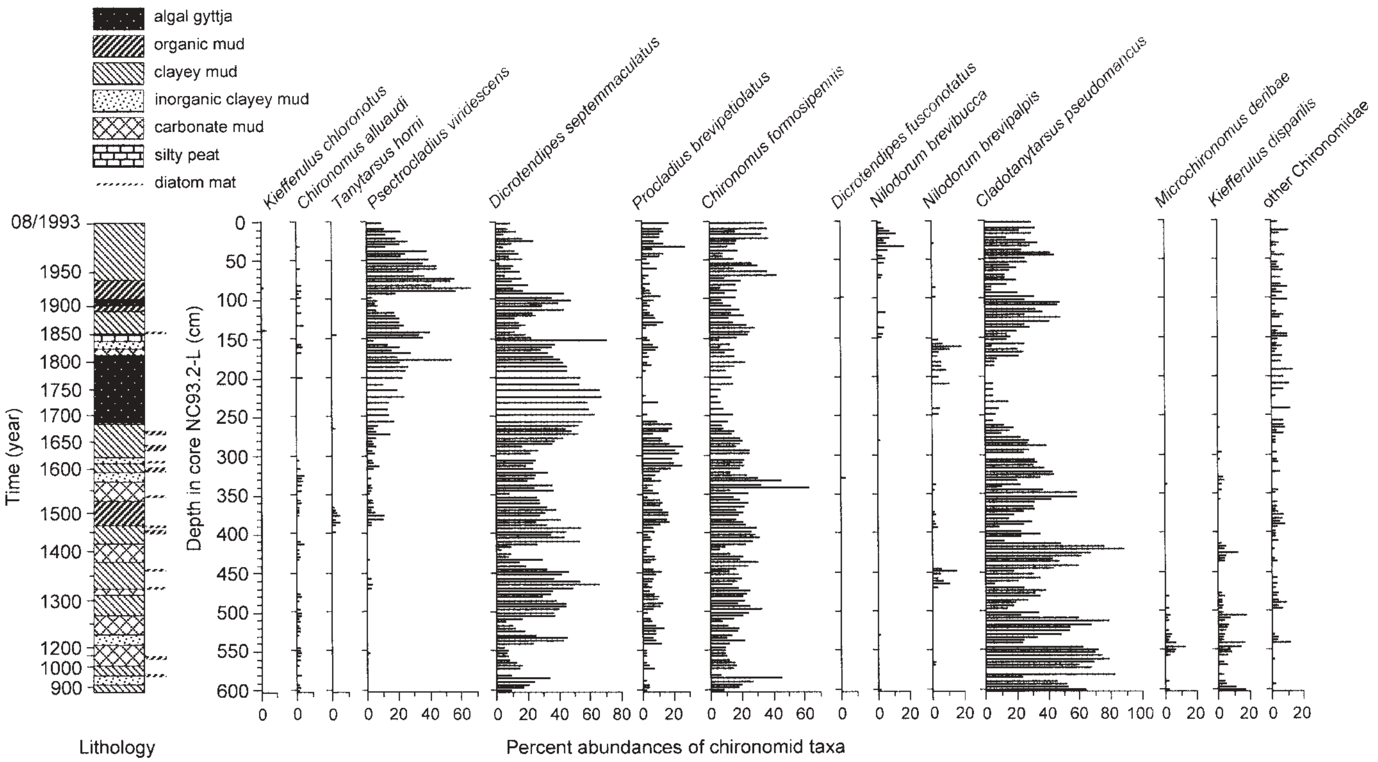
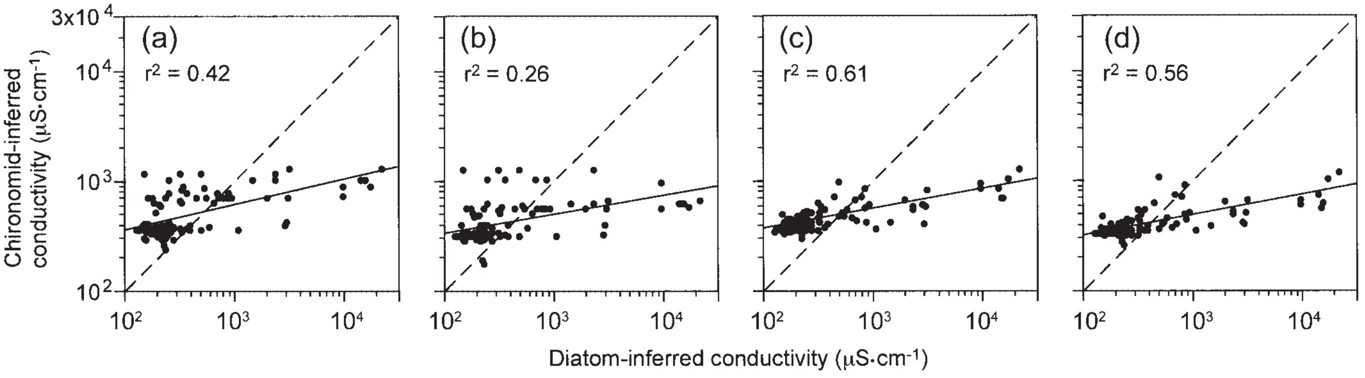


Fig. 8. Correlations between chironomid-inferred and diatom-inferred conductivity for the 1100-year Crescent Island Crater record (n = 130) using (a, b) simple and (c, d) hybrid presence–absence models without (a, c: P/A) and with (b, d: P/A$_{\text{tol}}$) tolerance down-weighing. Solid line: linear regression; broken line: equality of model solutions.



appearance or disappearance of taxa can generate signals. Consequently, the simple P/A and P/A$_{\text{tol}}$ models yield a limited number of possible outcomes (i.e., conductivity values) equal to the number of different species combinations in the fossil record. The effect is more prominent in the Crescent Island Crater record because its fossil assemblages have low Hill's N2 species diversity (Hill 1973; mean Hill's N2 = 5.8) compared with those from Lake Oloidien (mean Hill's N2 = 8.3) and more so in model output with tolerance down-weighing (P/A$_{\text{tol}}$) because WACALIB 3.5 awarded a very large tolerance range to two common fossil species with single occurrences in the modern calibration data set, thus effectively reducing their influence to zero. An associated problem is the disproportionate influence that rare species with distinct optima have on the reconstruction, as for example the conductivity minima at 140 and 84 cm depth in P/A and P/A$_{\text{tol}}$ reconstructions for Crescent Island Crater, because of isolated occurrences of *Kiefferulus chloronotus*.

Our hybrid P/A and P/A$_{\text{tol}}$ model applications avoid some of these shortcomings by giving species a weight proportional to their importance for the reconstruction, as suggested by their percent abundance in the fossil assemblages. In their application to Crescent Island Crater data, the hybrid P/A model without tolerance down-weighing is preferable to hybrid P/A$_{\text{tol}}$ because the former does not dilute the influence of the highly euryhaline *Cladotanytarsus pseudomancus* relative to other common species with more narrow tolerance ranges, hence producing a better signature of the conductivity minimum coinciding with peak 18th century lake level. Though the statistical robustness of these hybrid models is uncertain, we justify their use by the observation that our presence–absence calibration model based on published species lists is not dissimilar from an abundance-weighted calibration model with additional down-weighing of rare taxa. The hybrid model applications do not, however, solve deficiencies of poor species representation in the calibration data set.

Uneven distribution of residuals

Good correlation between chironomid- and diatom-inferred conductivity estimates in the long-term history of Lake Oloidien and Crescent Island Crater suggests a very significant influence of salinity on both diatom and chironomid species composition, relative to other environmental factors known to affect algae (nutrients, turbidity, substrate) and benthic invertebrates (substrate, food quality, oxygen). The dominant control of salinity on diatom species distribution in African lakes is further demonstrated by limited variation in the prediction error of the diatom-based inference model (Gasse et al. 1995), which is a reflection of high species diversity, fairly narrow salinity tolerance ranges, and repeated species turnover along the salinity gradient (Fritz et al. 1999). This contrasts with the very substantial variation in the prediction error of our chironomid-based estimates, seemingly because of relative complacency of chironomid species composition in fresh and slightly concentrated waters (<3000 $\mu S \cdot cm^{-1}$), followed by a nearly complete replacement of salt-tolerant freshwater species with true salt-loving species once the threshold of 3000 $\mu S \cdot cm^{-1}$ is crossed. Its most notable effect is that freshwater lakes with observed conductivity values between 20 and ~3000 $\mu S \cdot cm^{-1}$ yield predicted conductivity values in a much narrower range of ~150–1000 $\mu S \cdot cm^{-1}$. Consequently, our present chironomid-based inference models can differentiate only among fresh to slightly concentrated (<3000 $\mu S \cdot cm^{-1}$), mesosaline (~3000–15 000 $\mu S \cdot cm^{-1}$), and poly- to hypersaline African waters (>15 000 $\mu S \cdot cm^{-1}$).

This apparent threshold response of African chironomid faunas to salinity and the resulting bias in model prediction error is possibly an artifact of our construction of the calibration model with presence–absence data from published species lists with an average of only 3.8 species per lake. The handful of identified species of larval Chironomidae available for most lakes suggests that these collections typically represent only those taxa that thrive in local habitat conditions and not the larger contingent of species that occur near their environmental tolerance limits or in locally restricted types of microhabitat. If this is true, then more intensive live sampling would be expected to reveal greater overlap between freshwater and salt-lake chironomid faunas, more gradual species turnover along the conductivity gradient, and less pronounced bias in the prediction error of chironomid-based salinity-inference models.

However, comprehensive surveys of aquatic invertebrate distribution in African lakes (e.g., Hammer 1986; Tudorancea et al. 1989) show the reality of an abrupt transition between fresh and soda-lake faunas near 3000 $\mu S \cdot cm^{-1}$ and of the rather poor faunal differentiation with regard to salinity in the broad range of freshwater environments below that threshold. Consequently, the overall pattern of species distribution among lakes in the available calibration data set may well reflect ecological reality. Likely, the ultimate drivers of community response in these benthic aquatic invertebrates are not the species-specific physiological tolerances to salinity stress, but large-scale restructuring of benthic habitat accompanying drastic salinity change (Williams et al. 1990), for example, the wholesale disappearance of submerged macrophytes along with the sheltered mud habitat they provide and the coarse organic detritus they produce (McLachlan 1979). In the context of paleoenvironmental reconstruction, satisfactory agreement between chironomid- and diatom-based salinity inferences requires past salinity variations that encompassed a large portion of the full salinity gradient or at least crossed the all-important threshold between freshwater and salt-lake environments.

Limited amplitude of inferred conductivity variation

Chironomid-inferred conductivity during phases of hydrologic closure is systematically lower than the corresponding diatom-inferred conductivity, more so in Crescent Island Crater than in Lake Oloidien. As a result, slopes of the relationship between chironomid- and diatom-inferred conductivities are significantly different from unity. This is partly due to limited sensitivity of the chironomid-based calibration model in the freshwater range, as discussed above. Specifically, limited model sensitivity can explain the apparent overestimation of conductivity for (diatom-inferred) values below ~500 $\mu S \cdot cm^{-1}$ and underestimation for values above ~500 up to ~2000 $\mu S \cdot cm^{-1}$, evident in the Crescent Island Crater record. However, if model insensitivity were the main cause of this collapse in chironomid-inferred conductivity values, regressions between chironomid- and diatom-inferred conductivities would display a clear signature of the sudden transition in chironomid faunas between fresh and saline environments, and the correlation between chironomid- and diatom-inferred conductivities would be significantly reduced. Instead, chironomid-inferred values continue to be much lower than, but broadly proportional to, diatom-inferred values across the full range of values reconstructed in both fossil records, up to (diatom inferred) values of >20 000 $\mu S \cdot cm^{-1}$.

In contrast to the diatom assemblages deposited during early lowstand episodes in Crescent Island Crater, which are dominated by halophilic taxa (Verschuren et al. 2000*b*), corresponding chironomid assemblages contain a mixture of freshwater and halophilic taxa in which the latter (*Microchironomus deribae*, *Kiefferulus disparilis*) account for at most 24%. This is also the case in the Lake Oloidien record, with the exception of samples from within and immediately above the pre-1840 desiccation horizon. The large majority of saline-phase samples in both studied sediment records contain mixed freshwater–halophilic chironomid assemblages that lack modern analogs. Whereas the halophilic *Microchironomus deribae* has been reported from some freshwater lakes (Verschuren 1997), *Kiefferulus disparilis* and *Tanytarsus minutipalpis* have never been found living together with any true freshwater species. The incidence of no-analog situations would be reduced if transfer functions were developed from a calibration data set based on surface-sediment chironomid assemblages rather than the life collections used here. Since surface-sediment assemblages represent an integration of biological communities over several years, lakes which hover near the freshwater–saline transition today would likely yield mixed fossil assemblages similar to those found at depth in the Crescent Island Crater record, and introduce some degree of disharmonious species composition in the calibration data set.

Diatom floral composition and inferred conductivity (10 000 – 22 000 μS·cm^{-1}) indicate that during the Medieval Climatic Optimum, Crescent Island Crater did not hover near the freshwater–saline transition but was a true salt lake for extended periods of time. Similarly, diatom-inferred conductivity (12 700 – 13 600 μS·cm^{-1}; Verschuren et al. 1999*b*) and historical accounts from the mid-19th century (New 1874) indicate that Lake Oloidien was a true salt lake at that time, the type of African soda lake that today is inhabited exclusively by halobiontic chironomid species and the euryhaline *Cladotanytarsus pseudomancus*. Consequently, the mixed composition of chironomid assemblages deposited during past saline lowstands of both lakes must reflect significant postdepositional sediment mixing, with reworking of fossil assemblages deposited during earlier freshwater phases. Crescent Island Crater is highly sensitive to such mixing, because lake-level decline in the combined Lake Naivasha – Crescent Island Crater system causes resuspension of sediments recently deposited in the sector of Naivasha adjacent to the crater, which during an ensuing low stand contribute to sedimentation on the crater floor (Verschuren 1999).

The relative purity of soda-lake diatom assemblages deposited concurrently with mixed chironomid assemblages in both Lake Oloidien and Crescent Island Crater implies that chironomid larval remains must better survive cycles of resuspension and redeposition than do diatom frustules. Diatom preservation is controlled by the dissolved-silica concentration of bottom waters and the depth of sediment mixing relative to the rate of sediment accumulation (Lawson et al. 1978; Conley and Schelske 1989). In both large, stable and shallow, fluctuating lakes (Parker et al. 1977; Lent and Lyons 2001), most diatom silica is recycled to the water column before permanent burial. This process may be particularly strong in the shallow main basin of Lake Naivasha adjacent to Crescent Island Crater, considering its extensive areas of wind-induced erosion and transport relative to areas of sediment accumulation (Verschuren 1999). In contrast, preservation of chironomid remains is promoted by the chemical inertness of chitin and the resistance of sclerotized skeletal fragments to physical destruction (Frey 1988). Thus, differential preservation of diatoms and chironomids first buried in shallow sediments during fresh highstands and then redeposited during saline lowstands may result in greater contamination of those deposits with nonmatching chironomid fossils, as compared with diatoms.

Prospects

The statistical performance of the chironomid-based conductivity-inference models for African lakes, as reflected in coefficients of determination and RMSEs of prediction, is comparable to that of current diatom-based models, but threshold response of chironomid species composition to salinity change limits model sensitivity within the freshwater range. Given current limitations of the calibration data set, conductivity estimates produced by all four tested models matched historical instrumental data surprisingly well. The hybrid statistical procedure in which calibration models based on modern presence–absence data are applied to abundance-weighted fossil data rather than presence–absence data yielded the best agreement with diatom-inferred conductivity estimates, since it does not depend on complete replacement of individual species to generate variation. Weighing of species' influence inversely proportional to their estimated conductivity tolerance (the P/A$_{\mathrm{tol}}$ calibration model) resulted in muted signals of conductivity change in the freshwater range, in part by limiting the influence of one highly salt-tolerant species. The tendency of chironomid-inferred conductivity values for past saline phases in both test lakes to remain below corresponding diatom-inferred values is attributed to the combination of taphonomical processes in shallow fluctuating lakes with differential preservation of chironomid versus diatom fossils.

Besides diatoms and chironomids, the distribution of several other groups of aquatic biota with good fossil preservation, such as chrysophytes and cladocerans, have been investigated in relation to salinity. However, the performance of quantitative inference models based on these groups (Cumming et al. 1993; Zeeb and Smol 1995; Bos et al. 1996) is limited by the scarcity of truly halobiontic taxa. Model insensitivity at the high end of the salinity gradient also affects quantitative reconstructions based on Chironomidae of western Canada (Walker et al. 1995), where only two species tolerate conductivities above ~10 000 μS·cm^{-1}. African salt lakes are inhabited by at least three chironomid species in addition to the three halobiontic species currently included in the calibration data set (D. Verschuren, unpublished data), hence chironomid-based reconstruction of past changes in lakes' water balance holds great promise. Further improvements of the performance of chironomid-based inference models is contingent upon the construction of a comprehensive calibration data set using standardized collections of surface-sediment chironomid assemblages and associated modern environmental data.

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References

Barker, P., Gasse, F., Roberts, N., and Taieb, M. 1990. Taphonomy and diagenesis in diatom assemblages: a late Pleistocene palaeoecological study from Lake Magadi, Kenya. Hydrobiologia, **214**: 267–272.

Bayly, I.A.E. 1972. Salinity tolerance and osmotic behavior of animals in athalassic saline and marine hypersaline waters. Annu. Rev. Ecol. Syst. **3**: 233–268.

Birks, H.J.B. 1998. Numerical tools in palaeolimnology — progress, potentialities, and problems. J. Paleolimnol. **20**: 307–332.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C., and ter Braak, C.J.F. 1990. Diatoms and pH reconstruction. Phil. Trans. R. Soc. Lond. B Biol. Sci. **327**: 263–278.

Bos, D.G., Cumming, B.F., Watters, C.E., and Smol, J.P. 1996. The relationship between zooplankton, conductivity and lake-water ionic composition in 111 lakes from the Interior Plateau of British Columbia, Canada. Int. J. Salt Lake Res. **5**: 1–15.

Brooks, S.J., and Birks, H.J.B. 2000. Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, western Norway. J. Paleolimnol. **23**: 77–89.

Brooks, S.J., Mayle, F.E., and Lowe, J.J. 1997. Chironomid-based late-glacial climatic reconstruction for southeast Scotland. J. Quat. Sci. **12**: 161–167.

Conley, D.J., and Schelske, C.L. 1989. Processes controlling the benthic regeneration and sedimentary accumulation of biogenic silica in Lake Michigan. Arch. Hydrobiol. **116**: 23–43.

Cumming, B.F., Wilson, S.E., and Smol, J.P. 1993. Paleolimnological potential of chrysophyte cysts and scales and of sponge spicules as indicators of lake salinity. Int. J. Salt Lake Res. **2**: 87–92.

Dearing, J.A. 1997. Sedimentary indicators of lake-level changes in the humid temperate zone: a critical review. J. Paleolimnol. **18**: 1–14.

Frey, D.G. 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. J. Paleolimnol. **1**: 179–191.

Fritz, S.C., Cumming, B.F., Gasse, F., and Laird, K.R. 1999. Diatoms as indicators of hydrologic and climatic change in saline lakes. *In* The diatoms: applications to the environmental and earth sciences. *Edited by* E.F. Stoermer and J.P. Smol. Cambridge University Press, New York. pp. 41–72.

Gasse, F., Juggins, S., and Ben Khelifa, L. 1995. Diatom-based transfer functions for inferring hydrochemical characteristics of African paleolakes. Palaeogeogr. Palaeoclimatol. Palaeoecol. **117**: 31–54.

Gaudet, J.J., and Melack, J.M. 1981. Major ion chemistry in a tropical African lake basin. Freshw. Biol. **11**: 309–333.

Hammer, U.T. 1986. Saline lake ecosystems of the world. Monogr. Biol. 59. Junk, Dordrecht.

Hare, L., and Carter, J.C.H. 1987. Chironomidae (Diptera, Insecta) from the environs of a natural West African lake. Entomol. Scand. Suppl. **29**: 65–74.

Hill, M.O. 1973. Diversity and differences: a unifying notation and its consequences. Ecology, **54**: 427–432.

Laird, K.R., Fritz, S.C., Grimm, E.C., and Mueller, P.G. 1996. Century-scale paleoclimatic reconstruction from Moon Lake, a closed-basin lake in the northern Great Plains. Limnol. Oceanogr. **41**: 890–902.

Lawson, D.S., Hurd, D.C., and Pankratz, H.S. 1978. Silica dissolution rates of decomposing phytoplankton assemblages at various temperatures. Am. J. Sci. **278**: 1373–1393.

Lent, R.M., and Lyons, W.B. 2001. Biogeochemistry of silica in Devils Lake: implications for diatom preservation. J. Paleolimnol. **26**: 53–66.

Levesque, A.J., Mayle, F.E., Walker, I.R., and Cwynar, L.C. 1993. A previously unrecognized late-glacial cold event in eastern North America. Nature (Lond.), **361**: 623–626.

Line, J.M., ter Braak, C.J.F., and Birks, H.J.B. 1994. WACALIB version 3.3. A computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. J. Paleolimnol. **10**: 147–152.

Livingstone, D.A., and Melack, J.M. 1984. Some lakes of subsaharan Africa. *In* Lakes and reservoirs. *Edited by* F.B. Taub. Elsevier, Amsterdam. pp. 467–497.

McLachlan, A.J. 1979. Decline and recovery of the benthic invertebrate communities. Monogr. Biol. **35**: 143–160.

Mees, F., Verschuren, D., Nijs, R., and Dumont, H. 1991. Holocene evolution of the crater lake at Malha, Northwest Sudan. J. Paleolimnol. **5**: 227–253.

New, C. 1874. Life, wanderings, and labors in eastern Africa. 2nd ed. Hodder and Stoughton, London.

Parker, J.I., Conway, H.L., and Yaguchi, E.M. 1977. Dissolution of diatom frustules and recycling of amorphous silicon in Lake Michigan. J. Fish. Res. Board Can. **34**: 545–551.

Pinder, L.C.V. 1995. The habitats of chironomid larvae. *In* The Chironomidae: biology and ecology of non-biting midges. *Edited by* P.D. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman & Hall Ltd., London. pp. 107–135.

Smol, J.P., and Cumming, B.F. 2000. Tracking long-term changes in climate using algal indicators in lake sediments. J. Phycol. **36**: 986–1011.

Smol, J.P., Walker, I.R., and Leavitt, P.R. 1991. Paleolimnology and hindcasting climatic trends. Verh. Int. Ver. Theor. Angew. Limnol. **24**: 1240–1246.

Stoermer, E.F., and Smol, J.P. 1999. The diatoms: applications for the environmental and earth sciences. Cambridge Univsity Press, New York.

Street-Perrott, F.A., and Roberts, N. 1983. Fluctuations in closed-basin lakes as an indicator of past atmospheric circulation patterns. *In* Variations in the global water budget. *Edited by* A. Street-Perrott, M. Beran, and R. Ratcliffe. Reidel, Dordrecht. pp. 331–345.

Tudorancea, C., Baxter, R.M., and Fernando, C.H. 1989. A comparative limnological study of zoobenthic associations in lakes of the Ethiopian Rift Valley. Arch. Hydrobiol. Suppl. **83**: 121–174.

Vareschi, E., and Vareschi, A. 1984. The ecology of Lake Nakuru (Kenya). IV. Biomass and distribution of consumer organisms. Oecologia, **61**: 70–82.

Verschuren, D. 1996. Comparative paleolimnology in a system of four shallow tropical lake basins. *In* The limnology, climatology and paleoclimatology of the East African lakes. *Edited by* T.C. Johnson and E. Odada. Gordon & Breach, Newark, N.J. pp. 559–572.

Verschuren, D. 1997. Taxonomy and ecology of subfossil Chironomidae (Insecta: Diptera) from Rift Valley lakes in central Kenya. Arch. Hydrobiol. Beih. **107**: 467–512.

Verschuren, D. 1999. Sedimentation controls on the preservation and time resolution of sedimentary climate-proxy records from shallow fluctuating lakes. Quat. Sci. Rev. **18**: 821–837.

Verschuren, D. 2001. Reconstructing fluctuations of a shallow East African lake during the past 1800 years from sediment stratigraphy in a submerged crater basin. J. Paleolimnol. **25**: 297–311.

Verschuren, D., Cocquyt, C., Tibby, J., Roberts, N., and Leavitt, P.R. 1999*a*. Long-term dynamics of algal and invertebrate communities in a small, fluctuating tropical soda lake. Limnol. Oceanogr. **44**: 1216–1231.

Verschuren, D., Tibby, J., Leavitt, P.R., and Roberts, C.N. 1999*b*. The environmental history of a climate-sensitive lake in the former 'White Highlands' of central Kenya. Ambio, **28**: 494–501.

Verschuren, D., Tibby, J., Sabbe, K., and Roberts, N. 2000*a*. Effects of lake level, salinity and substrate on the invertebrate community of a fluctuating tropical lake. Ecology, **81**: 164–182.

Verschuren, D., Laird, K.R., and Cumming, B.F. 2000*b*. Rainfall and drought in equatorial East Africa during the past 1,100 years. Nature (Lond.), **403**: 410–414.

Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N., Leavitt, P.R., Brown, E.T., Talbot, M.R., and Hecky, R.E. 2002. History and timing of human impact on Lake Victoria, East Africa. Proc. R. Soc. Lond. B Biol. Sci. **269**: 289–294.

Walker, I.R. 1995. Chironomids as indicators of past environmental change. *In* The Chironomidae: biology and ecology of non-biting midges. *Edited by* P.D. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman & Hall Ltd., London. pp. 405–422.

Walker, I.R., Wilson, S., and Smol, J.P. 1995. Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. Can. J. Fish. Aquat. Sci. **52**: 950–960.

Williams, W.D. 1984. Chemical and biological features of salt lakes on the Eyre Peninsula, South Australia, and an explanation of regional differences in the fauna of Australian salt lakes. Verh. Int. Ver. Theor. Angew. Limnol. **22**: 1208–1215.

Williams, W.D., Boulton, A.J., and Taaffe, R.G. 1990. Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia, **197**: 257–266.

Zeeb, B.A., and Smol, J.P. 1995. A weighted-averaging regression and calibration model for inferring lakewater salinity using chrysophycean stomatocysts from western Canadian lakes. Int. J. Salt Lake Res. **4**: 1–23.