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EFFECTS OF DEPTH, SALINITY, AND SUBSTRATE ON THE INVERTEBRATE COMMUNITY OF A FLUCTUATING TROPICAL LAKE

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Abstract. Salinity is generally considered to be the dominant environmental factor regulating aquatic community structure in hydrologically closed lakes and wetlands, but it is not well known whether community response to long-term trends in hydrological balance is driven primarily by the direct physiological effect of salinity stress or by the habitat restructuring that accompanies changes in lake level and salinity. Attempts to separate the effects of various environmental factors on invertebrate populations in shallow fluctuating lakes through field study are hampered by the typically large temporal and spatial variation in species abundances and the long time scale of climate-driven habitat restructuring relative to the period of study. We used paleolimnological techniques to document long-term dynamics of the benthic invertebrate community inhabiting a shallow fluctuating lake in Kenya where during the period ~1870–1991 lake depth fluctuated between 4 and 19 m, and lakewater conductivity between ~250 and 14 000 $\mu\text{S}/\text{cm}$. Analyses of sediment texture, plant macrofossils, and fossil diatom assemblages in a ^{210}Pb -dated sediment core were combined with historical lake-level data to reconstruct continuous records of past changes in salinity and the distribution of various types of benthic habitat. Fossil invertebrate faunas recovered from the same core comprised 58 species of Ostracoda, chydorid Cladocera, and Chironomidae, with 26 common species together accounting for >95% of the recovered fossils. Uni- and multivariate statistical analyses of the faunal and environmental data revealed distinct species-specific responses to lake level, salinity, and papyrus-swamp development. Redundancy analysis and variation partitioning showed that salinity and swamp development together explained 51% of the observed historical variation in benthic community composition, and that their effects were independent. In the univariate analyses, six species (23%) showed a strong response to salinity. Nine species (35%) responded strongly to swamp development, which determines availability of submerged vegetated substrates and turbulence-free, littoral mud bottoms. Five species (19%) responded primarily to lake level, which affects the general distribution of sand and mud bottoms and the intensity of subaqueous spring discharge. The remaining six species (23%) showed no distinct pattern or correlation with the selected environmental factors. These results suggest that a significant portion of the documented correlation between salinity and invertebrate community structure along the full gradient of inland aquatic ecosystems may be an indirect effect of broad but diffuse relationships between salinity and the distribution of various types of benthic microhabitat. Decade-scale environmental change experienced by individual closed-basin lakes tends to remain limited to a relatively narrow portion of this gradient, where covariance between salinity and other ecological determinants may be weak. Therefore, local populations of benthic invertebrates will be regulated by the fluctuating availability of specific habitat and associated resources rather than by the limit of their osmoregulating capacity.

Key words: benthic community structure; Chironomidae; Chydoridae; environmental regulation; fluctuating ecosystem; Ostracoda; paleolimnology; redundancy analysis; resource limitation; salinity; variation partitioning.

INTRODUCTION

Inland aquatic ecosystems integrate all the atmospheric and terrestrial processes that occur in their

catchments, and are thus considered among the natural environments most sensitive to anthropogenic climate change (Firth and Fisher 1992, McKnight et al. 1996). As with all of today's stressed ecosystems (Kareiva et al. 1993), predicting the response to climate change of all the individual species that make up their core plant and animal communities remains a major challenge to the science of ecology. The exact effects of climate change on individual species will depend on how the expected changes in temperature and moisture availability will be translated to the species' immediate

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physical and biological environment, and on how tolerant or adaptable each species is to sustained trends or increased variability in a variety of potentially decisive environmental factors (Ives 1995).

It has long been established that over the full range of inland aquatic ecosystems, from dilute mountain tarns to hypersaline playas, species diversity and composition of local plant and animal communities are strongly influenced by the interplay between salinity and seasonal habitat stability (Beadle 1943, Bayly and Williams 1966, Hammer 1986). It is often assumed that salinity must then also be the dominant environmental factor driving long-term biological change in individual closed-basin lakes. However, regional surveys of aquatic invertebrate distribution (Rawson and Moore 1944, Tudorancea et al. 1989, Hammer 1993, Walker et al. 1995) actually show that "characteristic" freshwater and salt-lake faunas can be identified only at the extremes of the salinity gradient, and that community structure is poorly correlated with salinity over a wide range of intermediate salinities (Williams et al. 1990). The substantial salinity tolerance demonstrated by many aquatic invertebrates appears to conflict with the notion of ecological diversity in such species-rich taxa as the Chironomidae, Ostracoda, and Cladocera, which would predict more narrow niche separation, a clear unimodal response to salinity change, and consistent patterns of species replacement along the salinity gradient.

Poor correlation of community structure with salinity may indicate that over a wide portion of the salinity gradient the distribution of species among lakes is determined by environmental factors other than salinity (Williams 1984, Lancaster and Scudder 1987). One obvious class of environmental regulation that can create substantial variability in community structure among lakes involves top-down effects (Hunter and Price 1992, Osenberg and Mittelbach 1996, Polis et al. 1996). But in fluctuating ecosystems such as ephemeral streams and shallow closed-basin lakes, food webs are generally simple and uncohesive, and predator taxa abundant enough to regulate consumer populations are rare (Boulton et al. 1992, Closs and Lake 1994). An alternative hypothesis (Williams et al. 1990) proposes that species adapted to life in fluctuating lakes combine broad physiological tolerance to salinity variation with relatively strong dependence on a particular substrate, food resource, or other habitat feature of which the distribution may or may not covary with salinity. It predicts that the response of an aquatic invertebrate community to long-term environmental change will be dominated by the effects of changes in habitat availability or quality rather than by the direct physiological effect of salinity change itself. This distinction is important because at the decade-to-century time scale of anthropogenic climate change, the hydrology of closed-basin lakes and wetlands is dominated by transient dynamics in which lake level and salinity, each with their

own effects on benthic habitat diversity and distribution, often fail to covary (Langbein 1961, LaBaugh et al. 1996).

Field studies of benthic community regulation in fluctuating lakes are hampered by large temporal and spatial variation of population size (e.g., MacDonald 1956, Lévêque et al. 1983), the logistic difficulty of sampling so as to capture this variability (Tokeshi 1995), and the rather short time frame of a typical research program compared to that of the climate-driven hydrological cycles that bring about large-scale reorganization of invertebrate habitat. For example, a five-year study of the benthic invertebrate community of Lake Chad in the Sahel zone of North Africa (Dejoux et al. 1971, Dejoux 1976, 1983, Lévêque et al. 1983) revealed major shifts in community structure on both seasonal and interannual time scales, but no correlation could be established between the observed biological changes and the fluctuations of lake level and salinity that were thought to drive those changes. An eight-year study at Lake Chilwa in Malawi (Mclachlan and Mclachlan 1969, Mclachlan 1974, 1979) produced significant insights in the biological effects of drawdown and reflooding, but independent evaluation of the various environmental stress factors was difficult because they all changed simultaneously (Mclachlan 1979).

In this study we use the 120-yr paleolimnological record of a shallow closed-basin lake in Kenya to investigate factors contributing to long-term environmental regulation of benthic invertebrate populations in fluctuating tropical lake ecosystems. The spatially and temporally integrated nature of fossil assemblages recovered from lake sediments overcomes some of the difficulties plaguing the study of live aquatic-invertebrate populations (Dodson and Frey 1991), and allows long-term trends of species abundance to be observed as if raw field data had been processed through a low-pass filter (McKinney 1991). We first reconstruct the lake's environmental history using a combination of documentary evidence and sediment-core data. We then analyze the fossil distributions of benthic invertebrates against this background of environmental change, with lake depth, salinity, and swamp development selected as potential causative factors, or ecological determinants, of historical variation in population density.

METHODS

Description and recent history of the study site

Lake Oloidien (5.1 km²) is located at ~1885 m a.s.l. (above sea level) in the central valley of the Eastern Rift in Kenya, immediately southwest of Lake Naivasha (135 km²; Fig. 1). Highlands flanking the Rift Valley intercept most of the monsoonal rainfall in the region, resulting in a strong moisture deficit near the lakes. Rainfall and evaporation average 608 and 1865 mm per year with considerable interannual variation (Åse et al. 1986). The drainage basin of Lake Oloidien

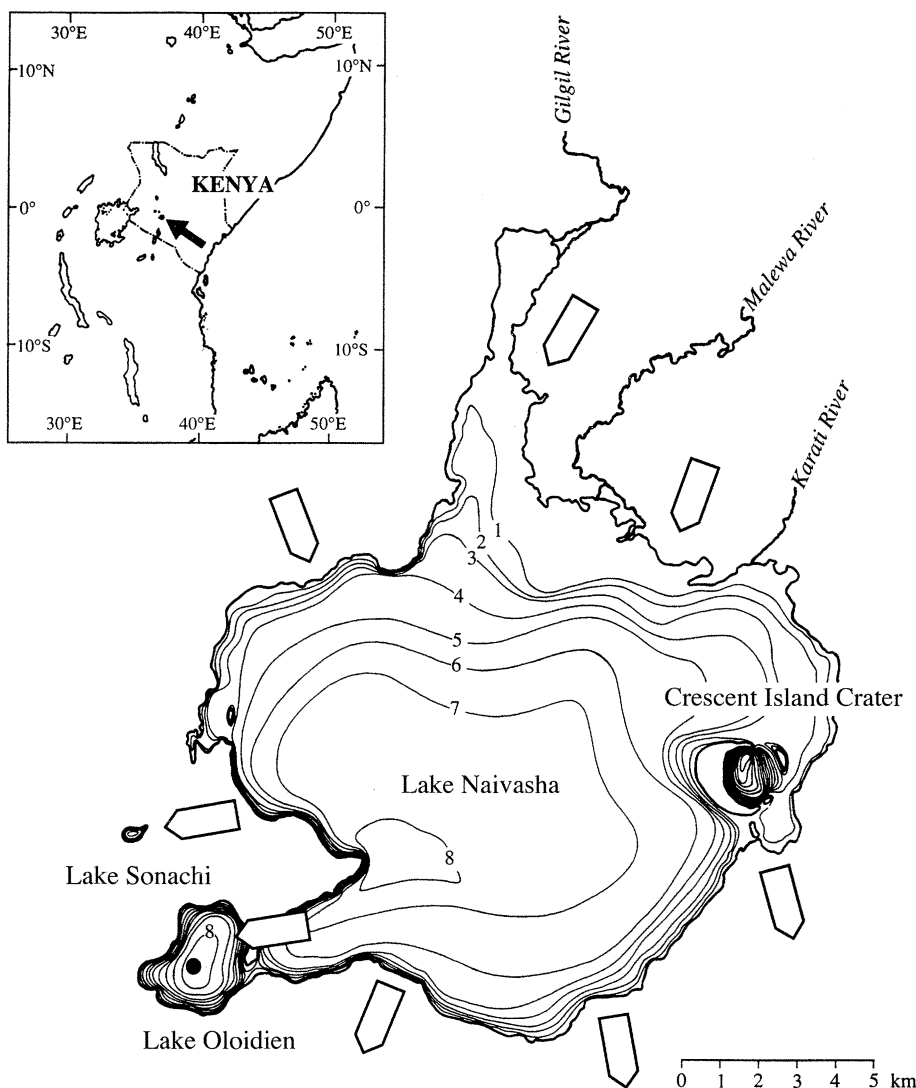


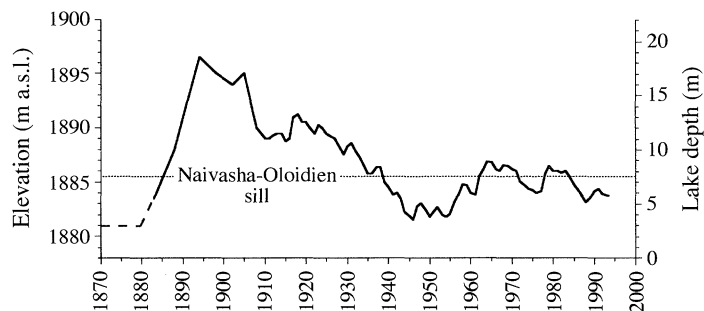
FIG. 1. Bathymetry of Lake Naivasha and its satellite basins Lake Oloidien and Crescent Island Crater (Eastern Rift Valley, Kenya; see inset) relative to a lake-surface elevation of 1885.8 m above sea level, with location of core NO91.1-S. White arrows show the direction of groundwater flow. The figure is modified after Gaudet and Melack (1981) and Åse et al. (1986).

is hydrologically closed so that water losses are due almost entirely to evaporation. Without river inflow directly into the lake nor significant surface runoff from the surrounding grass and scrub savanna, the level of Lake Oloidien must be maintained by rainfall on the lake surface and a considerable contribution of sub-surface inflow from Lake Naivasha through the permeable sill between them (Fig. 1). Lake Naivasha is hydrologically open, with river and groundwater inflow from the north and groundwater outflow to the south and southeast (Gaudet and Melack 1981). Crescent Island Crater is a small submerged crater basin along the eastern shore of Lake Naivasha and is also hydrologically open. Lake Naivasha and its two satellite basins are maintained by river input primarily from the Ma-

lewa River, which drains the Kinangop Plateau and Nyandarua Range that flank the Rift Valley on the east.

Long-term rainfall variability over the past 120 yr has caused the level of Lake Naivasha and its satellite basins to fluctuate considerably (Fig. 2). Local Maasai traditions recount that Lake Naivasha dried up almost completely during an extreme drought not long before the arrival of the first Europeans in 1883 (Åse et al. 1986); information received by missionaries around 1871 stating that "water is sweet on one side of [Lake Naivasha] and salt on the other" (Hemling 1987) no doubt refers to the contrasting salinity of Lake Naivasha and Lake Oloidien when separated from each other at low lake level. During such lowstands the hydrologically closed basin of Lake Oloidien becomes

FIG. 2. Lake Naivasha lake-level record, 1883–1993, relative to the elevation of lake bottom in Lake Oloidien and of the sill separating Lake Oloidien from Lake Naivasha. The figure is modified after Åse et al. (1986), with post-1983 data from Verschuren (1996).



saline due to evaporative concentration of dissolved salts, while Lake Naivasha remains fresh because salts are removed with the subsurface outflow (Gaudet and Melack 1981). By 1883 Lake Naivasha had begun a filling phase, rising rapidly to a historical maximum of 1896.5 m a.s.l. in 1894. During this highstand Lake Oloidien was broadly confluent with Lake Naivasha and fresh (Beadle 1932). The continuous lake-level record kept since 1908 shows high lake levels until ~1920, followed by a prolonged decline during the 1920s and 1930s that culminated in the historical lowstand of 1881.5 m a.s.l. in 1946. Lake level remained low until 1957, then started a new rise to 1887 m a.s.l. by 1964. Since then lake level has fluctuated around the elevation of the sill separating Lake Oloidien from Lake Naivasha, interrupted by short-lived lowstands in the early 1970s and late 1980s. Historically the depth of Lake Oloidien has ranged between 4 and 19 m, and its surface area between 4.0 and 7.5 km² (Verschuren 1996).

Diversity of benthic invertebrate habitat

At the intermediate lake levels prevailing today (lake depth ~6–8 m), Lake Oloidien has a mixing regime of continuous warm polymixis (Lewis 1983) in which temperature stratification develops during calm morning hours and is then destroyed by afternoon winds and nighttime convective mixing. Daily mixing of the entire water column generally keeps the entire lake floor well oxygenated (Melack 1976). At a current lakewater conductivity of ~1000 µS/cm, three major types of benthic invertebrate habitat exist in Lake Oloidien (Fig. 3B): submerged beds of *Potamogeton pectinatus* in the wave-agitated shallows on steep-sloping shores; sandy bottom in gaps between the weedbeds and on the gently sloping western shore; and stable mud bottom below an oxygenated water column in all offshore areas. The shifting shoreline of Lake Oloidien consists of volcanic sand grading to soils formed in Pleistocene lacustrine sediments; emergent littoral vegetation is absent.

During the period of confluence with Lake Naivasha ~1890–1940 (lake depth 10–19 m; Fig. 2), Lake Oloidien was fresh (<500 µS/cm) and offered benthic invertebrates a greater variety of microhabitats (Fig. 3A). Submerged macrophyte beds were composed of *Cer-*

atophyllum demersum, *Najas pectinata*, *Nymphaea caerulea*, *Nitella* spp., *P. pectinatus*, and several broad-leaved *Potamogeton* spp. (Beadle 1932, Jenkin 1932). Other vegetated substrates included the submerged parts of emergent littoral macrophytes such as *Cyperus papyrus*, and newly inundated terrestrial soils. The extensive belt of submerged and emergent littoral macrophytes dampened wave action nearshore, so that fine-grained muds could accumulate in shallow water between the vegetation. Sandy substrates probably persisted only on the western shore. At the time of highest lake level ~1900 (lake depth >15 m), Lake Oloidien may have been discontinuously polymictic (Lewis 1983) with complete mixing of the water column occurring only infrequently. Arguments in favor of discontinuous polymixis at that time are the convective mixing depth in nearby Crescent Island Crater, which is only 12–13 m, and the occasional occurrence of near-bottom oxygen depletion in Lake Oloidien even at today's depths of 6–8 m (Melack 1976). If complete mixing was uncommon, oxygenated mud bottoms must have been restricted to the sublittoral zone, and colonization of profundal mud bottoms would have required adaptation to low and fluctuating oxygen concentrations.

At the elevated salinities that prevailed during the lowstands of ~1870–1883 and 1946–1957, Lake Oloidien became so shallow (lake depth <4 m) that wind-driven turbulence affected a significant portion of the lake floor (Verschuren 1999). Submerged beds of *P. pectinatus* may have disappeared during those phases, either because salinity exceeded its physiological tolerance or because excessive seasonal shoreline migration caused repeated wetting and drying. Sand bottoms were common in all wave-agitated littoral zones (Fig. 3C). Farther offshore, mud bottoms were periodically disturbed by wave turbulence, which stirred up fine-grained sediments and prevented particulate organic matter from settling out of the water column.

Field and laboratory techniques

In August 1991 a 0.92m long sediment core (NO91.1-S) with undisturbed sediment–water interface was recovered from a central location (Fig. 1) in Lake Oloidien, using a single-drive piston corer (Wright

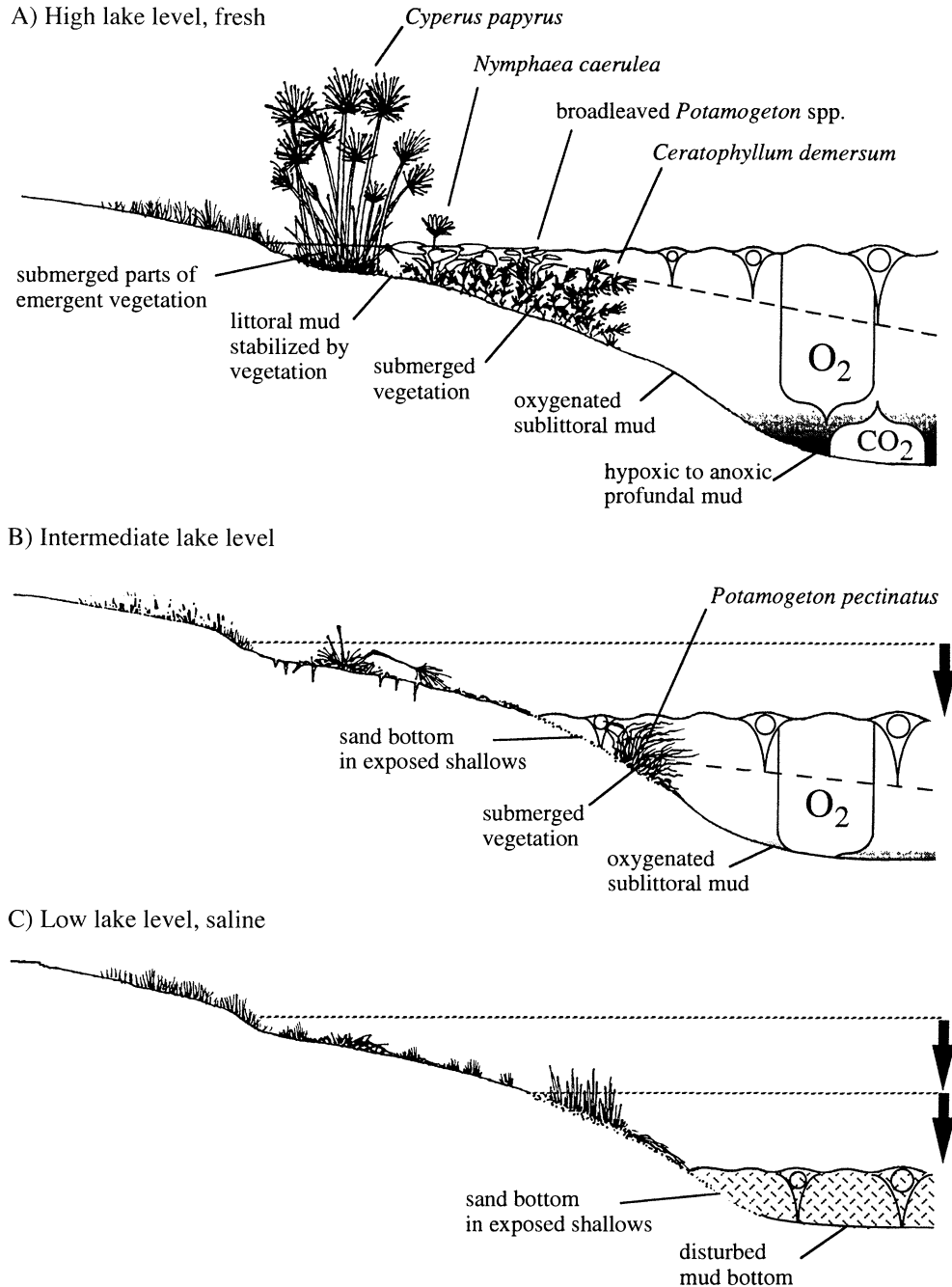


FIG. 3. Conceptual presentation of benthic habitat diversity in Lake Oloidien.

1980) operated from an anchored inflatable raft. The core was extruded upright in the field with a fixed-interval sectioning device (Verschuren 1993), and sequential 1-cm increments were transferred to watertight sampling bags for transport and storage. Water content (percentage H_2O by mass) and basic sediment composition (percentage organic matter, carbonate, and noncarbonate inorganic matter) of each 1-cm core increment were determined by drying overnight at $105^\circ C$,

burning at $550^\circ C$, and ashing at $1000^\circ C$ (Bengtsson and Enell 1986).

Fossil invertebrates were analyzed in 18 samples representing 2-cm thick core sections at 4-cm intervals in the upper 0.72 m of the profile. Subsamples measuring 10.5 mL for Ostracoda, 0.2–1.5 mL for chydorid Cladocera, and 2.0–3.0 mL for Chironomidae were prepared by dispersing the sediment matrix in warm 10% KOH for 45 min (Walker and Paterson 1985), and siev-

ing through 250- μ m and 105- μ m mesh sieves. Residues retained on each sieve were searched separately at 25–40 \times , and fossils were identified at 40–100 \times . In the event of uncertainty, specimens were picked from the residue and mounted in glycerine on microscope slides for examination at 100–1000 \times . Ostracoda were identified using primary taxonomic literature (Klie 1933, 1939, Lowndes 1936, Lindroth 1953, Martens 1993) and comparison with Lake Naivasha collections at the Natural History Museum, London (UK) and the Zoologiska Museet, Uppsala (Sweden). Chydoridae were identified with reference to Jenkin (1934), Smirnov (1971), and collections from various African lakes held at the University of Gent (Belgium). Chironomidae were identified following Verschuren (1997), who used both primary taxonomic literature and museum collections. Subsamples were always searched entirely, yielding on average 77 (4–320) ostracod valves, 138 (36–425) chydorid carapaces, and 129 (15–312) chironomid head capsules, for a total recovery of 6192 identified specimens belonging to 58 species. In the present analysis, three closely related predatory chironomids (*Ablabesmyia dusoleili*, *Monopelopia* sp., *Xenopelopia* sp.) were grouped under the tribe name Pentaneurini, and the data set was reduced to the 26 common species (taxa) that occur in at least half of the samples and together comprise >95% of all recovered fossils (Table 1). Fossil densities are expressed as the number of fossils per gram organic matter (Deevey et al. 1977), which partially corrects for sedimentation-rate variability (Verschuren 1999) and has been found to correlate well with live population biomass (Hann et al. 1994).

For each fossil invertebrate sample, lake depth at time of deposition was calculated by linking the historical lake-level record (Fig. 2) to sediment age determined by ^{210}Pb -dating (Verschuren 1999). ^{210}Pb -activity was measured through its granddaughter isotope ^{210}Po , with ^{208}Po used as an internal yield tracer. Sample preparation followed Eakins and Morrison (1978), and activity was measured for 28–72 h in an alpha spectroscopy system. Supported ^{210}Pb -activity was estimated as the asymptote of total activity at depth, and unsupported activity was calculated by subtracting average supported activity from total activity measured at each of 22 depth intervals. Chronology and sedimentation rates were calculated according to the constant-rate-of-supply (c.r.s.) model (Appleby and Oldfield 1978, Binford 1990).

Historical salinity fluctuations were reconstructed using quantitative estimates of past lakewater conductivity based on the composition of fossil diatom assemblages. Diatom analyses were performed on 24 samples representing 2-cm thick core sections at 4-cm intervals. Sample preparation was modified after Schrader (1974); 50- μ L aliquots of the resulting aqueous suspension were transferred to microscope slides and mounted in Naphrax (Northern Biological Supplies

TABLE 1. Ostracoda, Cladocera, and Chironomidae recovered from Lake Oloidien sediments, the percentage abundance of each species within its respective taxon, and the fraction of samples in which the species was present.

Taxon	Percentage	Fraction
Ostracoda, 12 species		
<i>Physocypris capensis</i>	38.3	13/18
<i>Potamocypris mastigophora</i>	4.1	14/18
<i>Zonocypris costata</i>	50.6	17/18
9 other species†	7.0	
Cladocera: Chydoridae, 22 species		
<i>Euryalona orientalis</i>	12.5	16/18
<i>Leydigia macrodonta</i>	1.6	16/18
<i>Leydigia propinqua</i>	11.7	18/18
<i>Alona</i> nr. <i>cambouei</i>	2.5	13/18
<i>Alona diaphana</i>	31.7	18/18
<i>Alona</i> nr. <i>pulchella</i>	2.2	18/18
<i>Alona rectangula</i>	16.3	18/18
<i>Biapertura verrucosa</i>	4.5	18/18
<i>Alonella excisa</i>	1.9	12/18
<i>Pleuroxus aduncus</i>	3.3	13/18
<i>Dunhevedia crassa</i>	1.8	15/18
<i>Chydorus eurynotus</i>	5.5	14/18
<i>Pseudochydorus globosus</i>	0.9	16/18
9 other species‡	3.5	
Insecta: Chironomidae, 24 species		
Pentaneurini§	1.2	7/18
<i>Procladius brevipetiolatus</i>	26.0	18/18
<i>Chironomus alluaudi</i>	0.9	11/18
<i>Chironomus formosipennis</i>	12.9	17/18
<i>Kiefferulus disparilis</i>	3.0	13/18
<i>Nilodorum brevipalpis</i>	1.2	13/18
<i>Dicrotendipes septemmaculatus</i>	4.0	15/18
<i>Microchironomus deribae</i>	10.7	14/18
<i>Tanytarsus horni</i>	8.5	11/18
<i>Cladotanytarsus pseudomancus</i>	26.6	18/18
12 other species	4.4	
Unidentified fossils	0.6	

Note: Species recovered from at least half the samples and contributing >1% to total group-taxon abundance were retained for statistical analysis.

† *Gomphocythere obtusata*, *Heterocypris congenera*, *Aocypris platybasis*, *Parastenocypris acocyproides*, *P. curvira-mi*, *P. junodi*, *Sclerocypris jenkiniae*, *Potamocypris palludum*, *Sarscypridopsis* nr. *trigonella*.

‡ *Alona guttata*, *Biapertura karua*, *Graptoleberis testudinaria*, *Alonella exigua*, *Pleuroxus* nr. *laevis*, *P. toumodensis*, *Chydorus parvus*, *C. nr. sphaericus*, *Ephemeroporus barroisi*.

§ *Ablabesmyia dusoleili*, *Monopelopia* sp., *Xenopelopia* sp.

|| *Corynoneura* nr. *scutellata*, *Cricotopus* nr. *scottae*, *Psectrocladius viridescens*, *Limnophyes natalensis*, *Dicrotendipes fusconotatus*, *Kiefferulus chloronotus*, *Nilodorum brevibucca*, *Parachironomus* sp., *Paratendipes* sp., *Polypedium* gr. *nubifer*, *Xenochironomus* sp., *Tanytarsus* sp. C.

Limited, Ipswich, UK). Diatoms were counted in transects at 1000 \times through differential interference contrast optics, and identified with reference to Krammer and Lange-Bertalot (1986, 1988, 1991), Gasse (1986), and Round et al. (1990). A preliminary zonation of fossil diatom assemblages was established using stratigraphically constrained numerical clustering (CON-ISS; Grimm 1987) of percent-abundance data from which rare taxa (no sample with >2%) had been removed. For quantitative inference of past conductivity we used the abundance-weighted conductivity optima

of individual diatom species established by canonical correspondence analysis and weighted-averaging regression (Birks et al. 1990, ter Braak 1990) of diatom assemblages in a reference data set of 164 African lakes with known water chemistry (Gasse et al. 1995). The performance of this prediction model, as evaluated by the correlation between inferred and observed conductivity of reference lakes, is $r^2 = 0.87$; the associated root mean square error of prediction (RMSE) is 0.39 log salinity units. Diatom-inferred conductivity is expressed as specific conductance at 25°C (K_{25}), hence historical field measurements mentioned in the text were also converted to K_{25} (Verschuren 1996); a conductivity of 1000 $\mu\text{S}/\text{cm}$ is roughly equivalent to a salinity of 1 g/kg (Williams and Sherwood 1994).

Historical changes in the relative distribution of vegetated, sand, and mud substrates were reconstructed by quantifying the sediment fractions of sand-sized mineral particles and coarse organic matter derived from aquatic macrophytes. The sediment matrix of 5.25 mL subsamples from 36 contiguous 2-cm core increments was dispersed in 0.25% alkaline detergent overnight, then rinsed through a 250- μm mesh sieve. Retained plant macrofossils (seeds and diagnostic parts of vegetative organs) were identified and counted at 20–40 \times . The residue was then transferred to ashless filter paper and its composition analyzed by mass loss upon burning and ashing, as above (Digerfeldt 1986). Coarse-particle residues weighing >0.5% of the total mineral or organic fractions of the sediment were retained as quantitatively significant.

Statistical analyses

Constrained and unconstrained ordination techniques (CANOCO 3.12; ter Braak 1990) were employed to study the relationships among samples in fossil species composition, and the relationships among species in their response to three selected environmental determinants (lake level, salinity, and papyrus-swamp development). We then used simple and multiple linear regression techniques (EViews 2.0; Lilien et al. 1995) to investigate the response of individual species to each environmental factor separately. Fossil species abundances (dependent or response variables) and the records of historical environmental change (explanatory or predictor variables) were log-transformed in both the uni- and multivariate analyses. Regressions were tested for serial autocorrelation by calculating the Durbin-Watson statistic (DW; Durbin and Watson 1951), a measure of the association between adjacent residuals, and the Akaike Information Criterion (AIC; Sakamoto et al. 1986), which intends to minimize the sum of squared residuals but places a penalty on extra variables added to the regression model. With three explanatory variables and $N = 18$, autocorrelation is significant ($P < 0.05$) when $DW < 0.93$, and a null hypothesis of no autocorrelation can be accepted when $DW > 1.69$ (Pindyck and Rubinfeld 1991). None of

our data series showed significant autocorrelation, and absence of autocorrelation was significant in 13 out of the 26 considered cases. For the 13 cases that yielded an inconclusive DW statistic, selection of the appropriate regression model was guided by AIC values for uncorrected regressions and the first two lag distributions.

Linear ordination was determined as the most appropriate multivariate technique for the present data set, based on observation of gradient lengths ≤ 1 standard deviation unit for the first four ordination axes in detrended correspondence analysis (DCA) (Jongman et al. 1995). First we used principal components analysis (PCA) to reduce complexity in the sample data on the basis of invertebrate community composition alone, and then redundancy analysis (RDA) to explicitly investigate the relationships between community composition and the three selected environmental variables. RDA analysis involved a forward selection procedure to obtain the smallest set of environmental variables explaining a statistically significant amount of the variance in the community data (ter Braak 1990). This procedure selected at each step the predictor variable that contributes most to the explained variance in the response variables; significance was tested using unrestricted Monte Carlo tests (4999 permutations). The relative contributions of the different environmental variables to the RDA ordination axes were assessed from their canonical coefficients and intra-set correlations, and their significance was judged by an approximate t test (ter Braak 1988). A series of partial RDAs was then used to decompose the variance in the response variables (i.e., the total sum of squares of the community data) into independent components. This variance partitioning allows assessment of which fractions of the explained variance are shared by two predictor variables, and which can be uniquely attributed to each of them (Borcard et al. 1992, Økland and Eilertsen 1994).

RESULTS

Litho- and chronostratigraphy

The historical sediment record of Lake Oloidien comprises the upper 0.71 m of core NO91.1-S. Recent sediments are mostly brown or dark brown massive clayey muds, grading to flocculent olive-brown muds near the surface (Fig. 4). The stratigraphy of organic-matter (OM) content and sediment texture defines three lithostratigraphic units, the boundaries of which reflect changes in bottom dynamics associated with the major trends of historical lake-level change (Verschuren 1999). Unit I (71–61 cm) was deposited during the 1870s–1880s lowstand when Lake Naivasha and Lake Oloidien stood lower than at any time during the 20th century (Fig. 2). The OM content of these sediments is low (12–16%), and carbonate (micrite) content is high (12–13%). A 1–3% admixture of quartz sand in-

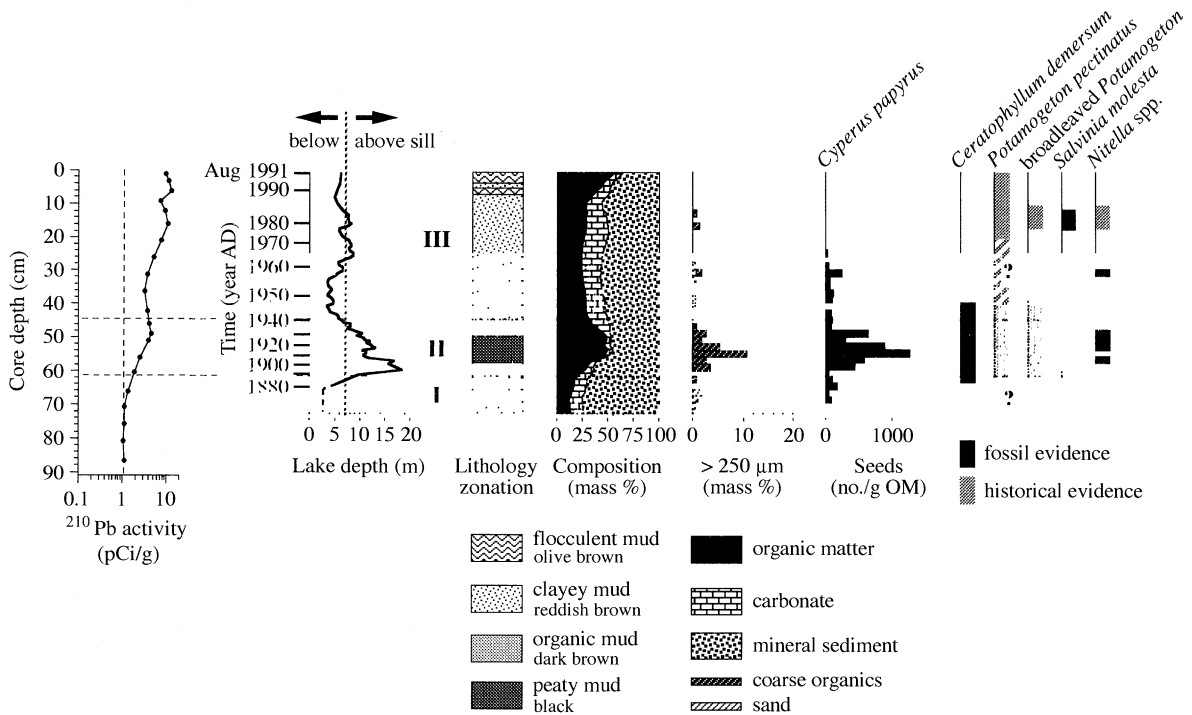


FIG. 4. Lithology, stratigraphic zonation (Units I–III), sediment composition, and macrofossil stratigraphy of core NO91.1-S in relation to the ^{210}Pb -derived sediment chronology and lake depth at the time of deposition. Broadleaved *Potamogeton* include freshwater species such as *P. schweinfurthii* and *P. octandrus*.

indicates proximity of the core site to high-energy littoral environments with considerable wind-driven bottom turbulence.

Unit II (61–45 cm) represents sedimentation during the highstand that lasted from ~1890 to 1940 (Fig. 2). These sediments stand out by their dark-brown color, which is due to the concentration of algal OM (up to 50%) as input rates of terrigenous mineral sediment were reduced (Verschuren 1999). They also contain up to 12% of nonalgal coarse OM, mostly remains of *Cyperus papyrus* and *Ceratophyllum demersum*. The presence of this plant debris in Unit II sediments creates a texture similar to that of surface muds found today in Lake Naivasha near submerged weedbeds and shore-fringing papyrus stands (Gaudet 1977; D. Verschuren, *personal observation*).

Unit III (45–0 cm) consists of calcareous clayey muds deposited after 1940 when lake level was low or intermediate (Fig. 2). The shift to lower OM content (24–30%) at the Unit II–III boundary is due to increased flux of terrigenous inorganic sediment offshore, including some sand (0.5–1%), during lake-level decline (Verschuren 1999). The sharp increase in OM content at the sediment surface reflects incomplete diagenesis of algal OM before permanent burial. High carbonate content of Unit III sediments (Fig. 4) is consistent with field data indicating supersaturation of Lake Oloidien water with regard to calcite, and a high pH (9.0–9.2) and low dissolved Ca/Na ratio (0.1) in

comparison with Lake Naivasha (7.7–8.5 and 0.6, respectively; Gaudet and Melack 1981). Low-carbonate Unit II sediments were deposited during the highstand when broad confluence between the basins resulted in the water chemistry of Lake Oloidien becoming similar to that of Lake Naivasha (Verschuren 1996).

The ^{210}Pb -derived sediment chronology of Lake Oloidien's 120-yr history (~1870–1991) is constrained by four stratigraphic marker horizons for which the inferred age at deposition is supported by independent evidence (Verschuren 1999): the base and top of Unit II dated to ~1890 and ~1940, fossils at 15–11 cm depth reflecting a 1980–1984 outbreak of the exotic water fern *Salvinia molesta*, and increased sediment accumulation at 9–8 cm depth reflecting a drawdown during 1987–1988. Stratigraphic similarity between core NO91.1-S and a second core collected later shows offshore sedimentation in Lake Oloidien to be spatially homogenous, in agreement with wave theory and empirical sedimentation models indicating that the impact of wind-driven turbulence on bottom dynamics in Lake Oloidien is limited to water depths of <2 m (Verschuren 1999). Consequently, the paleolimnological record of lake history incorporated in core NO91.1-S can be considered representative for the basin. High linear rates of sediment accumulation, and preservation of distinct sediment horizons in the flocculent surface muds (Fig. 4), argue against significant influence of

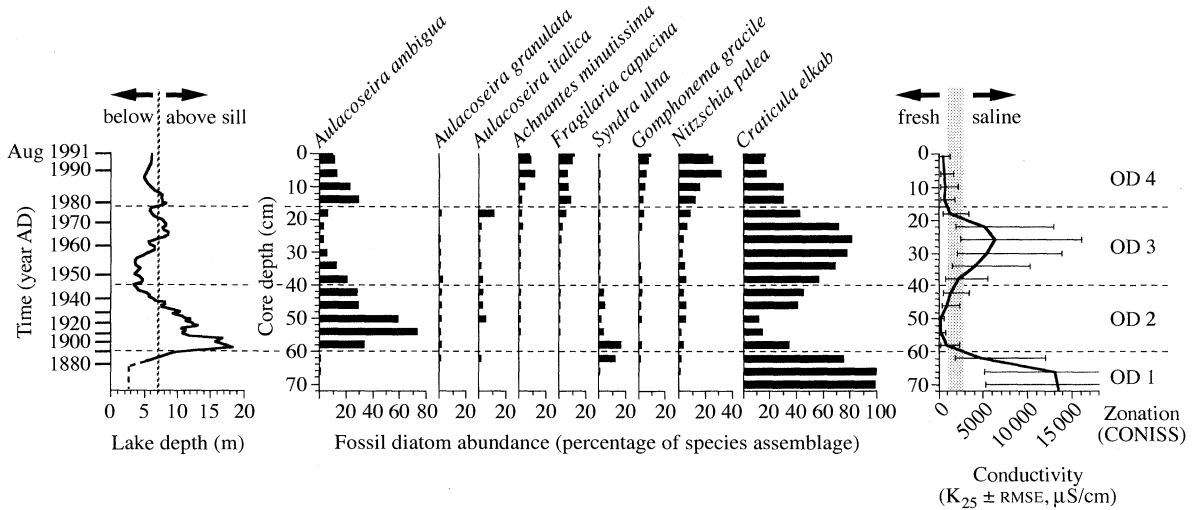


FIG. 5. Fossil diatom stratigraphy and zonation (OD1–OD4) of core NO91.1-S, and diatom-based salinity reconstruction (conductivity K_{25} , in $\mu\text{S}/\text{cm}$) for Lake Oloidien in relation to the ^{210}Pb -derived sediment chronology and lake depth at the time of deposition.

bioturbation on record resolution (Cohen 1984). Sedimentation-rate variability translates the constant 4-cm depth interval of fossil diatom and invertebrate analyses into a time resolution of reconstructed community dynamics of between 5 and 8 yr.

Stratigraphy of plant macrofossils and documentary evidence of submerged macrophytes

Unit I sediments (~1870–1890) contain very few plant macrofossils (Fig. 4), with the exception of a few papyrus seeds. In Unit II (~1890–1940) the distribution of papyrus seeds matches that of the coarse organic debris derived mostly from papyrus and *Ceratophyllum demersum* ($r^2 = 0.90$, $df = 8$, $P < 0.001$). Associated finds of *Najas pectinata* seeds and oogonia of the charophyte *Nitella* sp. provide evidence for development of diversified submerged macrophyte beds in Lake Oloidien during the highstand period of broad confluence with Lake Naivasha.

Remains of *Ceratophyllum demersum* become scarce near the top of Unit II, and disappear permanently from the record above the Unit II–III boundary in sediments deposited around the lake-level minimum of 1946. Admixture of papyrus debris also becomes insignificant ($<0.5\%$) in Unit III, but seeds are found in low numbers up to 23 cm depth. The depth interval 29–31 cm (~1960) represents a distinct peak in papyrus-seed abundance and contains the only *Nitella* fossils recovered from Unit III. Plant macrofossils in the upper half of Unit III are limited to remains of the exotic water fern *Salvinia molesta* at 11–15 cm, consistent with its presence in Lake Oloidien during an outbreak in the early 1980s (Harper 1984, Åse 1987).

The sediment record contains no seeds or other remains of *Potamogeton pectinatus*, the only common submerged macrophyte in Lake Oloidien today. *P. pec-*

tinatus is a euryhaline pondweed commonly found in shallow closed-basin lakes (Hammer 1986), but its persistence in Lake Oloidien through the 1946–1957 lowstand is uncertain. It was reported in the first local survey in the early 1970s (Gaudet 1977), and in the early 1980s it formed part of more diversified macrophyte beds that also included *P. schweinfurthii*, *Najas pectinata*, *Nitella oligospora*, and *N. furcata* (Clark et al. 1989, Harper et al. 1990). We assume that *P. pectinatus* and other *Potamogeton* spp. were also present during the early 20th-century period of broad confluence with Lake Naivasha, based on inferred similarity of Lake Oloidien environments with those in Lake Naivasha at that time (Beadle 1932, Jenkin 1932).

Fossil diatom stratigraphy and past salinity fluctuations

Fossil diatom floras representing the last 120 yr of Lake Oloidien history define four biostratigraphic zones, OD1 through OD4 (Fig. 5). The fossil flora of zone OD1 (71–60 cm), which corresponds to the 1870s–1880s lowstand, is dominated by *Craticula elkab*, a periphytic-benthic diatom characteristic of shallow saline-alkaline environments throughout East Africa (Gasse et al. 1983). Diatom-inferred lakewater conductivity reaches its highest reconstructed values of 12 000–14 000 $\mu\text{S}/\text{cm}$ in this zone. The inferred saline lowstand ended with the transgression of 1883–1894, first recorded by the appearance of the planktonic freshwater diatom *Synedra ulna* in the uppermost sample of OD1. Above the transition to OD2 (60–40 cm), *S. ulna* quickly reaches peak abundance and is then replaced by *Aulacoseira ambigua* and other *Aulacoseira* spp. that in African lakes are characteristic components of pelagic freshwater phytoplankton (Hecky and Kling 1987, Kilham 1990); the periphytic freshwater diatom

Nitzschia palea is present but uncommon. Diatom-inferred conductivity is $<1000 \mu\text{S}/\text{cm}$ throughout OD2, reaching a minimum of $300 \mu\text{S}/\text{cm}$ in sediments dated to the period 1910–1925. The halophilic diatom *C. elkab* comprises at least 10% of the fossil flora throughout OD2, and increases toward the OD2–OD3 boundary in sediments deposited during lake-level decline in the 1930s and early 1940s (Fig. 5).

The lower half of zone OD3 (40–16 cm) is marked by the further expansion of *C. elkab* during the 1946–1957 lowstand. Peak abundance of this species at 25–27 cm depth drives diatom-inferred conductivity to a maximum of $6500 \mu\text{S}/\text{cm}$ in sediments dated to around 1960. The upper third of OD3 documents renewed expansion of freshwater diatoms following the reconnection of Lake Oloidien with Lake Naivasha in the early 1960s. These now include the planktonic *Aulacoseira ambigua* and *A. italica*, the benthic-periphytic *Fragilaria capucina*, *Gomphonema gracile*, and *Achnanthes minutissima*, and *Nitzschia palea*, which can be both periphytic and planktonic (Gasse 1986). At the top of OD3 in sediments deposited around 1980, diatom-inferred conductivity has dropped to $\sim 1400 \mu\text{S}/\text{cm}$. Zone OD4 (16–0 cm) represents the diatom flora inhabiting the lake today. The planktonic *A. ambigua* comprises 30% of the fossil diatom flora in sediments deposited during a transgressive phase in the early 1980s, but then declines toward the sediment surface, replaced by the periphytic freshwater diatoms *F. capucina*, *G. gracile*, *A. minutissima*, and *Nitzschia palea*. Diatom-inferred conductivity remains fairly constant throughout OD4 at around $700 \mu\text{S}/\text{cm}$ (Fig. 5).

Solid test performance of the used diatom-based paleosalinity inference model (Gasse et al. 1995) notwithstanding, reconstructed conductivity values possess considerable uncertainty ranges (Fig. 5). For the purpose of this study, the timing of historical salinity fluctuations in relation to changes in invertebrate community composition is more important than the exact magnitude of those fluctuations. Still, reconstructed conductivity values are supported by good agreement with available field measurements. For example, the average value of $700 \mu\text{S}/\text{cm}$ reconstructed from diatom assemblages deposited in recent decades agrees with measurements of 700 – $1040 \mu\text{S}/\text{cm}$ for the period 1969–1974 (Kilham 1971, Melack 1976, Gaudet and Melack 1981), 620 – $750 \mu\text{S}/\text{cm}$ in the early 1980s (Clark et al. 1989), and around $1000 \mu\text{S}/\text{cm}$ during 1987–1991 (D. M. Harper, *personal communication*). Also, the diatom-inferred conductivity minimum of 300 – $350 \mu\text{S}/\text{cm}$ during the 1910s and 1920s matches the value predicted from broad confluence with Lake Naivasha at that time (Verschuren 1996), and is consistent with a measurement of $470 \mu\text{S}/\text{cm}$ in 1930 (Beadle 1932). No conductivity data are available from during the lowstand episodes of 1946–1957 and before 1890. However, diatom-inferred values of 12000 – $14000 \mu\text{S}/\text{cm}$ for the earlier lowstand are consistent

with information originating from local Maasai that Lake Oloidien was saline at that time (Hemings 1987), which to these herdsman presumably meant that it was not suitable for watering cattle.

Fossil distribution of benthic invertebrates

The stratigraphic distributions of benthic invertebrate species in core NO91.1-S display a range of distinct patterns (Fig. 6), reflecting a generally individualistic and species-specific response to decade-scale environmental change in Lake Oloidien. Some species (e.g., *Physocypria capensis*, *Procladius brevipetiolatus*, *Kiefferulus disparilis*, *Microchironomus deribae*) have fossil distributions that are positively or negatively correlated with the record of diatom-inferred salinity. Fossil distributions of some species (e.g., *Euryalona orientalis*, *Alonella excisa*, *Pentaneurini*, *Tanytarsus horni*) match the stratigraphy of fossil papyrus seeds. Other distributions are less obviously related to these environmental variables (e.g., *Zonocypris costata*, *Dunhevedia crassa*), or lack distinct trends (e.g., *Chironomus formosipennis*).

Multivariate statistical analysis of these faunal data reveals that more than half of observed variation in invertebrate community composition through time is captured in two dimensions: PCA axes 1 and 2 together explain 65% of the observed variance (eigenvalues of 0.48 and 0.17; Table 2). PCA sample scores (Fig. 7) comprise four nonoverlapping groups, defining the four biostratigraphic zones (Fig. 6: OI1 through OI4) that describe the general change in community composition through time. Zone boundaries generally coincide with those of the diatom zonation, except that the OI3–OI4 boundary is located at 20 cm depth rather than 16 cm (Fig. 6 vs. Fig. 5). RDA analysis with forward selection of the three selected predictor variables (salinity, papyrus, and lake depth) indicates that only salinity and papyrus contribute significantly and independently to explained variation in the faunal data: axes 1 and 2 of the constrained ordination together explain 51% of the observed variance (eigenvalues of 0.36 and 0.15). High species–environment correlations for both axes ($R = 0.86$ and 0.96 ; Table 2) indicate that PCA and RDA yield comparable results (Jongman et al. 1995) and thus that the relative position of samples in an RDA ordination diagram (not shown) will be similar to that in the PCA ordination diagram (Fig. 7).

Axis 1 of both PCA and RDA arranges samples and species along a gradient of papyrus-swamp development (Figs. 7 and 8); low canonical and intra-set correlation coefficients for the predictor variable salinity (Table 2) indicate that salinity does not contribute significantly to this axis. The position of most species on the right side of the RDA diagram reflects the overall positive influence of papyrus swamp on their abundance; only *Dunhevedia crassa* exhibits negative correlation with this variable. Seven species (*Euryalona orientalis*, *Pleuroxus aduncus*, *Tanytarsus horni*, *Pen-*

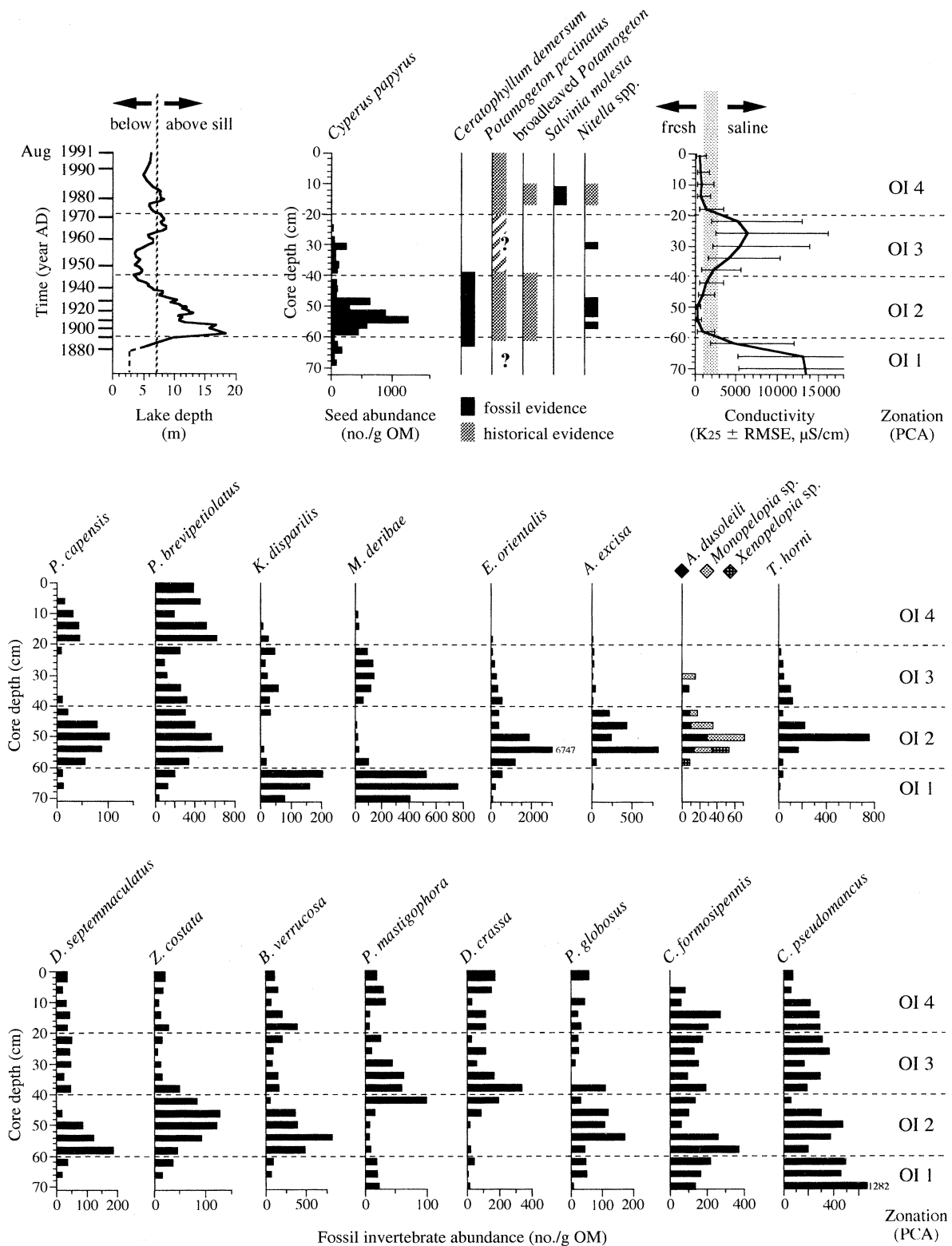


FIG. 6. Fossil distribution of benthic-invertebrate taxa (Ostracoda, Cladocera, Chironomidae) and stratigraphic zonation of fossil communities (OI1–OI4) in core NO91.1-S in relation to changes in lake depth, salinity, and the diversity of vegetated substrates in Lake Oloidien over the past 120 years. Note the variable scale of organic-specific fossil concentrations on the horizontal axes.

TABLE 2. Diagnostic results of PCA and RDA on fossil invertebrate faunas in core NO91.1-S from Lake Oloidien.

Analysis	Diagnostic	Predictor	Axis 1	Axis 2	Axis 3	Axis 4
PCA	eigenvalue		0.48	0.17	0.08	0.06
RDA	eigenvalue		0.36	0.15		
RDA	species-environment correlation		0.86	0.96		
RDA	canonical coefficients	papyrus	1.01†	0.05		
		salinity	0.11	1.01†		
RDA	inter-set correlations	papyrus	0.86	-0.11		
		salinity	-0.04	0.95		

† $|t| > 2.1$ (ter Braak 1988).

taneurini, *Chydorus eurynotus*, *Alonella excisa*, *Alona* nr. *cambouei*) have >40% of their variance fitted by RDA axis 1, implying that their historical occurrence in Lake Oloidien has been controlled primarily by the presence of papyrus swamp. Ordination axis 2 arranges samples and species along a salinity gradient (Figs. 7 and 8); papyrus does not contribute significantly to this axis (Table 2). True halophilic species (*Kiefferulus disparilis*, *Microchironomus deribae*) and some freshwater species (*Physocypria capensis*, *Procladius brevipetiolatus*, *Leydigia propinqua*, *Biapertura verrucosa*, *Alona diaphana*) show strong correlation with this axis,

suggesting a rather direct control of lakewater salinity on their historical occurrence in Lake Oloidien.

The almost perpendicular position of the arrows representing salinity and papyrus in the RDA diagram (Fig. 8) indicates that the effects of salinity and swamp development on benthic invertebrate community structure in Lake Oloidien are largely independent. Variance partitioning corroborates this observation: removing papyrus as a covariable from RDA does not affect the fraction of variation in the faunal data explained by salinity, and vice versa (Table 3). The analysis suggests that 35.6% of past variation in community structure can be attributed to the effects of swamp development,

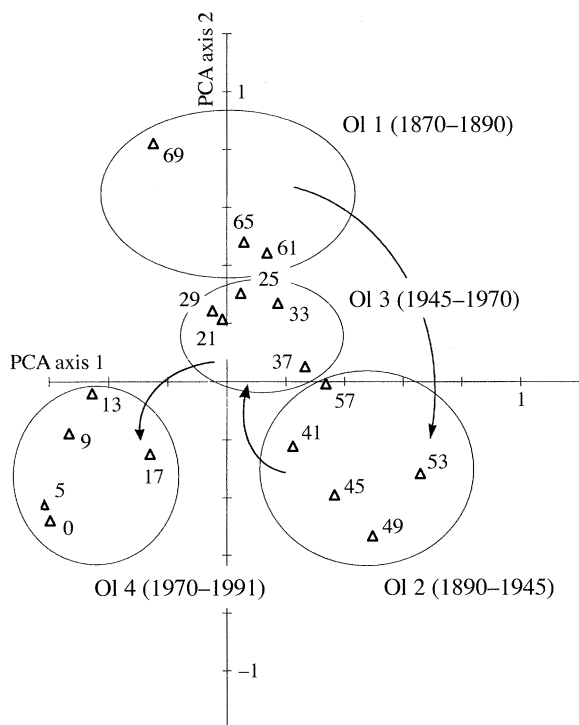


FIG. 7. PCA ordination of fossil invertebrate faunas in core NO91.1-S, showing separation of samples in four groups defining stratigraphic zones OI1 through OI4. PCA axes 1 and 2 together explain 65% of observed historical variance in the faunal data. Sample scores were multiplied by 0.37 to fit the coordinate system of the RDA ordination in Fig. 8.

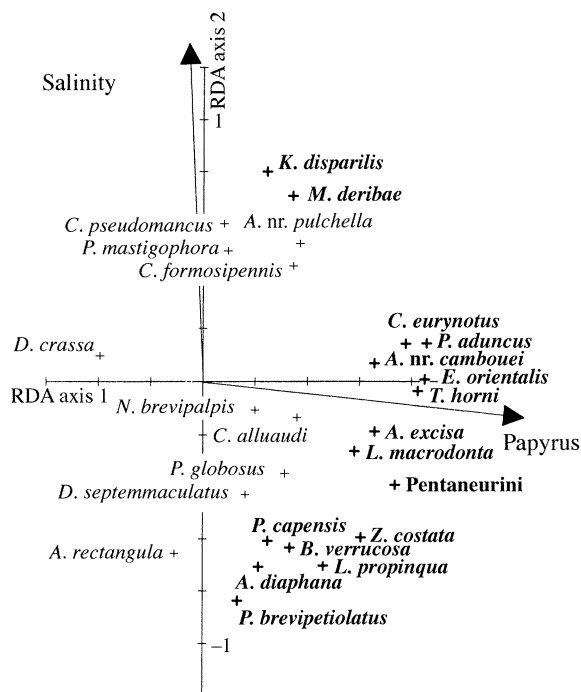


FIG. 8. RDA correlation biplot of the fossil distributions of invertebrate species and the predictor variables salinity and papyrus in Lake Oloidien. RDA axes 1 and 2 together explain 51% of the variance in the species data. Species in bold type have >40% of their fossil distribution accounted for by swamp development and salinity (cf. Table 4).

TABLE 3. Partitioning of the variance in the faunal data set, based on RDA using papyrus, salinity, and lake depth as sole predictor variables, and partial RDA in which one or two environmental factors have been removed as covariable.

Predictor variable	Covariables	% variance explained	P
Papyrus	none	35.6	<0.001***
Papyrus	salinity	35.6	<0.001***
Salinity	none	15.2	0.045*
Salinity	papyrus	15.2	<0.001***
Lake depth	none	15.1	0.035*
Lake depth	papyrus	8.1	0.030*
Lake depth	salinity	13.9	0.036*
Lake depth	papyrus and salinity	5.2	0.095 ^{NS}

Note: The P values are based on Monte Carlo permutation.

and 15.2% to salinity. Lake depth explains a comparable amount (15.1%), but the fraction of variation explained after partialling out the effects of salinity and papyrus (5.2%) is no longer significant, due mainly to covariation between lake depth and papyrus (Table 3).

Multiple linear regression of the fossil distributions of individual invertebrate species against the historical records of lake depth, salinity, and swamp development

generally corroborates the results of multivariate statistics (Table 4). The distribution of 20 (77%) of the 26 common benthic invertebrates in Lake Oloidien displays a significant ($P < 0.05$) to highly significant ($P < 0.001$) linear relationship with one (or two) of the three selected environmental variables. Six of the seven species that suggested a strong salinity effect in RDA show strong correlation with salinity in multiple regression, and all eight species that suggested a strong effect of papyrus swamp in RDA also show correlation with papyrus in multiple regression. Multiple regression does appear to reveal a greater role for lake depth in the regulation of invertebrate populations than was suggested by multivariate statistics. In total, six species (23%) display strongest response to salinity, nine (35%) to papyrus, and five (19%) to lake depth; fossil distributions of the six remaining species (23%) do not show a significant relationship with either depth, salinity, or papyrus.

DISCUSSION

Covariation between lake level, salinity, and swamp development

Our conceptual scheme of benthic habitat diversity in Lake Oloidien (Fig. 3) reflects the broad inverse relationship between lake level and salinity character-

TABLE 4. Effects of papyrus swamp, salinity, and lake depth on the abundance of invertebrate species, based on redundancy analysis and multiple linear regression of fossil distributions in core NO91.1-S against diatom-inferred conductivity, fossil papyrus-seed abundance, and lake depth at the time of burial.

Species	RDA1	RDA2	P			R ²	N	df	DW	AIC
			Papyrus	Salinity	Depth					
<i>Euryalona orientalis</i>	++	—	<0.001***	0.554	0.587	0.77	17	3, 13	2.10*	—
<i>Pleuroxus aduncus</i>	++	—	<0.001***	0.087	0.558	0.71	18	3, 14	1.99*	+
<i>Tanytarsus horni</i>	++	—	<0.001***	0.384	0.358	0.64	18	3, 14	1.35†	—
Pentaneurini	++	—	<0.001***	0.085	0.770	0.63	18	3, 14	1.49	+
<i>Chydorus eurynotus</i>	++	—	<0.001***	0.207	0.750	0.55	18	3, 14	0.98†	—
<i>Alonella excisa</i>	++	—	0.011*	0.913	0.556	0.37	18	3, 14	1.21†	—
<i>Alona</i> nr. <i>cambouei</i>	++	—	0.014*	0.276	0.367	0.36	18	3, 14	2.00*	+
<i>Kiefferulus disparilis</i>	—	++	0.227	<0.001***	0.678	0.66	17	3, 13	1.80*	+
<i>Procladius brevipetiolatus</i>	—	++	0.708	<0.001***	0.531	0.67	18	3, 14	1.77*	+
<i>Alona diaphana</i>	—	++	0.158	<0.001***	0.181	0.52	18	3, 14	1.15	+
<i>Microchironomus deribae</i>	—	++	0.195	0.001**	0.133	0.53	18	4, 13	1.83*	+
<i>Physocypris capensis</i>	—	++	0.505	0.004**	0.377	0.72	17	4, 12	1.04	—
<i>Leydigia propinqua</i>	+	++	0.020*	0.005**	0.632	0.65	18	3, 14	2.12*	+
<i>Biapertura verrucosa</i>	—	++	0.406	0.166	0.008**	0.65	18	3, 14	2.15*	+
<i>Zonocypris costata</i>	+	+	<0.001***	0.002**	0.822	0.83	18	5, 12	1.35	—
<i>Dicrotendipes septemmaculatus</i>	—	—	0.027*	0.916	0.001**	0.82	17	4, 12	1.47	—
<i>Dunhevedia crassa</i>	—	—	0.718	0.816	0.005**	0.47	15	3, 11	2.36*	+
<i>Chironomus alluaudi</i>	—	—	0.162	0.126	0.015*	0.41	18	3, 14	2.80*	—
<i>Potamocypis mastigophora</i>	—	—	0.161	0.917	0.042*	0.30	16	3, 12	1.44	+
<i>Leydigia macrodonta</i>	+	—	0.026*	0.559	0.783	0.29	18	3, 14	2.18*	+
<i>Alona</i> nr. <i>pulchella</i>	—	—	0.182	0.058	0.215	0.23	18	3, 14	1.76*	+
<i>Alona rectangula</i>	—	+	0.442	0.118	0.263	0.29	18	3, 14	1.35	+
<i>Pseudochydorus globosus</i>	—	—	0.403	0.876	0.232	0.12	18	3, 14	2.49*	+
<i>Chironomus formosipennis</i>	—	—	0.782	0.243	0.149	0.02	18	4, 13	1.42	—
<i>Nilodorum brevipalpis</i>	—	—	0.748	0.664	0.258	−0.05	18	3, 14	1.65	+
<i>Cladotanytarsus pseudomancus</i>	—	+	0.165	0.861	0.820	0.12	18	4, 13	1.39	—

Note: The RDA1 and RDA2 columns report the fit to RDA axes 1 and 2 (−, <20%; +, >20%; ++, >40%; ter Braak and Wiertz 1994); DW is Durbin-Watson statistic, shown as significant ($P < 0.05$) when there is no serial autocorrelation in the faunal data; AIC is the Akaike Information Criterion, given as + when met by the regression model without autoregressor terms.

† DW statistic is low due to strings of zero values in both the dependent and explanatory variables.

izing closed-basin lakes, and limited salinity tolerance of many aquatic macrophytes (Hammer 1986); lushly vegetated freshwater conditions tend to prevail at high lake level and poorly vegetated saline conditions tend to prevail at low lake level. At Lake Oloidien, low lake level (depth < 4 m) before 1890 coincided with high conductivity (>10 000 $\mu\text{S}/\text{cm}$) and absence of aquatic vegetation (Fig. 6). During the 1890–1930 period of broad confluence with Lake Naivasha, high lake level (depth ≥ 10 m) coincided with freshwater conditions (≤ 500 $\mu\text{S}/\text{cm}$) and extensive development of papyrus swamp and associated submerged macrophyte beds (Fig. 6).

Variance partitioning of the fossil data (Table 3) supports the notion of covariation between lake depth and papyrus in Lake Oloidien; swamp development requires broad confluence with Lake Naivasha. Little covariation between lake depth and salinity, on the other hand, suggests lack of a clear linear relationship between these two environmental variables. Lake depth and reconstructed salinity fail to covary particularly in the period after 1940 (Fig. 5). First, diatom-inferred conductivity reconstructed from sediments deposited at lowest lake level in 1946 is only ~ 2000 $\mu\text{S}/\text{cm}$. Salinity had not yet increased beyond this modest value because the lowstand was reached only six years after Lake Oloidien had become disconnected from fresh Lake Naivasha (~ 400 $\mu\text{S}/\text{cm}$; Verschuren 1996). Further salinity increase to its reconstructed peak in the late 1950s occurred during the decade 1946–1957 of below-average rainfall (Åse et al. 1986) and continuous strong evaporative concentration at low lake level. Second, reconstructed conductivity values indicate that Lake Oloidien did not return to freshwater conditions (< 1000 $\mu\text{S}/\text{cm}$) until ~ 1970 , while the lowstand had ended with renewed lake-level rise during 1958–1964. Probably, only the reunion of Lake Oloidien with Lake Naivasha in the mid-1960s halted and then reversed the trend of increasing salinity. The clearing in 1975–1977 of rooted papyrus swamp that had covered the Naivasha–Oloidien sill (Åse 1987) promoted freshwater inflow from Lake Naivasha during a second transgressive phase in the late 1970s to early 1980s (Fig. 2). Although the hydrological relationship of Lake Oloidien and Lake Naivasha may be particular, the observed nonlinearity between lake level and salinity is not unique to Lake Oloidien but typical for the transient dynamics that dominate closed-basin hydrology at this time scale (Langbein 1961, LaBaugh et al. 1996).

The lack of covariance between salinity and papyrus in Lake Oloidien is mainly due to the failure of papyrus swamp to become reestablished after the return of freshwater conditions in the 1970s (Fig. 6). Lake Oloidien became sufficiently fresh to allow temporary expansion of submerged macrophytes (Harper 1984, Clark et al. 1989), but there was no regrowth of the papyrus that had been abundantly present during the 1890–1930 highstand. This may be due to several fac-

tors. First, *Cyperus papyrus* is less tolerant of elevated salinity and pH than most other tropical aquatic macrophytes (Howard-Williams 1979, Hammer 1986). Second, with a conductivity of 620–1000 $\mu\text{S}/\text{cm}$ and pH of 9.0–9.2 Lake Oloidien remained significantly more alkaline than Lake Naivasha (233–480 $\mu\text{S}/\text{cm}$; pH 7.7–8.5), where papyrus fringes much of the shoreline today (Harper et al. 1990). Third, germination of papyrus from seed may have been hampered by residual saline porewater in littoral soils (Gaudet 1977). This failure of papyrus to recolonize Lake Oloidien in recent decades despite local conditions well within the tolerance range of most freshwater invertebrates (Williams 1981, Frey 1993), together with lack of covariance between salinity and lake depth, are instrumental to our use of Lake Oloidien's history as a natural experiment into the environmental regulation of a tropical benthic invertebrate community.

Long-term dynamics of the benthic-invertebrate community

Multivariate and univariate statistics both indicate that the presence of papyrus swamp and its associated weedbeds exerted major environmental control on benthic invertebrate community composition in Lake Oloidien. Papyrus explains more than a third of all historical variation in the faunal data (Table 3), and the preponderance of species on the positive side of the papyrus gradient (Fig. 8: RDA axis 1) is a measure of its favorable influence on species diversity. Also in multiple regression (Table 4), more than a third of considered species displays strong response to papyrus. The effects of salinity on community composition, albeit distinct, appear to have been subordinate to those of papyrus and largely independent from them.

The direct physiological effect of high salinity on freshwater biota is osmoregulatory stress (Bayly 1972). Cladocera are typical freshwater organisms in that most species are unable to cope with conductivities above 3000 $\mu\text{S}/\text{cm}$, i.e., a salinity of 3 g/kg (Williams 1981, Frey 1993). Salt-tolerant species within the chydorid Cladocera, as well as many freshwater Ostracoda and Chironomidae, push beyond this limit by means of hyper-osmotic regulation (Bayly 1972, Aladin 1991). Hypo-osmotic regulation has been demonstrated in some halobiont Chironomidae only (Sutcliffe 1960, Lauer 1969), while halobiont Ostracoda are osmotic conformers rather than regulators (Bayly 1972). The strongly positive correlation of *Kiefferulus disparilis* and *Microchironomus deribae* abundance with salinity observed in the Lake Oloidien record (Table 4; Figs. 8 and 9) agrees with faunistic data showing these halobionts to avoid freshwater lakes but thrive in salinities of up to 40 000 $\mu\text{S}/\text{cm}$ (Harrison 1987, Verschuren 1997). The chironomid *Procladius brevipes* and ostracod *Physocypria capensis* display a strongly negative relationship with salinity (Fig. 9). In the case of *P. capensis* this reflects its intolerance for even slightly

elevated salinity (Cohen et al. 1983) and predicts restriction to lakes with a positive water balance. The fact that *Physocypris* is unusual among nonmarine Ostracoda for its swimming rather than benthic lifestyle (Klie 1938) may not be coincidental to its strong salinity response and apparent independence from the variation in benthic habitat diversity linked to changes in lake depth and swamp development.

Most of the common chydorid Cladocera found in Lake Oloidien have occasionally been reported from saline lakes (see Luyten 1934, Löffler 1961, Flößner 1972, Hammer 1986, Frey 1993), demonstrating the tolerance to elevated salinity that promotes faunal resilience to the long-term hydrological instability characterizing their environment. All five chydorid species that show a strong response to papyrus (Fig. 8, Table 4) are typical inhabitants of vegetated littoral habitats where they feed on periphyton (Flößner 1972, White-side and Swindoll 1988, Hann 1990). For example, *Alonella excisa* is an indicator taxon for reed swamp in Europe (Luyten 1934, Amoros 1984). Faunistic data for species with exclusively tropical distribution are scarce, but in Lake Naivasha *Alona* nr. *cambouei* was found most abundantly among submerged macrophytes bordering papyrus swamp (Jenkin 1934). The Chironomidae that show a strong response to papyrus are also all typical members of the so-called "weedbed-fauna" of shallow African lakes fringed with papyrus swamp (Harrison 1987, Kibret and Harrison 1989). Among these, *D. septemmaculatus* is particular in that it has no particular association with papyrus or any other aquatic macrophyte but uses vegetated substrates for tube-building above the mud surface (Gilinsky 1984, Merritt and Cummins 1984). This may explain why it persisted in Lake Oloidien after the demise of papyrus swamp and today occurs in the sparse beds of *Potamogeton pectinatus*.

Because forward selection of predictor variables in RDA withheld only papyrus and salinity as significant environmental factors (Fig. 8), variation partitioning failed to resolve the direct influence on benthic community composition exerted by lake depth. The fraction of total faunal variation explained by lake depth is comparable to that explained by salinity (Table 3), but separation of its overall effect suffers from partial covariance with papyrus. Univariate analysis of the faunal data did identify five species that responded more strongly to lake depth than to either salinity or papyrus (Table 4). The negative relationship of *Dunhevedia crassa* with lake depth is explained by its preference for wave-agitated shallows where particulate organic matter and associated bacteria are in continuous suspension (Fryer 1968); decline toward the conductivity maximum of the late 1950s and rarity during the pre-1890 lowstand reflects its inability to exploit this resource when shallow conditions are accompanied by high salinity. Negative correlation with lake depth in the ostracod *Potamocypris mastigophora* may be re-

lated to its preference for silty and sandy substrates (Tudorancea et al. 1989), which tend to expand during lowstands due to the greater impact of wind stress on sedimentation (Håkanson and Jansson 1983). *Potamocypris* spp. are also known to dwell in areas of subaqueous groundwater discharge (Forester and Smith 1993), which similarly tends to intensify during lowstands (Almendinger 1990). The apparent response of *D. septemmaculatus* to lake depth may be an artifact of its former and current associations with a range of vegetated substrates (cf. above).

The apparently limited effect of either salinity, lake depth, or papyrus on the distribution of six remaining species may be due to failure of this study to capture the environmental factors that control their populations. For some of these taxa, lack of a clear response to the historical range of environmental fluctuation in Lake Oloidien is not unexpected. For example, the data support the status of *Cladotanytarsus pseudomancus* as the most salt-tolerant freshwater chironomid in Africa (Harrison 1987, Verschuren 1997). In the case of the obligate necrophagous chydorid *Pseudochydorus globosus*, long-term persistence in Lake Oloidien is consistent with field data indicating that distribution of its food of decaying animal remains (Fryer 1968) is largely independent of salinity or substrate type (Luyten 1934, Flößner 1972).

CONCLUSION

The eventful history of Lake Oloidien created a 120-yr field experiment permitting paleolimnological analysis of long-term environmental regulation of benthic invertebrate communities in a fluctuating tropical lake. Temporal resolution on the order of 5–8 yr allowed separation of the effects of lake level, salinity, and papyrus-swamp development, while averaging (smoothing) the short-term and spatial variability in population abundance that often confounds sought-after patterns in field studies (Tilman 1989, Anderson 1995, Carpenter 1996). Although establishment of correlation between population abundance and selected environmental factors may fall short of elucidating the proximate cause for population expansion and decline, the results of this study prompt two conclusions.

First, our data support critiques (Hammer and Heselstine 1988, Williams et al. 1990) of the ecological significance of salinity in individual closed-basin lakes. They suggest that a significant portion of observed regional correlation between salinity and benthic-invertebrate community composition (Tudorancea et al. 1989, Walker et al. 1995) may be an indirect effect of broad but diffuse relationships between salinity and the distribution of specific types of benthic habitat. Because medium-term (i.e., decade-scale) environmental change in individual closed-basin lakes usually remains limited to a relatively narrow portion of this salinity gradient, direct osmoregulatory stress may play a subordinate role in the regulation of local invertebrate

community structure. Population abundance will be controlled more directly by the availability of preferred substrate and microhabitat, which itself is determined by lake depth and the chemical ecology of local aquatic vegetation. In principle, the same may also be true for the regional correlation between salinity and diatom community composition on which depends the diatom-based salinity reconstruction. However, superior test performance of diatom-based salinity-inference models (Wilson et al. 1994, Gasse et al. 1995) as compared to similar models using Cladocera or Chironomidae (Walker et al. 1995, Bos et al. 1996) demonstrates that water chemistry alone explains a substantially larger fraction of the species composition of diatom communities than of benthic-invertebrate communities.

Second, independence of the effects of salinity and papyrus on the benthic-invertebrate community of Lake Oloidien reflects both the lack of covariance between these environmental factors and the generally individualistic nature of species response to long-term environmental change. This observation is consistent with the predicted (Menge and Sutherland 1976, Pimm 1982) and observed (Closs and Lake 1994) simplicity of community structure in fluctuating aquatic systems, and illustrates the rather uncohesive and ephemeral nature of insect species associations that becomes even more evident at time scales of 10^3 – 10^4 yr (Elias 1994). Groups of species respond similarly to environmental change if their habitat or limiting resource is under similar environmental control. Synchronous response of a third of the 26 common invertebrate species in Lake Oloidien to expansion and decline of papyrus swamp is consistent with field data documenting high species diversity in vegetated habitats (Merritt and Cummins 1984, Harrison 1987, Hann 1990), and predicts that the maximum rate of change in aquatic-invertebrate community structure along a regional salinity gradient will coincide with the tolerance limits of keystone aquatic macrophytes.

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