

Long-term dynamics of algal and invertebrate communities in a small, fluctuating tropical soda lake

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Abstract

Lake Sonachi, Kenya, is a small alkaline-saline crater lake that over the past 175 years has experienced considerable fluctuations in lake depth ($Z_{\max} = 3\text{--}18\text{ m}$) and an alternation of meromictic and holomictic episodes lasting from a few years to several decades. Paleolimnological methods were used to reconstruct the long-term dynamics of algal and invertebrate communities in Lake Sonachi in relation to the historical evolution of their physical and chemical environment. Multivariate statistical analysis revealed only weak correlation between the stratigraphic distributions of fossil algal pigments, diatoms, and chironomid larvae in ²¹⁰Pb-dated sediment cores and the documented or reconstructed variation in lake depth, mixing regime, and surface-water conductivity. The eventful biological history of Lake Sonachi exemplifies the complexity of long-term community dynamics in tropical African soda lakes and reveals how phytoplankton community structure can exert direct control on benthic and planktonic invertebrate communities. The modest phytoplankton abundance and photosynthetic activity of Lake Sonachi when compared with other tropical African soda lakes represent recent lake conditions, resulting from a dramatic decline of filamentous cyanobacteria (e.g., *Spirulina platensis*) between the 1930s and 1970s and incomplete replacement by the small coccoid cyanobacteria (e.g., *Synechococcus bacillaris*), which are dominant today. This reduction in algal biomass favored benthic and planktonic invertebrates by reducing the prevalence of complete water-column anoxia associated with intense nighttime respiration of cyanobacterial blooms. Anoxia-intolerant halobiont chironomids expanded during an episode of low lake level ($Z_{\max} < 4\text{ m}$), holomixis, and high conductivity ($>9,000\ \mu\text{S cm}^{-1}$) in the late 1940s and 1950s, whereas they had failed to do so under similar conditions in the late 19th century when algal abundance was high. Planktonic cladocerans developed high population densities only during two short meromictic phases in the 1970s when conductivity was modest ($3,000\text{--}6,000\ \mu\text{S cm}^{-1}$) and algal abundance was low. The decline of filamentous cyanobacteria also increased water-column transparency but apparently did not increase benthic diatom abundance.

Alkaline-saline lakes, or soda lakes, in tropical Africa are inhabited by specialized biota that can tolerate high water temperature, high salinity, and low oxygen solubility (Hecky and Kilham 1973; Talling 1992). Most of these organisms also possess highly developed strategies of diapause and dis-

persal that allow them to persist in arid landscapes where scarce aquatic habitats are hydrologically unstable and of marginal quality. Floristic and faunistic surveys conducted over the past 70 yr (Beadle 1932; Jenkin 1936; Hecky and Kilham 1973; LaBarbera and Kilham 1974; Gasse et al.

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1983; Wood and Talling 1988; Tudorancea et al. 1989) established that the biological diversity and community structure of African soda lakes are controlled primarily by salinity and the degree of environmental stability. Because many African soda-lake taxa are widely distributed in a large range of salinities, one would expect the response of soda-lake communities to climatically driven environmental change at time scales of years to decades to be rather small. However, field monitoring of individual soda lakes (Kalk 1979; McLachlan 1979; Vareschi and Vareschi 1984; Melack 1988) has indicated that the algal and invertebrate communities of these lakes are highly sensitive to environmental change and that taxa can become locally extirpated following salinity fluctuations well within known tolerance ranges. These observations indicate that soda-lake communities are regulated by a variety of environmental factors, among which salinity may be important but not necessarily decisive for survival. Other factors may include nutrient or food availability, temporal variation in dissolved oxygen, water-column transparency, and the stability of various substrata available to benthic organisms. Unfortunately, covariance of these factors in the course of both seasonal and multiannual hydrological cycles has made it difficult to separate their respective effects on observed patterns of species replacement and community reorganization (McLachlan 1979; Melack 1988).

Hydrological models and long-term monitoring of shallow closed-basin lakes (Langbein 1961; Crowe 1993; LaBaugh et al. 1996) indicate that on time scales of years to decades these systems display significant nonlinearity between depth and salinity. Thus, if changes in biologically important environmental factors such as substrate quality or oxygen concentration can be mechanistically linked to changes in lake depth or salinity, it should be possible to independently evaluate their effects on a biological community by collecting environmental and community data over a sufficiently long period of time. Paleolimnology can provide such long-term data, if the sediment record of biological history is continuous and contains information that can be resolved at the appropriate time scale (Anderson 1995). We used paleolimnological methods to investigate the long-term regulation of algal and invertebrate communities in Lake Sonachi, a small soda lake in Kenya that combines a 115-yr record of documented lake-level fluctuations with a detailed sedimentary record of the consequent changes in mixing regime and bottom dynamics (Verschuren 1999a). This is the first direct comparison of taxonomically resolved community data from an African soda lake with environmental data at the ecologically relevant time scale of multiannual hydrological cycles.

Study site

Lake Sonachi is a small (0.14 km²), shallow ($Z_{\max} = 4.25$ m in 1993), alkaline-saline crater lake located at 1,884 m above sea level in the semiarid Rift Valley of central Kenya. Much of the monsoonal rainfall in the region is intercepted by surrounding highlands, so that annual rainfall averages only 680 mm (1951–1980; MacIntyre and Melack 1982; Åse et al. 1986) whereas annual evaporation is 1,865 mm

(1966–1982; Åse et al. 1986). The water level of Lake Sonachi is maintained against this strong moisture deficit by subsurface flow from nearby Lake Naivasha, a large (135 km²) but similarly shallow ($Z_{\max} = 6$ m) freshwater lake fed by rivers draining the wet highlands of the Kinangop Plateau and Nyandarua Range (Gaudet and Melack 1981; Darling et al. 1990). Historical depth soundings in Lake Sonachi (1929–1993; $n = 17$), hydrological data (MacIntyre and Melack 1982; Darling et al. 1990), and observations of synchronous lake-level change (Njuguna 1988) all point to a strong groundwater connection between the two lakes and suggest that the continuous 115-yr lake-level record of Lake Naivasha can be extrapolated to Lake Sonachi (Fig. 1; Verschuren 1999a).

The salt budget of Lake Sonachi is controlled by rainfall and evaporation at the surface and dissolution of sedimentary evaporites by percolating groundwater. Wind shelter from the high crater rim promotes shallow density stratification, with the chemocline typically at 4 m depth. The upper water column undergoes a daily cycle of thermal stratification (2–3°C) in the morning and mixing in the afternoon and at night (Melack 1982). Low lake level ($Z_{\max} \leq 5$ m) prevailing since 1985 precludes year-round density stratification, but Lake Sonachi was meromictic during much of the 1970s and early 1980s at lake levels only slightly higher than today ($Z_{\max} = 7$ –8 m; MacIntyre and Melack 1982; Njuguna 1988) and also during the period 1890–1945 (Verschuren 1999a). As in other African soda lakes, the ionic composition of lake water is dominated by sodium and bicarbonate, and pH is very high (9.0–10.3; Kilham 1971; Melack 1981). Surface-water conductivity (K_{25}) since 1929 ranged from 3,000 to 11,550 $\mu\text{S cm}^{-1}$, and years with good data coverage show seasonal fluctuation on the order of 1,000–2,000 $\mu\text{S cm}^{-1}$ (Verschuren 1996).

Field study in the 1970s established that Lake Sonachi is phosphorus limited (Peters and MacIntyre 1976; Melack et al. 1982), and both phytoplankton abundance (21–68 mg chlorophyll *a* [Chl *a*] m^{-3}) and photosynthetic activity (150–870 mg O₂ $\text{m}^{-2} \text{h}^{-1}$) at that time were modest compared with those of other African soda lakes (Melack 1981, 1982). In 1980–1981, the algal community was dominated by small coccoid cyanobacteria, with *Synechococcus bacillaris* contributing an average of 53% (16–75%) to monthly algal biomass (Njuguna 1988). Other common planktonic cyanobacteria were *Lyngbya limnetica*, *Synechocystis aquatilis*, *Spirulina laxissima*, and *Spirulina platensis*, whereas planktonic diatoms and green algae were scarce; *Nitzschia* spp. averaged 2% of monthly algal biomass, and *Nannochloris* sp. reached 1% only in the dry season. In 1979, the same assortment of cyanobacteria was found but green algae also included *Chlorella* sp. and *Oocystis parva* (Kalff and Watson 1986). Modern phytoplankton composition contrasts with that observed in 1929 and 1931 (Beadle 1932; Rich 1932; Jenkin 1936), which appeared to be entirely dominated by filamentous cyanobacteria, most notably *S. platensis*. Diatom flora in littoral plankton and periphyton collected in the 1970s (Melack 1982; Gasse 1986) contained *Anomoeoneis sphaerophora*, *Craticula elkab*, *Navicula cryptocephala* var. *veneta*, *Nitzschia frustulum*, *Nitzschia* cf. *latens*, *Nitzschia sigma*, and *Rhopalodia gibberula*.

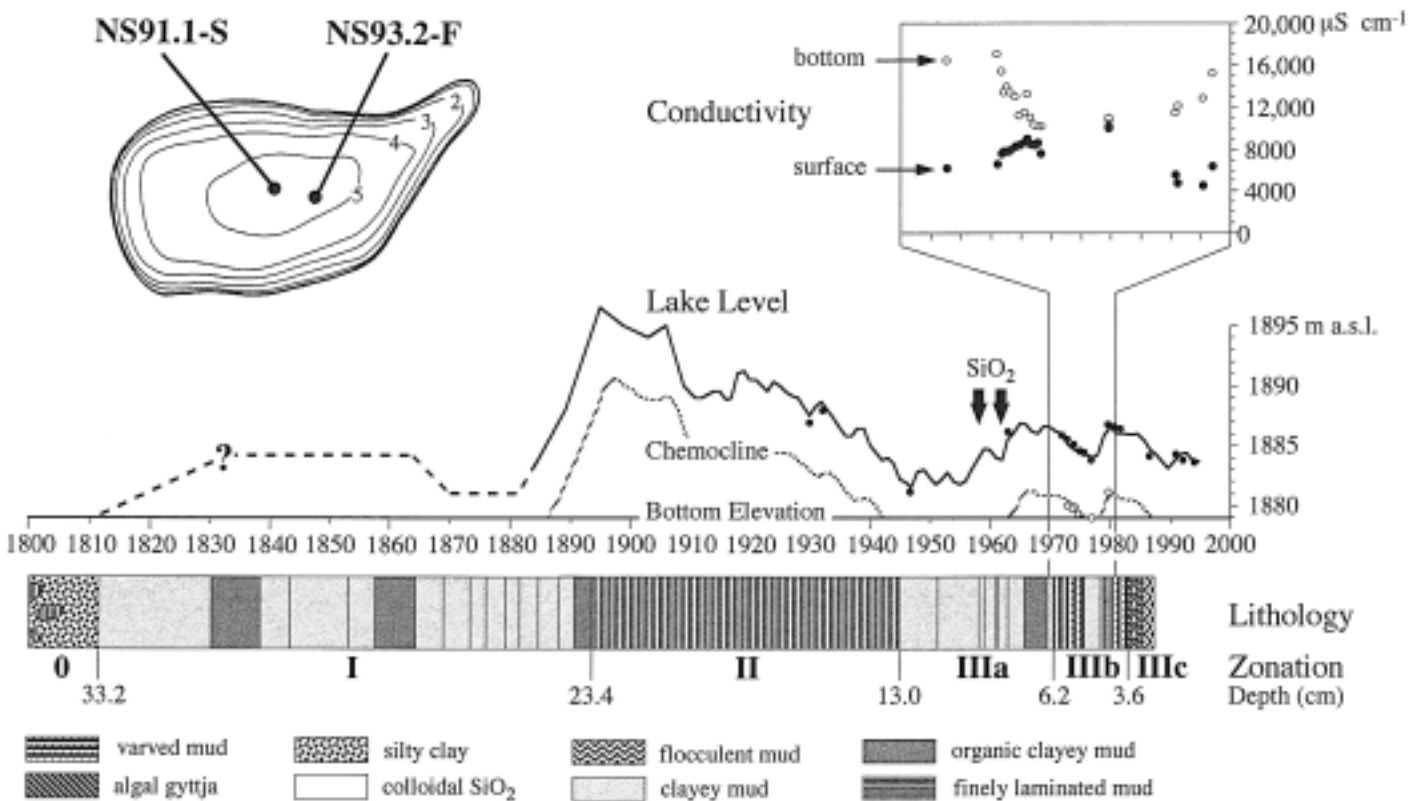


Fig. 1. Sediment chronology, lithology, and stratigraphic zonation (units 0–IIIc) of freeze-core NS93.2-F from Lake Sonachi, fitted to a linear time axis for comparison with historical fluctuations in lake depth (●, solid line) and measured or inferred chemocline depth (○, dashed line). *Inset*: Bathymetry of Lake Sonachi with core sites. Modified from Verschuren (1999a).

The zooplankton community of Lake Sonachi is poor in species and apparently erratic in its occurrence. De Beauchamp (1932) found the salt-tolerant planktonic rotifer *Brachionus dimidiatus* in 1929, and Beadle (1932) encountered the calanoid copepod *Paradiaptomus africanus* in 1931. No zooplankton have been reported since then, although this may in part reflect the scarcity of zooplankton sampling in later field studies. In 1984 (Clark et al. 1989), the nearshore zoobenthos consisted exclusively of larval Chironomidae (*Kiefferulus disparilis*, *Microtendipes* sp., and *Cladotanytarsus pseudomancus*), with a total density of 13,500 organisms m^{-2} . Other aquatic insects reported to occur in Lake Sonachi include eight species of salt-tolerant Hemiptera and three species of Coleoptera (Hutchinson 1932; Clark et al. 1989).

Methods

Chronostratigraphy of the Lake Sonachi sediment record—The stratigraphy of fossil algal pigments, diatoms, and aquatic invertebrates in two sediment cores describes the environmental history of Lake Sonachi since its last complete desiccation in the early 19th century. Field techniques, core lithology, and chronostratigraphy were previously described by Verschuren (1999a). Piston-core NS91.1-S (35 cm long) was collected in 1991 and extruded in the field with a fixed-interval (1.0 cm) sectioning device (Verschuren 1993). Freeze-core NS93.2-F (37.2 cm) was collected in 1993, returned from the field intact, and sectioned in 50 in-

crements of variable thickness (0.3–1.7 cm) with a miniature chisel while cooled on a bed of dry ice. Increment boundaries were chosen to coincide with visible lithostratigraphic boundaries so that fossil data obtained from each increment could be directly related to specific bottom dynamics at the time of burial. Freeze-coring caused slight resuspension of flocculent material at the mud–water interface; consequently, the reference depth of 0.0 cm in NS93.2-F was assigned to the uppermost undisturbed sediment horizon, which corresponds to a sediment depth of 2.5 cm depth in NS91.1-S. Core chronologies were determined by ^{210}Pb dating, with sediment ages and accumulation rates calculated using the constant rate of supply (CRS) model (Appleby and Oldfield 1978). Consistent depth–age relationships were obtained by setting the collection date of core NS93.2-F to 1988, equal to sediment age at 2.5 cm depth in NS91.1-S.

Recent offshore sediments in Lake Sonachi consist of alternating sections of finely and coarsely laminated muds, reflecting changes in bottom dynamics over time as determined by lake depth and mixing regime (Verschuren 1999a; Fig. 1). These soft muds overlie the stiff silty clays of a desiccation surface (unit 0) that was formed when the lake dried completely in the early 19th century. Lacustrine muds deposited since that time comprise three well-defined lithostratigraphic units that are common to all four basins of the Lake Naivasha system (Verschuren 1999b). Unit I (33.2–23.4 cm depth in NS93.2-F, 30–22 cm in NS91.1-S) consists of coarsely laminated muds deposited under a holomictic

regime at low or intermediate lake level between the early 19th century lake filling and about 1890 (Åse et al. 1986). Unit II (23.4–13.0 cm, 22–15 cm) consists of finely laminated (~1 mm) organic clayey muds, deposited between 1890 and 1945 during a period of stable meromixis and mostly high lake level. Unit III (13.0–0.0 cm, 15–0 cm) contains both coarsely and finely laminated muds deposited after 1945. Subunit IIIa (13.0–6.2 cm, 15–9 cm) consists of coarsely laminated ochreous muds deposited under a holomictic regime during the lowstand of 1945–1957 and subsequent lake-level rise in the late 1950s and 1960s; the sequence is interbedded by two pale horizons of colloidal, nonbiogenic amorphous silica that precipitated out of the water column at the start of renewed lake-level rise in the late 1950s (Verschuren 1999a). Subunit IIIb (6.2–3.6 cm, 9–5 cm) comprises two sections of finely laminated muds deposited when Lake Sonachi was meromictic during the 1970s and early 1980s. This subunit is interbedded by a 4-mm-thick horizon of unlaminated ochreous mud deposited under an inferred holomictic regime during a short-lived lowstand in the late 1970s. Subunit IIIc (3.6–0.0 cm, 5–0 cm) was deposited under holomixis and low lake levels since 1983 and consists of layers of olive-green gyttja alternating with flocculent muds containing partly decomposed algal remains. Correspondence between changes in mixing regime inferred from the lithology and the historical record of lake depth (Fig. 1), and little variation in measured chemocline depth (4.1 ± 0.4 m, $n = 7$), support arguments based on wave theory (Verschuren 1999b) that chemocline depth may be assumed constant through time (Fig. 1; cf. Lowe et al. 1997).

A high degree of similarity between the ^{210}Pb activity profiles of both cores and strong correlation between their time-normalized organic-matter stratigraphies ($r^2 = 0.71$, $P < 0.001$) indicate that temporal variation in sedimentation at the two core sites has been similar (Verschuren 1999a) and thus that fossil data from both cores are representative of lake history. In NS93.2-F, which has the highest time resolution and offers strict correspondence of sample boundaries with visible sedimentary structure, the chronology of inferred changes in mixing regime is anchored in six marker horizons supported by independent historical evidence and four horizons that can be linked to the historical lake-level record by assuming constancy of chemocline depth over time (Verschuren 1999a). Excellent agreement between the ^{210}Pb -inferred ages of these horizons and the documented or estimated age of the events that created them provides a solid basis for use of lithostratigraphy as a record of past changes in mixing regime.

Laboratory procedures—Fossil algal pigments were analyzed in 50 contiguous depth increments of core NS93.2-F. Pigments were extracted from freeze-dried subsamples in an 80:15:5 mixture of acetone:methanol:water and quantified by reverse-phase high-performance liquid chromatography. Carotenoids, chlorophylls, and their derivative compounds were identified on the basis of spectrophotometric characteristics and cochromatography with authentic standards (Leavitt et al. 1989; Leavitt and Findlay 1994). Lake Sonachi sediments contain >50 pigments, but many of these occur

infrequently or at low concentration. Our analysis here is restricted to β -carotene, a chemically stable pigment indicating total algal abundance (Leavitt et al. 1989, 1994), and the common taxon-specific pigments alloxanthin (cryptophytes), diatoxanthin (diatoms), myxoxanthophyll (filamentous cyanobacteria), lutein-zeaxanthin (green algae and cyanobacteria), and chlorophyll *b* (Chl *b*) (green algae). The relative abundance of green algae and cyanobacteria was estimated by comparing lutein-zeaxanthin concentrations with those of Chl *b* and its pheopigment derivative pheophytin *b*. The relative abundance of filamentous and nonfilamentous cyanobacteria was estimated by comparing the percent abundances of myxoxanthophyll and lutein-zeaxanthin relative to the those of the three other major taxon-specific pigments. The fossil pigment data are presented here as organic-matter (OM)-specific pigment concentrations ($\text{nmol pigment [g OM]}^{-1}$) because comparison of long-term live plankton data with varved fossil pigment records indicate that this metric most accurately captures historical variations in algal abundance and community composition (Leavitt and Findlay 1994; Leavitt et al. 1997). In many lakes, postdepositional pigment degradation can bias estimates of algal abundance based on fossil pigment accumulation rates (Leavitt and Findlay 1994). Organic-matter-specific pigment concentrations are less influenced by such preservation artifacts because bulk organic matter and algal pigments degrade at a similar rate (Leavitt 1993; Leavitt and Findlay 1994). Comparison of surface sediment and downcore fossil pigment assemblages in Canadian closed-basin lakes further demonstrated that fossil pigments accurately record the patterns and thresholds of algal community change known from surveys of the living algae (Vinebrooke et al. 1998).

Fifty samples from core NS93.2-F were processed for quantitative diatom analysis by oxidation with hydrogen peroxide, digestion in acetic acid, and repeated dilution (Schradler 1974). Aliquots (50- μl) of the final dilution were transferred to microscope slides and mounted in Naphrax[®]. Diatoms were identified with reference to the works of Gasse (1986), Krammer and Lange-Bertalot (1986, 1988, 1991), and Round et al. (1990) and were counted at $\times 1,000$ magnification with a Leitz Diaplan microscope equipped with differential interference contrast optics. Diatom preservation is generally good in the lacustrine muds above unit 0, with the fraction of broken valves averaging 19% ($\pm 13\%$; coefficient of variation [CV] = 0.68) of total counts. Total diatom abundance is presented as number of frustules [$\text{g dry weight}]^{-1}$. Total abundance varies over four orders of magnitude between individual sediment horizons, hence patterns of diatom accumulation ($\text{frustules cm}^{-2} \text{ yr}^{-1}$) are similar to those of diatom abundance, notwithstanding six-fold variation in bulk sediment accumulation rate (Verschuren 1999a). These patterns also dominate accumulation profiles of individual species; therefore, stratigraphic zonation of species assemblages and other statistical procedures were based on percent abundance. To eliminate undue influence of rare taxa, only taxa reaching 2% in at least one sample ($n = 27$) were included in these analyses. Diatom-inferred values of past surface-water conductivity were calculated with a weighted-average regression and calibration model (ter Braak 1990) based on conductivity optima for individual

taxa derived from a reference data set of diatom floras in 164 African lakes with known water chemistry (Gasse et al. 1995). Problematic morphotypes, e.g. *Nitzschia* cf. *latens* and *Nitzschia* cf. *fonticola*, were assigned values for the nominate species, although they may not necessarily occupy the same ecological space (Cox 1994). Because of underrepresentation in the reference data set, the conductivity optima of *Nitzschia pura* and *N. cf. latens* are rather poorly defined, which may have introduced a bias in the absolute values of conductivity estimates for depth horizons in which these species are common. Descriptive salinity classification is modified after that of Gasse et al. (1987): freshwater: <500 $\mu\text{S cm}^{-1}$, oligosaline: 500–5,000 $\mu\text{S cm}^{-1}$, mesosaline: 5,000–20,000 $\mu\text{S cm}^{-1}$, polysaline: 20,000–40,000 $\mu\text{S cm}^{-1}$, and metasaline: >40,000 $\mu\text{S cm}^{-1}$.

Fossil invertebrates were analyzed in 34 contiguous 1-cm increments of core NS91.1-S. Subsamples (2.0–10.0 ml) were prepared by dispersing the sediment matrix in warm 10% potassium hydroxide (Walker and Paterson 1985) and rinsing through 250- μm and 105- μm mesh sieves. The retained residues were scanned at $\times 25$ under a Wild M10 dissecting microscope, and remains of planktonic cladocerans, benthic cladocerans, chironomids, and other aquatic arthropods were identified at $\times 40$ –100. Cladocerans were identified with reference to the works of Jenkin (1934), Goulden (1968), Smirnov (1971) and a collection of intact specimens from Lake Naivasha. Chironomids were identified using primary taxonomic literature and reference material from private and museum collections (Verschuren 1997). In the event of uncertainty, specimens were picked from the residue and mounted in glycerine on semipermanent microscope slides for identification at $\times 400$. All prepared samples were searched entirely, and counts for each taxon in the two size fractions were summed. The samples yielded an average of 104 (31–192) chironomid fossils; cladoceran fossils (0–257 per sample) were concentrated in a few horizons at 4–10 cm depth. The invertebrate data are presented as fossil accumulation rates (fossils $\text{cm}^{-2} \text{yr}^{-1}$), based on studies suggesting that their preservation in sediments of this age is complete and taxon independent (Walker et al. 1984; Frey 1988). Statistical treatment was limited to the eight most common chironomid species, which together comprise an average of 97% (81–100%) of the fossil chironomid sum.

Statistical procedures—Biostratigraphic zonation of fossil pigment, diatom, and chironomid assemblages was established with the stratigraphically constrained clustering procedure CONISS (Grimm 1987), and compared with lithostratigraphy to evaluate community response to changes in mixing regime. Guided by the biostratigraphic zonation to label and group samples (i.e., species assemblages or communities), correspondence analysis (CA) was used to visualize changes in community composition through time in relation to the two main directions of variation in the data. Samples from unit 0 were omitted because desiccation and subaerial reworking of these sediments is likely to have corrupted fossil preservation. Rare taxa were downweighted to limit their influence on the general pattern of community change, and Hill's scaling (ter Braak 1990) was used to minimize the shortening of ecological distance at the ends of

the ordination axes that is inherent to CA; otherwise the analyses involved no data manipulation or transformation. Detrended correspondence analysis yielded sample configurations similar to those of CA for all three data sets; hence, detrending was not warranted and the results of the statistically more neutral CA were retained. Community response to lake depth and salinity was evaluated by canonical correspondence analyses (CCA), a direct gradient technique in which the fossil distributions are treated as response variables and the documented or reconstructed changes in specific environmental factors as predictor variables (ter Braak and Prentice 1988; Sluiter et al. 1995). The lake depth corresponding to a particular core sample was calculated by linking the historical lake-depth record of Lake Naivasha (Fig. 1) to ^{210}Pb -inferred sample ages; samples deposited before 1880 (>26.6 cm depth in NS93.2-F, >25.0 cm in NS91.1-S) were excluded from this analysis. Because diatom-inferred conductivity estimates were used as a proxy for salinity, CCA constrained to salinity was performed only on the fossil pigment and chironomid data. Statistical significance of CCA Axis 1 for both data sets was tested with Monte Carlo permutation tests (ter Braak 1990; Lotter and Birks 1993). All the multivariate statistical analyses of the fossil and environmental data were performed with the program CANOCO 3.12 (ter Braak 1990).

Results

Algal pigments—Concentrations of β -carotene and all taxon-specific pigments are low in unit 0 (Fig. 2), reflecting the severe degradation of algal pigments during subaerial exposure on a dry lake bed. Fossil pigment concentrations increase sharply immediately above unit 0, in agreement with the lithostratigraphic evidence for lake filling at the base of unit I. The high concentrations ($\sim 1,000$ – $4,000 \text{ nmol [g OM]}^{-1}$) of β -carotene, myxoxanthophyll, and lutein-zeaxanthin in Lake Sonachi sediments are characteristic of meromictic (Brown et al. 1984; Leavitt et al. 1989) and eutrophic (Leavitt et al. 1994) lakes with good pigment preservation. Taxon-specific pigments derived from cyanobacteria (lutein-zeaxanthin, myxoxanthophyll) are an order of magnitude more abundant than pigments with similar chemical stability (Hurley and Armstrong 1990; Leavitt and Carpenter 1989) derived from eukaryotic algae (diatoxanthin, alloxanthin), clearly indicating that the algal community of Lake Sonachi has always been dominated by cyanobacteria. Low concentrations of Chl *b* (Fig. 2) and absence of its derivatives pheophytin *b* and pheophorbide *b* (not shown) indicate that green algae were always rare and that the high lutein-zeaxanthin concentrations are realized primarily by zeaxanthin derived from cyanobacteria.

CCA of organic-matter-specific pigment concentrations defines six biostratigraphic zones, P1–P6 (Fig. 2), that correlate favorably with the lithostratigraphic record of past changes in mixing regime, except that zone P3 singles out a group of unit II samples that combine high concentrations of myxoxanthophyll and lutein-zeaxanthin with low concentrations of Chl *b*. The near-identical relative abundance of the two cyanobacterial pigments in zone P3 (Fig. 2) suggests

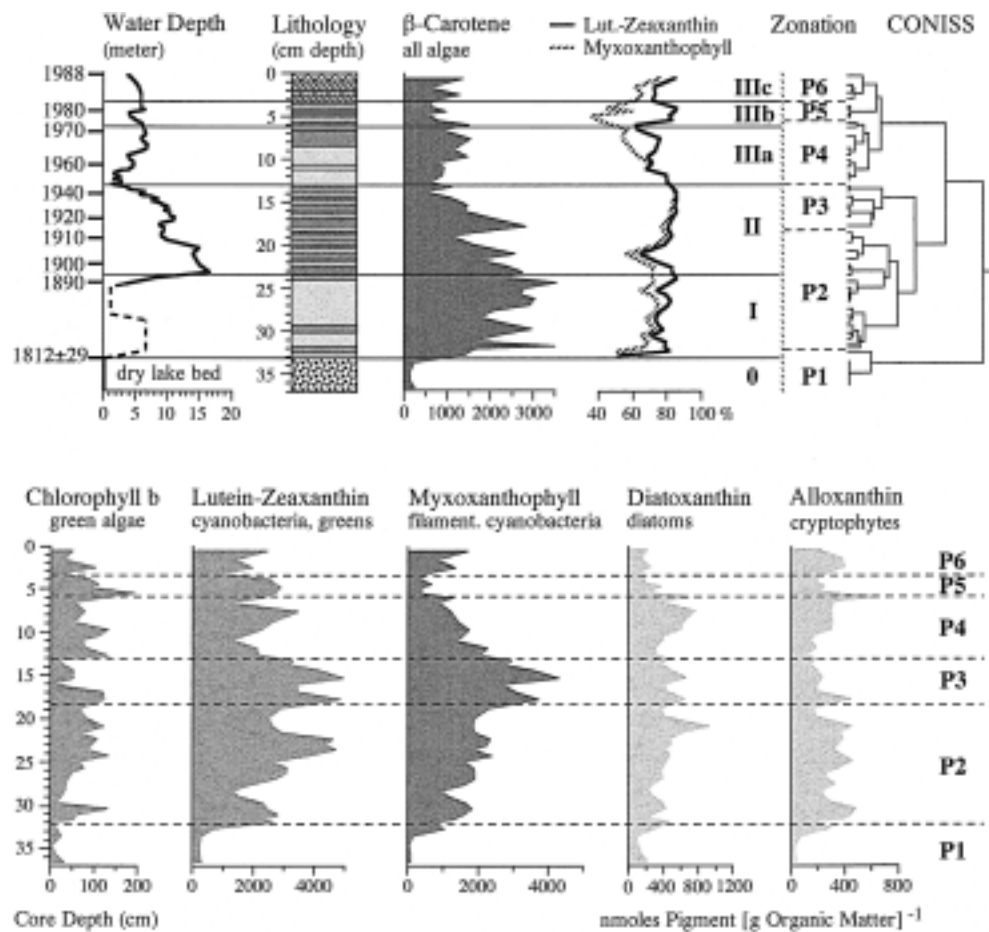


Fig. 2. Organic-matter-specific concentrations, percent abundances, and stratigraphic zonation (P1–P6) of fossil algal pigments in freeze-core NS93.2-F in relation to core chronology, lithology, and the historical lake-level record. Note the variable scale of pigment concentration units.

predominance of filamentous cyanobacteria during this period of highest algal biomass. Despite the inferred dominant contribution of cyanobacteria to total algal abundance, stratigraphic patterns of lutein-zeaxanthin and myxoxanthophyll differ from that of β -carotene. β -Carotene reaches peak concentrations in zone P2, followed by a 50–75% decrease towards the top of P3 and relatively constant values in P4–P6. Myxoxanthophyll declines from maximum concentrations of $>4,000$ nmol [g OM] $^{-1}$ in zone P3 sediments deposited around 1930 to minima of <500 nmol [g OM] $^{-1}$ in zone P5 during the 1970s and early 1980s. Stratigraphic patterns of lutein-zeaxanthin generally follow those of myxoxanthophyll, except that high percent abundance of lutein-zeaxanthin relative to myxoxanthophyll in upper P4, P5, and P6 sediments (Fig. 2) indicates that nonfilamentous cyanobacteria partly compensated for the recent decline in filamentous cyanobacteria. Fossil concentrations of alloxanthin and diatoxanthin are low and show few distinct patterns, except that diatoxanthin reaches peak concentrations at about 32 cm (dated to about 1810–1820), 22–21 cm (1900–1906), and 10–7 cm (1958–1973), during episodes of lake transgression (Fig. 1).

Diatoms—Fossil diatom analysis in core NS93.2-F yielded 93 taxa, most of which are regular elements of the African soda-lake flora. In particular, the common diatoms *Anomoeoneis sphaerophora*, *Rhopalodia gibberula*, *Craticula elkab*, *Nitzschia* cf. *latens*, and *N. pura* form an assemblage characteristic of shallow alkaline-saline lakes with conductivities of $>10,000$ $\mu\text{S cm}^{-1}$ and a pH of >9.4 (Hecky and Kilham 1973; Gasse 1986).

Biostratigraphic zonation of the fossil diatom flora comprises six zones, D1–D6, that show little obvious relationship with the lithostratigraphic record of past mixing regimes (Fig. 3). Zone D1 (37.2–30.1 cm) groups samples from unit 0 and the lower third of unit I. Unit 0 samples form a sub-zone with a high degree of internal similarity, consistent with their recovery from the disturbed muds of a desiccation horizon. These samples contain mostly meso- and polysaline halophilic diatoms (*Anomoeoneis sphaerophora*, *Craticula elkab*, *Nitzschia* cf. *latens*, *N. pura*). Zone D1 samples from unit I were deposited during the initial phase of early 19th century lake filling. They show strong development of the benthic mesosaline *A. sphaerophora* followed by invasion of freshwater-oligosaline taxa (*Nitzschia fonticola*, *Fragilaria*

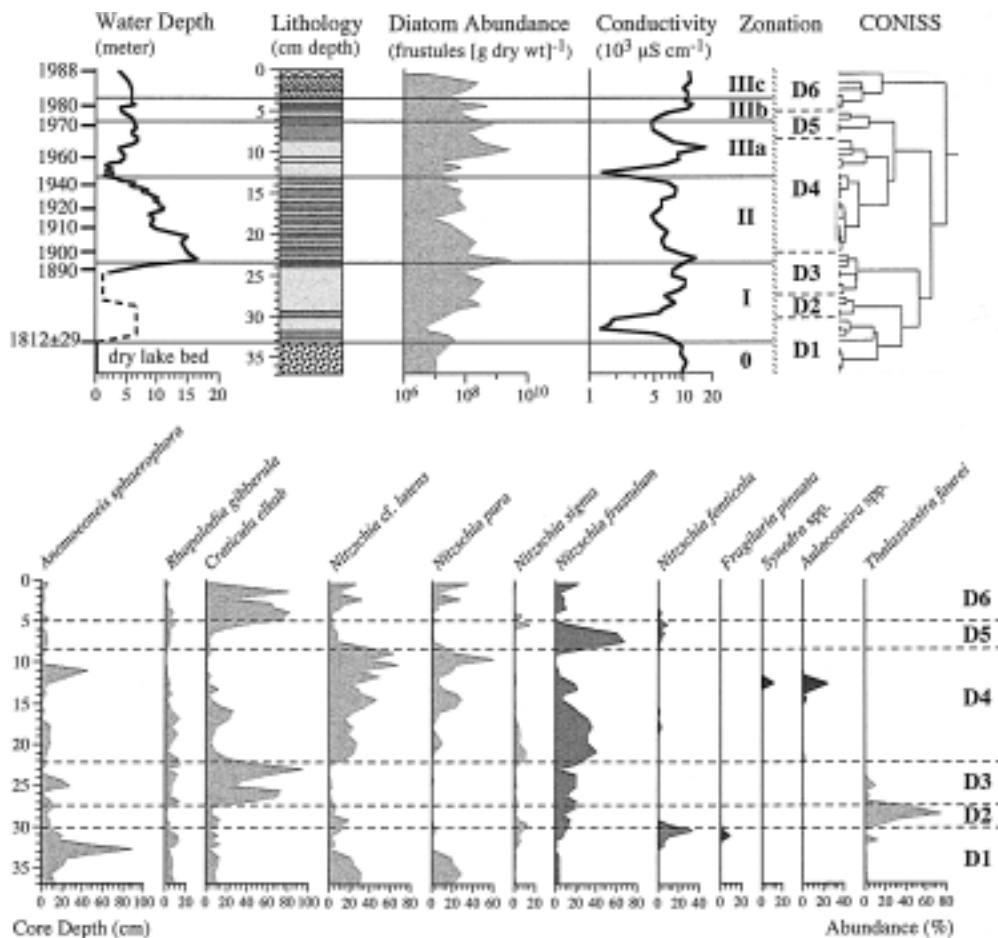


Fig. 3. Total diatom density, percent abundances, inferred surface-water conductivity, and stratigraphic zonation (D1–D6) of fossil diatoms in freeze-core NS93.2-F in relation to core chronology, lithology, and the historical lake-level record.

pinnata) and declines of the halophilic taxa *N. pura*, *N. cf. latens*, and *N. frustulum*. Diatom-inferred conductivity indicates that Lake Sonachi started out at ca. $7,000 \mu\text{S cm}^{-1}$ and then freshened to ca. $1,500 \mu\text{S cm}^{-1}$ by about 1850.

Zone D2 (30.1–27.3 cm) represents a 20-yr period in the mid-19th century when Lake Sonachi apparently became deeper but also more saline. Diatom-inferred conductivity increased to $5,500$ – $8,200 \mu\text{S cm}^{-1}$ with the expansion of *Nitzschia cf. latens* and *N. sigma*, emergence of the mesosaline pelagic species *Thalassiosira faurei*, and disappearance of freshwater taxa (Fig. 3).

Zone D3 (27.3–22.2 cm) broadly coincides with the lowstand period before 1883 (Fig. 1). Diatom assemblages in this zone are mainly composed of mesosaline benthic taxa (*Rhopalodia gibberula*, *Craticula elkab*, *Nitzschia frustulum*); diatom-inferred conductivity ranges between $7,000$ and $13,000 \mu\text{S cm}^{-1}$, with variability driven primarily by fluctuations in *Anomoeoneis sphaerophora* and *C. elkab*.

Zone D4 (22.2–8.4 cm) comprises lake history from ca. 1900 to 1966, which includes the early 20th century period of high lake level, progressive decline to the historical lowstand of the late 1940s and early 1950s, and subsequent rise during the late 1950s and early 1960s (Fig. 1). This zone

starts with a drastic reduction of *Craticula elkab* and increased abundance of facultatively planktonic species with mostly lower salinity optima (*Nitzschia frustulum*, *N. cf. latens*, *N. sigma*), translated into a 50% decline of diatom-inferred conductivity to $4,500$ – $6,000 \mu\text{S cm}^{-1}$. This evidence for freshening of Lake Sonachi in the early 20th century is followed by a gradual increase of inferred conductivity as *N. cf. latens* and *N. pura* expand at the expense of *N. frustulum* and *N. sigma*. Diatom-inferred conductivity reaches a maximum of $17,000 \mu\text{S cm}^{-1}$ near the top of D4 where the community is dominated by the polysaline *N. pura*. However, this overall trend is punctuated by considerable variation in fossil assemblages and reconstructed conductivity. Specifically, sediments deposited at low lake level in the late 1940s contain the characteristic freshwater planktonic diatoms *Aulacoseira* spp. and *Synedra* spp. These freshwater taxa did not persist long, but their presence depresses diatom-inferred conductivity to a minimum of $1,400 \mu\text{S cm}^{-1}$ (Fig. 3).

Zone D5 (8.4–5.0 cm) encompasses ca. 1966 to 1976, a period when lake level stabilized at 1,886 m above sea level (Fig. 1). Inferred conductivity drops from its peak at the top of D4 to $4,700$ – $5,300 \mu\text{S cm}^{-1}$ due to strong declines of

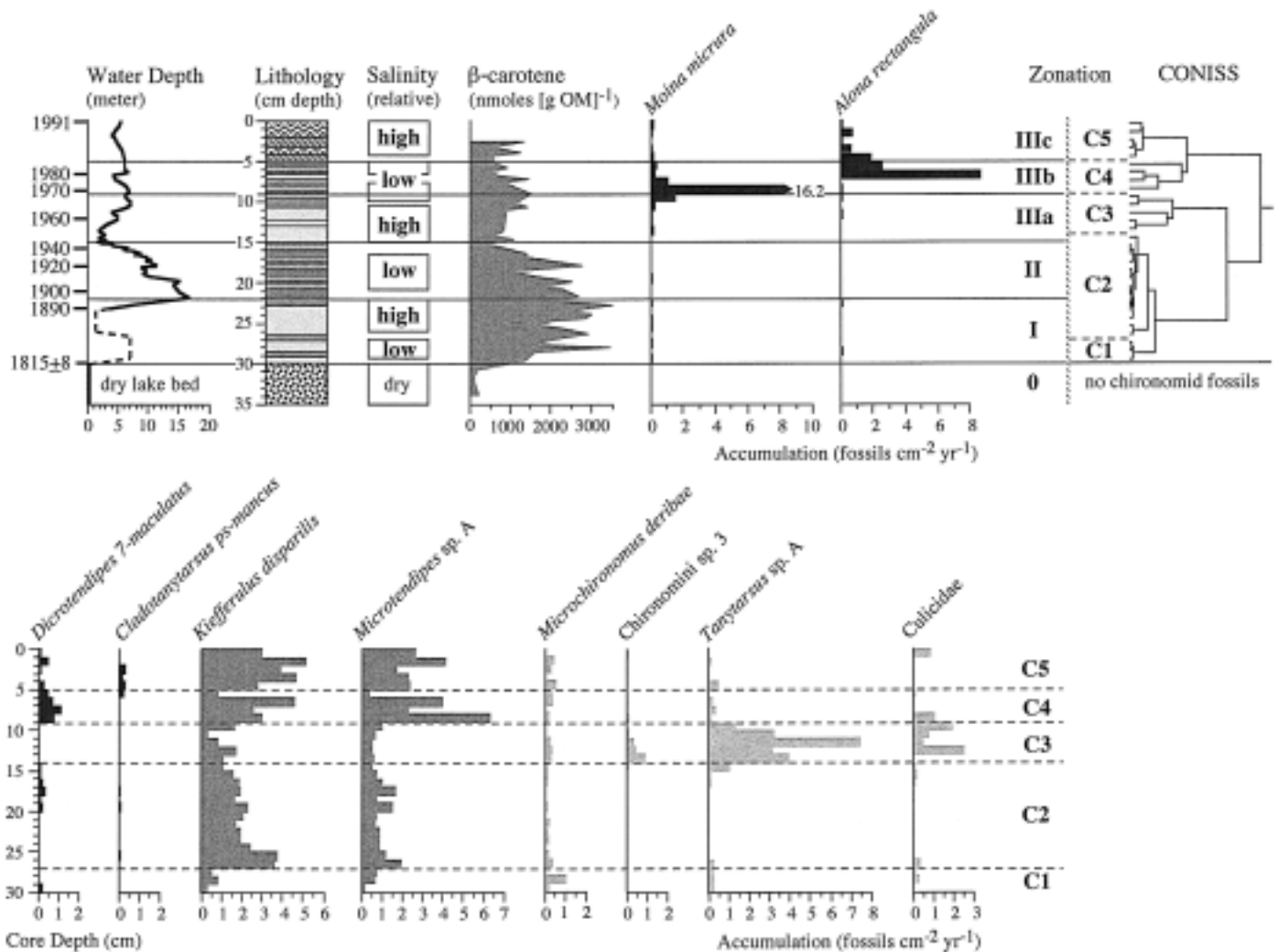


Fig. 4. Accumulation rates and stratigraphic zonation (C1–C5) of fossil Cladocera, Chironomidae, and Culicidae in piston-core NS91.1-S in relation to core chronology, lithology, historical lake depth, diatom-inferred conductivity, and the β -carotene record of total algal abundance.

Nitzschia pura and *N. cf. latens* and a prominent rise of *N. frustulum* (Fig. 3). Oligosaline *N. fonticola* is also present, reaching a maximum of 10% during the 1970s. Reconstructed conductivity increases again to $6,700 \mu\text{S cm}^{-1}$ towards the top of D5, mainly reflecting increased abundance of *Craticula elkab* at the expense of *N. frustulum*.

Zone D6 (5.0–0.0 cm) represents the diatom flora after 1976, a period that encompassed both renewed lake-level rise until 1980 and gradual decline after that (Fig. 1). This fluctuation has not been recorded in the fossil diatom assemblages, which show continued dominance of *Craticula elkab* and diatom-inferred conductivity stable at $10,000\text{--}12,000 \mu\text{S cm}^{-1}$ (Fig. 3).

Aquatic invertebrates—Fossil invertebrate communities of Lake Sonachi are composed mainly of chironomids; cladocerans are present only intermittently, and ostracods are absent. Except for scarce remains of *Bosmina longirostris*, *Euryalona orientalis*, *Alona nr. pulchella*, *Chydorus nr. sphaericus*, *C. parvus*, and *Pseudochydorus globosus*, cla-

docerans are entirely limited to two species, *Moina micrura* (67% of the fossil sum) and *Alona rectangula* (31%). The planktonic *M. micrura* is represented by its ephippia, the annual production of which is considered proportional to average population density (Pražáková and Fott 1994; Verschuren and Marnell 1997). *Moina* occurs mainly in a single horizon of peak accumulation ($1.6 \times 10^5 \text{ m}^{-2} \text{ yr}^{-1}$) in the lower half of subunit IIIb, coincident with documented meromixis in the early 1970s (Fig. 1). This peak population abundance developed from low abundances in the 1960s, as represented by the upper half of subunit IIIa (Fig. 4). It is unlikely that these deeper ephippia resulted from postburial downmixing of subunit IIIb specimens, because preservation of finely laminated sediments implies absence of bioturbation (Verschuren 1999a). *Moina* ephippia also occur in low numbers in the upper half of subunit IIIb and in subunit IIIc. *Alona rectangula* is a benthic species that becomes planktonic in lakes where waters are turbid with a suspension of fine organic particles (Kalk 1979). In the Lake Sonachi record, it occurs concentrated in a single horizon of peak ac-

cumulation ($8.9 \times 10^4 \text{ m}^{-2} \text{ yr}^{-1}$) in the middle of subunit IIIb, i.e., 2 cm above the *Moina* peak and contemporaneous with a short meromictic phase in the early 1980s (Fig. 1). Fossil abundance declines above the initial peak to low levels near the sediment surface; only a few isolated specimens were recovered from unit I and subunit IIIa (Fig. 4).

Fossil chironomid faunas of Lake Sonachi comprise one species of Orthoclaadiinae, eight of Chironomini, and two of Tanytarsini; no members of the Tanypodinae were found. Biostratigraphic zonation defines five zones, C1–C5, that correlate favorably with the record of past mixing regimes except that zone C1 emphasizes faunal uniqueness during the episode of initial lake filling ca. 1815–1850 and that C2 suggests only limited response to lake-level rise and onset of meromixis in the 1890s (Fig. 4). Overall the fauna is dominated by two anoxia-tolerant halobiont species, *Kiefferulus disparilis* (47%) and *Microtendipes* sp. A (30%). The third most common species, *Tanytarsus* sp. A, is also a halobiont but is intolerant to anoxia. It occurs most prominently in zone C3, largely coincident with subunit IIIa, the holomictic regime that prevailed during the 1940s–1950s low-stand and subsequent lake-level rise. An unidentified taxon named Chironomini sp. 3 and larvae of culicid mosquitoes exhibit fossil distributions similar to that of *Tanytarsus* sp. A. The halophilic component of the chironomid fauna is completed by *Microchironomus deribae*, an anoxia-intolerant species that appears to have been common during the lake-filling period but later persisted only in low numbers.

Five percent of the chironomid fossils belong to freshwater taxa with varying degrees of tolerance to the high salinities typical of African soda lakes (Verschuren 1997). Of these, *Dicrotendipes septemmaculatus* is present in upper C2 and C4 sediments deposited during meromictic phases and is largely absent in core sections corresponding to holomictic periods (Fig. 4). *Cladotanytarsus pseudomancus* occurs infrequently throughout the core profile but is fairly common only in C5, which represents the late-1980s phase of lake-level decline. *Chironomus formosipennis*, *Chironomus alluaudi*, *Nilodorum brevipalpis*, and an Orthoclaadiinae nr. *Smittia* (not shown) are present as only a few isolated occurrences.

Community response to lake level, mixing regime, and salinity—CA of the fossil pigment data reveals that most of the variation in algal community composition through time can be captured in two dimensions: CA axes 1 and 2 together explain 79% of the observed variance (Table 1). The majority of sample scores are aligned with axis 1, reflecting comparable concentrations of myxoxanthophyll and lutein-zeaxanthin along a gradient of increasing β -carotene (Fig. 5a). Axis 2 primarily reflects the relative abundance of the two cyanobacterial pigments, with zone P5 samples from the period of unstable meromixis in the 1970s and early 1980s singled out by their low myxoxanthophyll and high Chl *b* concentrations. Good separation of samples from zones adjacent to each other supports the biostratigraphic zonation, with the exception of upper P2 and lower P4 samples, which plot among P3 samples on the basis of near-identical relative abundances of myxoxanthophyll and lutein-zeaxanthin (Fig. 2).

Table 1. Eigenvalues of ordination axes 1–4 generated by correspondence analysis of fossil pigments; diatoms, and chironomid assemblages in the Lake Sonachi sediment record, the cumulative percentage of data set variance explained by those axes, and the sum of all unconstrained eigenvalues as a measure of absolute variance in each data set.

Data set	Axes				Sum
	1	2	3	4	
Pigments					
Eigenvalues	0.049	0.026	0.011	0.005	0.095
% variance	51.2	78.9	91.0	96.7	
Diatoms					
Eigenvalues	0.436	0.374	0.269	0.221	1.873
% variance	23.3	43.2	57.6	69.4	
Chironomids					
Eigenvalues	0.483	0.099	0.072	0.044	0.730
% variance	66.3	79.9	89.7	95.8	

CA of diatom abundance percentages suggests that past changes in the diatom flora of Lake Sonachi are complex and multidimensional: CA axes 1 and 2 together explain only 43% of the observed variance (Table 1; Fig. 5b). Sample scores generally support the distinctiveness of the diatom floras of zones D2, D3 + D6, and D4, which are dominated, respectively, by *Thalassiosira faurei*, *Craticula elkab*, and the species pair *Nitzschia pura* + *N. cf. latens*. However, neither of the two principal axes can be obviously related to known environmental gradients. For example, because of their common occurrence in zone D4, species scores of the meso- and polysaline diatoms *N. cf. latens* and *N. pura* plot along axis 1 together with those of the freshwater genera *Aulacoseira* and *Synedra*. The two groups are separated only along CA axis 4 (not shown), which explains 12% of the observed variance in the diatom data (Table 1).

In the fossil chironomid data set (Fig. 5c), CA axes 1 and 2 together explain 80% of the observed variance (Table 1). Axis 1 by itself already explains 66% of the variance, indicating that much of the change in chironomid faunal composition through time can be captured in one dimension. Axis 1 appears to reflect a gradient of decreasing anoxia tolerance from *Kiefferulus disparilis* and *Microtendipes* sp. A to *Tanytarsus* sp. A and Chironomini sp. 3. Near complete separation of samples from zones adjacent to each other confirms the biostratigraphic zonation and its association with the record of past mixing regimes. However, CA axis 1 does not reflect a gradient in mixing regime; C2, C4, and C5 remain unseparated on this axis but include faunas living under both meromictic and holomictic regimes. Separation of C4 from C2 + C5 along axis 2 is controlled by the relative abundance of *Dicrotendipes septemmaculatus*.

CCA with forward selection of lake depth and diatom-inferred conductivity as predictor variables captured only a small amount of the historical variation in algal and invertebrate communities. CCA axis 1 of the fossil pigment data correlates more closely with reconstructed conductivity ($r = 0.39$) than axis 2 correlates with lake depth ($r = 0.23$), but neither axis explains a significant fraction of the variance

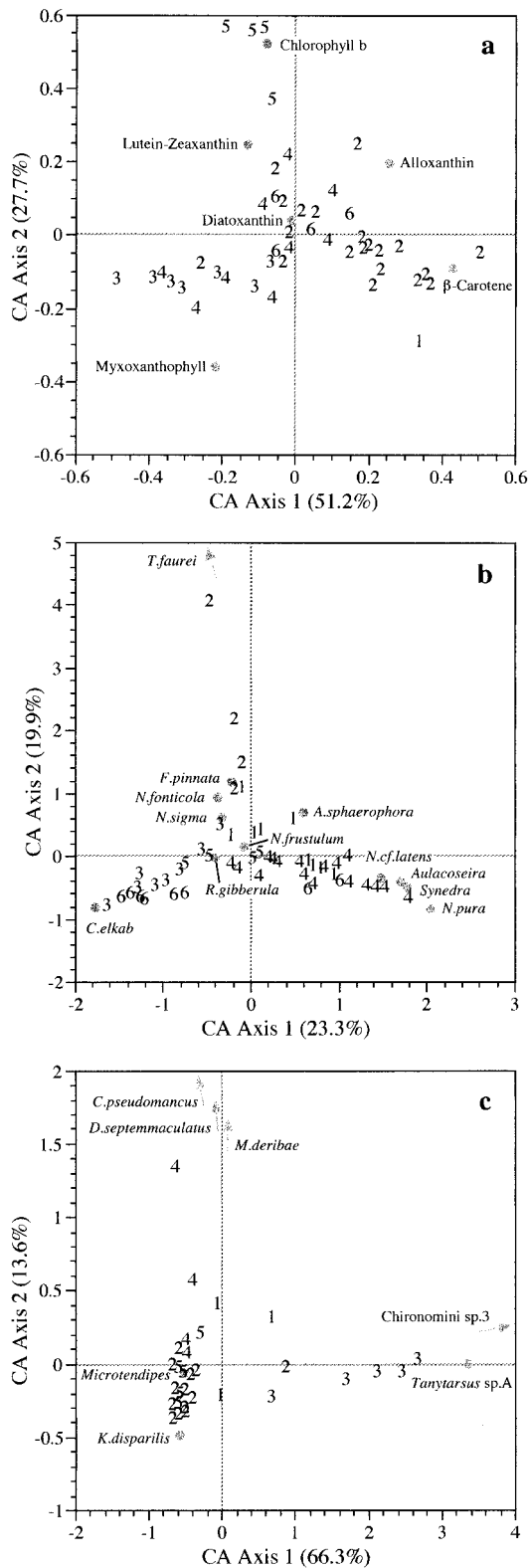


Fig. 5. Correspondence analysis (CA) ordination of pigments (a) and diatom (b) and chironomid (c) species and fossil assemblages in the recent sediment record of Lake Sonachi. Sample labeling follows CONISS-based biostratigraphic zonation as shown in Figs. 2–4. Species scores for pigments were multiplied by 0.25 to fit sample-score scaling of the ordination axes.

Table 2. Results of canonical correspondence analysis (axes 1 and 2) on fossil pigments and chironomid assemblages, with lake depth and diatom-inferred conductivity as explanatory variables.

Data set	% variance	P*	r†	
			Depth	Salinity
Pigments				
Axis 1	6.9	0.9	0.12	0.39
Axis 2	0.5		0.23	−0.06
Chironomids				
Axis 1	10.9	0.7	0.40	0.17
Axis 2	1.3		0.24	−0.35

* Based on Monte Carlo permutation.

† Intraset correlation.

(Table 2). CCA of the fossil chironomid faunas suggests slightly better correlation with lake depth ($r = 0.40$) than with reconstructed conductivity ($r = -0.35$), but here also neither axis is significant. CCA of the fossil diatom data with lake depth as the sole predictor variable had axis 1 explain only 3.7% of the observed variation, which likewise was not significant ($P = 0.82$).

Discussion

Long-term dynamics of the algal community—Patterns in fossil pigment stratigraphy indicate that during most of the 19th century and in the early 20th century algal abundance in Lake Sonachi was significantly greater than it is today (~100–300%) and that under conditions of stable meromixis between ca. 1915 and 1945 the algal community must have been characterized by dense, possibly unialgal blooms of filamentous cyanobacteria. Relatively low downcore variability in concentrations of the labile pigment Chl *a* ($103 \pm 76 \text{ nmol [g OM]}^{-1}$), consistently high Chl *a*:pheophytin *a* ratios (~0.5), and the permanence of bottom anoxia implied by the preservation of sediment lamination throughout the core suggests that there have been no systematic changes in the preservation of algal pigments relative to that of bulk organic matter (Leavitt and Carpenter 1989; Leavitt 1993). Normally, prolonged exposure to oxygen promotes selective loss of labile chlorophylls or their conversion to more chemically stable derivatives (Hurley and Armstrong 1990; Leavitt 1993). Because all reported carotenoids have similar chemical stabilities (Hurley and Armstrong 1990; Leavitt and Findlay 1994), compositional changes in the fossil pigment spectrum are more likely to have resulted from corresponding changes in the algal communities rather than selective pigment deposition and preservation. Consequently, the observed declines in β -carotene and myxoxanthophyll probably do record actual changes in algal abundance and community composition over the past half century. Inferred early 20th century conditions in Lake Sonachi resemble those prevailing today in more typical examples of chemically stratified African soda lakes, where algal production by dominant *Spirulina* spp. can be extremely high (Talling et al. 1973; Melack 1979; Wood and Talling 1988; Talling 1992). Collapse of a productive *Spirulina*-dominated algal

community in Lake Sonachi must have occurred between the early 1930s and the 1970s; *S. platensis* was still abundant in 1931 (Beadle 1932).

Patterns in the relative abundance of taxon-specific pigments (Fig. 2) suggest that the decline of filamentous cyanobacteria followed disruption of meromixis in the mid-1940s and continued through the subsequent period of holomixis until the 1970s. Nonfilamentous cyanobacteria also declined during the 1940s–1950s lowstand but recovered following renewed lake-level rise in the 1960s. These fossil data agree with documented evidence for replacement between the 1930s (Beadle 1932) and the late 1970s (Njuguna 1988) of *Spirulina platensis* by *Synechococcus bacillaris* as the dominant cyanobacterial taxon in Lake Sonachi. Similar patterns of community reorganization, also accompanied by a reduction of total algal abundance, were observed following the 1970s drawdown of Lake Nakuru and Lake Elmenteita further north in the Rift Valley (Vareschi 1982; Melack 1988). Melack (1988) proposed that these changes resulted when improved bottom oxygenation at low lake level impeded recycling of nutrients from the sediments. In Lake Sonachi, dominance of the anoxia-intolerant chironomid *Tanytarsus* sp. A during the 1940s–1950s lowstand (Fig. 4) is consistent with a situation in which expansion of oxygenated areas of the lake floor would have contributed to algal community reorganization. Still, preservation of sediment lamination throughout the corresponding core section (Fig. 1, subunit IIIa) indicates that at least the offshore lake bottom near the core sites remained anoxic and unaffected by wind-driven turbulence in lake depths as shallow as 3 m (Fig. 1). Similar to the situation in other African soda lakes, bottom anoxia in Lake Sonachi (Melack 1982) is promoted by the high bacterial oxygen demands for decomposition of sinking cyanobacterial blooms (Talling 1992). In contrast with more exposed soda lakes, this anoxia can persist through lowstands because superior wind shelter by its high crater rim (Melack 1981) limits the frequency of deep-mixing events that can replenish the depleted oxygen (Verschuren 1999a).

Whereas nonfilamentous cyanobacteria maintained relatively constant levels in recent decades, filamentous cyanobacteria declined further after the renewed onset of meromixis around 1970 (Fig. 2, subunit IIIb and zone P5); clear separation of zone P5 samples in the CA ordination (Fig. 5a) confirms the uniqueness of algal community structure during the episode of unstable meromixis in the 1970s and early 1980s. This inferred second phase of algal community reorganization correlates with field evidence for dominance of nonfilamentous cyanobacteria (76% of phytoplankton biomass) and relative unimportance of *Spirulina laxissima* and *S. platensis* (12%) at that time (Melack 1981; Melack et al. 1982; Njuguna 1988). Jellison and Melack (1993) found that algal production in Mono Lake, California, was depressed during meromixis because of poor nutrient regeneration from the dense and anoxic lower water column into the photic zone. However, it is unclear why meromixis in Lake Sonachi disfavored filamentous cyanobacteria in the 1970s when these algae thrived during meromixis in the period 1890–1945. It has been proposed (Vareschi and Jacobs 1985) that the copepod *Paradiaptomus africanus* may contribute to the

high productivity of African soda lakes by mediating nutrient recycling within the circulating upper water column. The fact that *P. africanus* has not recently been reported from Lake Sonachi but was abundant during *Spirulina* dominance in the 1930s (Beadle 1932) suggests a possible role in the observed algal changes, but poor preservation of copepods in the fossil record precludes evaluation of the mechanism involved.

Long-term dynamics of the diatom flora—The fossil diatom flora of Lake Sonachi correctly recorded several important events in lake history. First, the importance of freshwater and oligosaline taxa (*Fragilaria pinnata*, *Nitzschia fonticola*, *N. frustulum*) at the base of unit I is consistent with expected freshening of the water column during the initial phase of early 19th century lake filling. Second, the 1870s–1880s lowstand is characterized by clear dominance of the benthic mesosaline taxon *Craticula elkab*, which as expected declined in favor of facultatively planktonic taxa with lower salinity optima (*N. frustulum*, *N. sigma*) following the major 1890s transgression and subsequent onset of meromixis. High percentages (>20%) of *N. frustulum* correlate with lithological evidence for meromixis in both unit II and subunit IIIa (Fig. 3), consistent with the expected reduction of surface-water salinity at those times. Third, diatom-inferred conductivity estimates at the top of the core agree with today's surface-water conductivity of 10,000–11,000 $\mu\text{S cm}^{-1}$ (Verschuren 1996). The reconstructed salinity history indicates that freshening of Lake Sonachi following the 1940s–1950s lowstand was delayed until the late 1960s when lake level had completed its 5-m rise (Fig. 1), consistent with the hypothesis (Verschuren 1999a) that the 1957–1964 transgression resulted from hydrological adjustment to Lake Naivasha rather than from strong increases in local rainfall.

Despite apparent truthfulness of the fossil diatom record in reflecting several major events in lake history, correlation between inferred conductivity and the main direction of variation in the fossil diatom assemblages (CA axis 1) is only marginally significant ($r = 0.37$, $P = 0.013$, $n = 45$; samples from desiccation horizon unit 0 excluded). CCA (Table 2) and stratigraphically constrained cluster analysis (Fig. 3) also show little correlation between diatom community structure and historical changes in lake depth or mixing regime. Available field data are too incomplete to permit comparison between diatom-inferred and observed conductivity values through lake history, but strong correlation between lake depth and observed surface-water conductivity during the decade 1970–1980 ($r = 0.96$, $P < 0.001$) contrasts with the lack of correlation between lake depth and diatom-inferred conductivity ($r^2 = 0.20$, $P = 0.8$) for the group of five core increments deposited during that period. Overall, the poor relationship between diatom community structure and presumed important environmental variables suggests that (1) postdepositional processes affected the representation of living diatom floras in the fossil record, (2) Lake Sonachi salinity did not always change in direct relation to lake level as it did in the 1970s, or (3) long-term dynamics of diatom populations in African soda lakes are more com-

plex than would be predicted from the climate-driven changes in their physical and chemical environment.

Diatom-inferred conductivity estimates can be biased when fossil assemblages have been affected by taphonomic processes such as sediment mixing, reworking of older sediments, and differential dissolution (Gasse et al. 1997). For example, the delayed decline of the mesosaline *Craticula elkab* in favor of oligosaline planktonic taxa following the 1890s lake-level rise may in part be due to reworking of *C. elkab*-containing deposits during rapid transgression. Although the preservation of fine sedimentary structure throughout the core profile (excluding unit 0) argues against a significant effect of this process on overall diatom stratigraphy, it does cause the second-highest value of reconstructed conductivity to coincide with high lake level and lithological evidence of meromixis (Fig. 3). Another potentially important bias can occur if the living diatom flora creating a fossil assemblage does not reflect annual mean surface-water conductivity. In Lake Sonachi, diatoms account on average for only 2% of total phytoplankton biomass, with considerable month-to-month variability (0.0–6.7%, CV = 1.13; Njuguna 1988). Hence, a short-lived seasonal bloom can strongly influence the composition of fossil assemblages that integrate over longer time intervals, e.g., when annual freshwater inflows briefly cap a saline water column before being mixed. This phenomenon may explain the unexpected combination of the stenotopic freshwater taxa *Aulacoseira* and *Synedra* with the polysaline diatoms *Nitzschia cf. latens* and *N. pura* in assemblages deposited at low lake level in the late 1940s (Figs. 3, 5b); a possible analog has been observed in nearby Lake Oloidien, where *Aulacoseira* spp. were abundant only during the rainy month of November 1963 and not in subsequent drier months when surface-water conductivity was high (Lind 1965).

An alternative hypothesis for the origin of these mixed assemblages is that fossils of the freshwater taxa were brought to Lake Sonachi through deflation of Lake Naivasha sediments that became exposed as peripheral mudflats during the 1940s lowstand. This hypothesis is supported by the fact that all the species involved (*Aulacoseira ambigua*, *A. granulata* var. *angustissima*, *A. italica* var. *bacilligera*, *Synedra acus* var. *radians*, *S. cunningtonii*, *S. rumpens* var. *fragilaroides*, *S. tenera*) also occur in early 20th century sediments from Lake Naivasha (C. Cocquyt, unpubl. data). If true, the allochthonous nature of these fossils would require their exclusion from the analysis of past community change in Lake Sonachi. However, a modified diatom CA without *Aulacoseira* and *Synedra* was virtually identical to that using the complete data set. The correspondingly modified diatom CCA also did not markedly improve the relationship between diatom community structure and lake depth (axis 1 explained 4.7% of the variance vs. 3.7%).

An explanation for delayed freshening of Lake Sonachi following the 1957–1964 lake-level rise can be found in a complex hydrology characterized by nonlinearity between lake depth and salinity. Lake Sonachi's response to positive rainfall anomalies lacks the amplification effect that Lake Naivasha displays by virtue of its large drainage basin (2,378 km²) and efficient river network. Consequently, lake-level rise in Lake Sonachi is more likely to be realized through

its subsurface connection to Lake Naivasha rather than an increase in local rainfall. The associated dissolution of sedimentary evaporites by percolating groundwater increases Lake Sonachi's salt budget, thus maintaining high salinity (MacIntyre and Melack 1982) during transgression and preventing the density stratification required for meromixis (Verschuren 1999a). Besides delayed freshening after the 1957–1964 rise, this process may also explain why the early to mid-19th century diatom flora infers increasing salinity simultaneously with a deepening of the water column (Figs. 3, 5b: zone D2) and why following the 1883–1894 transgression diatom-inferred freshening did not start until after the establishment of meromixis (Fig. 3: zone D3–D4 boundary located 1.3 cm above the unit I–II boundary).

Multidimensionality of the fossil diatom record can also indicate that the diatom flora at certain times responded to environmental factors other than salinity. Excluding the possibly allochthonous freshwater component, the most prominent separation of fossil diatom floras along CA axes 1 and 2 (Fig. 5b) is determined by alternating dominance of the benthic-epiphytic *Craticula elkab* (D3 and D6), the facultatively planktonic species pair *Nitzschia pura* + *N. cf. latens* (D4), and the planktonic *Thalassiosira faurei* (D2), suggesting that changes in the suitability of benthic and pelagic habitats may have influenced community structure. We can also speculate that meromixis in Lake Sonachi may have created distinct chemical habitats that allowed coexistence of species with distinct salinity optima; benthic taxa in shallow bottom environments are more influenced than planktonic taxa by inflow of saline groundwater (Hammer and Heseltine 1988). Another potential influence on algal community structure in soda lakes is water-column transparency (Talling 1992). In Lake Elmenteita, for example, loss of *Spirulina* from the water column in the 1970s led to a significant transparency increase that allowed benthic diatoms to become the major primary producers (Melack 1988). In Lake Sonachi, the decline of filamentous cyanobacteria also promoted transparency, measured as an increase in Secchi disk depth from 0.05–0.10 m in 1930 (Beadle 1932) to 0.30–1.20 m in the 1970s (Melack 1981), but this transparency does not appear to have stimulated total diatom abundance (as diatoxanthin; Fig. 2) nor resulted in sustained positive trends in the percent abundance of known benthic taxa such as *Anomoeoneis sphaerophora*, *Rhopalodia gibberula*, and *C. elkab* (Fig. 3).

Long-term dynamics of the invertebrate fauna—Preservation of fine sedimentary structure throughout the core profiles indicates that the offshore lake bottom of Lake Sonachi has always been anoxic and, hence, that benthic invertebrates must always have been restricted to peripheral bottom areas in contact with the circulating upper water column (Verschuren 1999a). Dissolved oxygen in these shallow areas is independent of lake level but strongly influenced by algal abundance. In poorly mixed African soda lakes, intense nighttime respiration by dense cyanobacterial populations often results in complete deoxygenation of the upper water column (Talling 1992). Although benthic habitat increased significantly during lowstands as steep bottom gradients near the present shoreline gave way to a more gently sloping lake

floor (Fig. 1), which species were favored to exploit this habitat would have been determined in large measure by the prevailing oxygen regime.

The halobiont chironomid *Kiefferulus disparilis* is a characteristic taxon of African meromictic soda lakes prone to nighttime deoxygenation, and although it is functionally adapted to a diet of filamentous cyanobacteria, its distribution and local success appear to be related more to the oxygen regime than to algal community composition (Tudorancea et al. 1989; Verschuren 1997). The importance of this species in Lake Sonachi (Figs. 4, 5c) reflects the rather marginal quality of the lake's benthic habitat during both meromictic and holomictic episodes. The anoxia-intolerant chironomid *Tanytarsus* sp. A is the only chironomid known to thrive in metasaline African soda lakes (Verschuren 1997). Invasion and dominance of *Tanytarsus* sp. A during holomixis between 1945 and 1970 is thus consistent with the combined occurrence at that time of high inferred salinity (8,000–17,000 $\mu\text{S cm}^{-1}$), expansion of shallow benthic habitat, and reduced risk of nighttime anoxia due to declining algal abundance. Significantly, *Tanytarsus* sp. A had failed to invade Lake Sonachi during the 1870s–1880s lowstand when algal abundance was high, despite the fact that lake depth, mixing regime, and inferred conductivity (7,500–13,000 $\mu\text{S cm}^{-1}$) were comparable to conditions in the late 1940s and early 1950s (Fig. 4). An improved oxygen regime resulting from the elimination of dense cyanobacterial blooms may thus have been the decisive factor allowing expansion of *Tanytarsus* sp. A and other anoxia-intolerant insects (Chironomini sp. 3, culicid larvae) during the mid-20th century lowstand. *Microchironomus deribae* has oxygen requirements and preferences for silty substrata of low organic content similar to those of *Tanytarsus* sp. A (Tudorancea et al. 1989; Verschuren 1997) but is replaced by it when conductivity exceeds 12,000 $\mu\text{S cm}^{-1}$ (Vareschi and Vareschi 1984). In Lake Sonachi, *M. deribae* was common only during lake filling in the early 19th century (Fig. 4). With rising lake level, increased algal abundance, and eventual transition to meromixis, *M. deribae* must have become restricted to a narrow zone near shore, where wave-induced turbulence prevents anoxia. *M. deribae* was unable to take advantage of expanded bottom habitat and improved oxygenation in the late 1940s, possibly because high salinity favored *Tanytarsus* sp. A instead.

Similar environmental controls also appear to have governed the occurrence of planktonic cladocerans in Lake Sonachi. *Moina micrura* and *Alona rectangula* both rank among the small minority of cladocerans that reproduce in salinities above 3‰ (Frey 1993; Green 1993). *Moina* persists in conductivities of up to 6,000 $\mu\text{S cm}^{-1}$ but is sensitive to nighttime anoxia (Kalk 1979). In Lake Sonachi, it became established during holomixis in the 1950s (Fig. 4), but initial populations may have been hampered by high conductivity ($\geq 10,000 \mu\text{S cm}^{-1}$). Documented (Fig. 1) and inferred (Fig. 3) freshening of the epilimnion to 5,000–7,000 $\mu\text{S cm}^{-1}$ in the late 1960s and early 1970s allowed a short-lived population explosion during meromixis in the early 1970s, followed by reduction back to marginality in the mid-1970s when lake level had dropped and conductivity had risen to 11,000 $\mu\text{S cm}^{-1}$. Upon renewed freshening in 1979–1980

(Fig. 1; not recorded by the diatom flora), *Moina* was overshadowed by strong development of *Alona rectangula* (Fig. 4). Also, *Alona* was reduced to marginality when conductivity again rose above 7,000 $\mu\text{S cm}^{-1}$ during the mid-1980s (Verschuren 1996). Thus, sizable populations of both cladoceran taxa in Lake Sonachi occurred only in the 1970s when conductivity minima coincided with low algal abundance. Cladoceran zooplankton were rare or absent during earlier periods of low conductivity when algal abundance was high. As with the anoxia-intolerant zoobenthos, a favorable oxygen regime dependent on modest algal abundance may have been conducive to their short-lived success. These fossil data are consistent with the observation that cladocerans were absent in Lake Sonachi in 1929 (Jenkin 1934) when algal biomass was high and have never been reported from small hypereutrophic soda lakes elsewhere in Africa.

Synthesis and conclusion

Despite the considerable lake-level and salinity fluctuations of Lake Sonachi over the past 175 yr, multivariate statistical analyses of fossil pigments, diatoms, and invertebrate assemblages showed only weak relationships of long-term dynamics in the local biological communities with three potentially important environmental variables. This weak relationship may be due partly to limitations of the sediment record as an archive of lake history, exemplified by the uncertainty regarding the origin of mixed diatom assemblages deposited during the 1940s lowstand, as well as limitations in the method used to reconstruct past salinity based on fossil diatom assemblages recovered from that sediment record. It may also be due partly to nonlinearities between lake depth, salinity, and mixing regime, since major changes in algal and invertebrate community composition over the past half century do seem to correlate with lithology-inferred transitions between holomixis and meromixis. At time scales of centuries or longer, deep-water columns in closed-basin lakes usually are correlated with meromixis and low surface-water salinity, and shallow-water columns are correlated with holomixis and high salinity. At time scales of years to decades, however, benthic and planktonic habitats can be strongly affected by transient hydrological dynamics during which the correlation between lake depth and salinity is weak (LaBaugh et al. 1996; Poiani et al. 1996). At Lake Sonachi, documented and inferred nonlinearity among lake level, salinity, and mixing regime is the result of the crater's particular hydrologic relationship with Lake Naivasha and the distinct response of each lake to long-term trends in rainfall over their combined catchment (Verschuren 1999a). In a broader context, the limited predictive power of lake depth and salinity in long-term community regulation appears to reflect the generally complex and individualistic response of salt-lake biota to changes in their physical and chemical environment.

The long-term dynamics of biological communities in Lake Sonachi documented in this study are best explained by explicitly recognizing interactions and probable causality between biological and environmental changes. During high

lake level and stable meromixis in the period 1915–1945, the composition and abundance of Lake Sonachi's phytoplankton community resembled that of other small African soda lakes, and reduced algal abundance after that time favored the populations of anoxia-intolerant cladocerans and chironomids that are rare elsewhere. Phytoplankton and zooplankton communities of the 1970s and early 1980s, when Lake Sonachi balanced on the threshold between meromixis and holomixis following a long period of holomixis and low lake level, were unique in the lake's 175-yr history. The reported decline of filamentous cyanobacteria in Lake Sonachi may have arisen from progressive reduction in nutrient availability, first because expansion of oxygenated bottom areas during holomixis in the period 1945–1970 impeded nutrient release from the sediments and then because meromixis in the 1970s impeded nutrient regeneration from the anoxic lower water column to the photic zone. Under this scenario, however, fossil evidence for high algal abundances during both holomixis and meromixis in the 19th and early 20th century remain unexplained. Long-term changes in nutrient supply linked to vegetation succession in the crater catchment and the continuous loss of nutrients through burial in accumulating lake sediments may impose additional complexity on ecosystem processes that create essentially unique environmental conditions during each successive phase of lake history. If so, starting conditions for long-term community dynamics in African soda lakes would only be restored when a future episode of hyperaridity reinitiates terrestrial vegetation succession, and wind deflation of organic lake sediments from a dry lake bed redistributes sequestered nutrients throughout the catchment.

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