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ORIGINAL PAPER

Spatial variability of chironomid death assemblages in the surface sediments of a fluctuating tropical lake (Lake Naivasha, Kenya)

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Abstract Studies addressing within-lake variability of fossil chironomid assemblages are very few, and all deal with hydrologically stable temperate lakes where the question of spatial integration mostly relates to the mixing of faunal assemblages associated with shallow, warm-water habitat and those associated with deeper, cold-water habitat. Here we study within-lake variability of surface-sediment chironomid assemblages in the fairly large (~100–170 km^2 since 1983) and shallow ($Z_{\max}$ = 5–8 m) fluctuating tropical lake basin of Lake Naivasha, Kenya, and compare the patterns observed with those in two smaller adjacent basins, one similarly shallow (Lake Oloidien, 5.1–5.7 km^2, 5–8 m), the other deep and stratified (Crescent Island Crater, 1.9 km^2, 14–17 m). Chironomid assemblages were analysed in core-top samples and surface sediments along inshore to offshore transects, and how well individual samples represented the total (basin-wide mean) subfossil assemblage was considered both in terms of taxon richness and taxon percent composition. Within-lake variability of subfossil chironomid concentrations (with generally higher absolute values in nearshore samples) could be explained by effects of sediment winnowing and focusing, whereas between-lake variability reflected their relative susceptibility to wind-driven sediment disturbance or bottom anoxia. In all study lakes, but most significantly in lakes Naivasha and Oloidien, species distribution in the subfossil chironomid assemblages showed a strong nearshore to offshore gradient, which in these shallow lakes, reflects the dominant control of substrate and food quality on species distribution in the living community. Particularly in the larger basins, nearshore samples better represented the total lake assemblage than offshore samples, because the former always contained a component of mud-dwelling species whereas the latter often lacked a component of macrophyte-dwelling species. Our results show that although sedimentation dynamics in the shallow, wind-stressed Lake Naivasha is dominated by frequent resuspension and random sediment redistribution, the near- to offshore gradient in chironomid habitat remains imprinted on subfossil assemblages. We conclude that also in shallow fluctuating lakes, given sufficient size, incomplete pre-burial spatial integration of habitat-specific chironomid assemblages can be exploited for within-lake calibration of environmental gradients.

Keywords Africa · Chironomidae · Fossil remains · Lake Naivasha · Paleoclimate reconstruction · Spatial variability · Taphonomy

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Introduction

Chironomids are a family of true flies (Insecta: Diptera) of which the larvae constitute one of the most abundant bottom-dwelling macro-invertebrates in aquatic ecosystems (Cranston 1995). They inhabit the uppermost sediments of both littoral and profundal (deep-water) environments, cling on or burrow into aquatic plants, tunnel in moist wood, or parasitize other invertebrates (Oliver and Roussel 1983). Chironomid species show great capacity to respond rapidly to changes in their aquatic environment, and their heavily sclerotised chitinous head capsules, shed during ecdysis (moulting), preserve well in lake sediments. Therefore, chironomids are considered among the best indicators currently available to infer past environmental conditions in lakes, and many quantitative inference models have been developed for chemical (salinity, total phosphorus, oxygen), physical (temperature), morphometric (water depth), and biological (chlorophyll and macrophytes) variables (see Walker 2001).

Lake sediments are among the few continuous proxy archives that provide long-term information about past environmental conditions, and in addition to chironomids they preserve fossil remains of various other aquatic biota (macrophytes, pollen, Cladocera, diatoms, etc.). Macro and microfossils contained in these sediments are not evenly distributed in a lake, due to specific habitat preferences of the taxa of interest (e.g. Frey 1988; Hofmann 1988; Moos et al. 2005; Zhao et al. 2006), sedimentation dynamics (sediment focusing, erosion and redistribution; e.g. Davis and Brubaker 1973; Anderson 1990), and diagenesis within the fossil assemblages which may affect certain taxa more strongly than others (e.g. Walker et al. 1984; Barker et al. 1991). Sediment focusing (*sensu* Likens and Davis 1975) occurs when sediments in the shallower regions of a lake are resuspended and settle in deeper water, not only producing higher rates of sediment accumulation there but also introducing fossils derived from terrestrial and nearshore aquatic environments to the offshore sediment record. Often affecting the interpretations made in biological paleolimnology (e.g. Davis and Ford 1982; Battarbee and Flower 1984; Charles et al. 1991), sediment focusing also affects the within-lake distribution of chironomid remains buried in lake sediments. Despite the tendency that remains of littoral taxa are largely retained in shallow-water sediments (Iovino 1975; Walker et al. 1984; Frey 1988), mid-lake fossil chironomid assemblages in large or deep stratified lakes are often dominated by littoral taxa (Stark 1976; Wiederholm 1979; Schmäh 1993; Brodersen and Lindegaard 1999), because population production in bottom habitats that are colder, less well oxygenated, or on soft unstable substrate can be an order of magnitude lower than production in littoral habitat (Graham and Burns 1983; Pinder 1995; Tokeshi 1995). The importance of sediment focusing in individual lakes varies with differences in morphometry and physical limnology (e.g. Hilton 1985; Blais and Kalff 1995), and accordingly also the relative magnitude of a nearshore contribution to mid-lake chironomid assemblages. For example, in a large lake with complex morphometry this contribution was found to be proportional to local basin slope (Kansanen 1986). When complete dominance of deepwater assemblages by littoral species occurs, it suggests lack of a proper deepwater community, for example in the permanently anoxic hypolimnia of chemically stratified lakes (e.g. Mees et al. 1991). Excepting this special situation, complete numerical integration of inshore and offshore communities in mid-lake fossil assemblages is probably rare (Frey 1988): even in a set of small (<0.15 km^2), shallow (7.3–9.2 m) lakes studied by Heiri (2004), pre-burial transport failed to obscure clear depth-related gradients of chironomid habitat in the subfossil assemblages recovered from surface sediments. Complete spatial integration of fossils is, of course, no prerequisite for trustworthy paleoenvironmental reconstruction. It suffices that changes in the fossil percent abundances of taxa associated with a specific microhabitat are indicative of the actual former changes in the relative distribution of that microhabitat in the study lake (Verschuren et al. 2000).

All the currently available studies addressing within-lake variability of fossil chironomid assemblages (Stark 1976; Kansanen 1986; Schmäh 1993; Heiri 2004) dealt with hydrologically stable north-temperate lakes. In such lakes, especially in deep stratifying ones, the question of spatial integration mostly relates to the mixing of faunal assemblages associated with shallow habitat that is warm and well oxygenated with assemblages from deeper habitat that is cooler and (seasonally) less well oxygenated (cf. Heiri et al. 2003). In this study, we assess spatial variability of fossil chironomid assemblages within a fairly large (~100–170 km^2 since 1983) and shallow ($Z_{\max}$ = 5–8 m) fluctuating tropical lake basin (Lake Naivasha, Kenya) and two smaller adjacent lake basins, one similarly shallow (Lake Oloidien: 5.1–5.7 km^2, 5–8 m), the other deep and stratified [Crescent Island Crater (CIC): 1.9 km^2, 14–17 m]. Vulnerable to wind stress, almost the entire bottom surface of Lake Naivasha is above the critical depth of quiet sediment accumulation (Håkanson 1977), consequently random sediment resuspension and redistribution (Hilton 1985) are the dominant mechanisms of sediment deposition (Verschuren 1999). Through comparison with the smaller, less exposed basins nearby, we here investigate the extent to which this frequent sediment disturbance enhances the spatial integration of chironomid fossils, and may increase the degree to which single-core fossil assemblages are representative of the chironomid communities formerly inhabiting the lake and all its benthic habitat types. In discussing the representativeness of single samples we take into account both relative taxon richness (i.e. its proportion of the total number of taxa found in a lake, cf. Heiri 2004) and the relative abundance of common taxa, because these form the basis of abundance-weighted averaging methods used in modern quantitative paleoenvironmental reconstructions.

Material and methods

Study sites and laboratory analyses

For this study, we analysed subfossil chironomid assemblages in 43 surface-sediment samples taken along near- to offshore transects in Lake Naivasha and its satellite basins CIC and Oloidien, in the central valley of the Eastern Rift in Kenya (Fig. 1). The main basin of Lake Naivasha is a large (~100–170 km^2), shallow ($Z_{\max}$ in 1983 = 8 m; Z_{mean} = 4.8 m), wind-stressed lake. With a wave base at 6 m depth, undisturbed

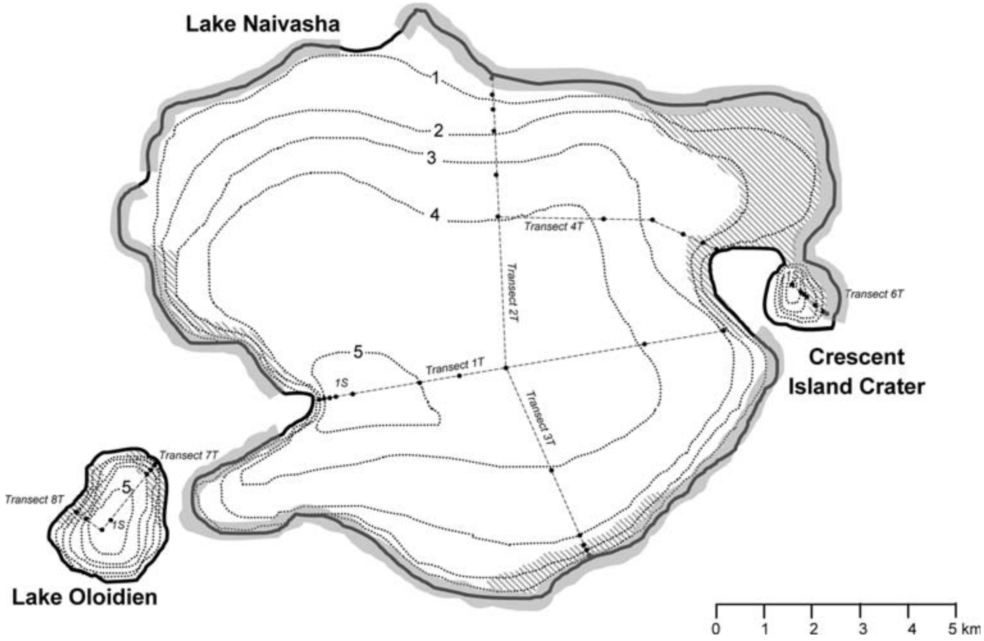

Fig. 1 Bathymetry and location of inshore to offshore sampling transects in Lake Naivasha and its satellite basins Oloidien and Crescent Island Crater (Eastern Rift Valley, Kenya), with distribution of submerged (cross-hatching) and emergent macrophytes (shaded area along shoreline). Map modified after Gouder de Beauregard et al. (1998)

accumulation of fine-grained sediments occurs in only 26% of its bottom area when Z_{max} = 8 m (Verschuren 1999). When Z_{max} is equal or less than 6 m, such as has been the case for most of the past 20 years, the entire lake bottom is subject to periodic wind-driven disturbance. The main basin (hereafter referred to as Lake Naivasha) is further hydrologically open and fresh (300 µS/cm) with groundwater flowing towards the lake from the north and exiting in the south and southeast (Gaudet and Melack 1981). CIC is a small (1.9 km^2), fresh (500 µS/cm) and deep (Z_{max} = 17 m in 1983; Z_{mean} = 9.0 m) submerged crater basin along the east shore of Lake Naivasha. The shorter wind fetch limits the local wave base to 3.4 m depth. Combined with the great mean-depth, this allows fine-grained accumulation in 83% of its bottom area when Z_{max} is 17 m, and not likely much less today at Z_{max} values of 14–15 m. CIC is also hydrologically open, due to confluence with the main basin and groundwater throughflow. Lake Oloidien is slightly larger than CIC (5.1–5.7 km^2) but as shallow as Lake Naivasha (Z_{max} = 8 m in 1983; Z_{mean} = 6.1 m). Local wave base is at 3.3 m, allowing fine-grained accumulation in 83% of the bottom area when Z_{max} is 8 m, and ~70% today. Lake Oloidien is hydrologically closed, and its lake water slightly concentrated (1,200 µS/cm in 1996). All three studied lake basins are continuously warm polymictic, a mixing regime in which thermal stratification (here, 3–4°C) develops daily during calm sunny morning hours and is then destroyed by strong afternoon winds and night-time convective circulation (Lewis 1983). At the current lake level, Lake Naivasha and Lake Oloidien probably circulate to the bottom almost every night. In CIC, daily convective circulation extends down to about 10–12 m (Brierley et al. 1987). Deeper wind-driven mixing (due to evaporative cooling at the surface) reaches the bottom frequently enough to prevent seasonal anoxia (Melack 1979), however possibly short-lived hypoxic conditions do occur (Brierley et al. 1987; DV, personal observation); more detail on the study sites is given in Verschuren (1996).

Surface-sediment samples (n = 40) were collected in 1996 with a rod-operated single-drive piston corer to recover the sediment-water interface intact at all locations (Fig. 1), including areas of sediment accumulation, erosion and transport. They were supplemented with three core-top samples collected in 1991 (Oloidien, N091-1S) and 1993 (Naivasha, NM93-1S and CIC, NC93-1S).

The upper sections (1–3 or 1–6 cm in low-yield samples) of each short core were prepared for fossil chironomid analysis by dispersing in warm 10% KOH (Walker and Paterson 1985), and rinsing through stacked 250- and 106-µm mesh sieves. Judging from the three ^{210}Pb-dated cores, sedimentation rates are high in areas of net (though not necessarily continuous) accumulation, with surface sediments (0–6 cm) representing the last 2–4 years. The often highly flocculent surface layer (0–1 cm) contained few chironomid fossils, and was reserved for other analyses. All chironomid fossils in both size fractions were picked at 30× and mounted in glycerine on microscope slides. Identification was done with a compound microscope at 100–400× by reference to Verschuren (1997) and taxonomic literature mentioned therein. Here nomenclature is updated in accordance with the regional East African dataset of Eggermont and Verschuren (2004a, b). Depending on fossil density and surface-sediment water content, between 0.5 and 48.7 g of wet mud was processed to yield the ~35–60 head capsules desired for numerical analysis (Heiri and Lotter 2001; Quinlan and Smol 2001). Criteria for counting fragmentary fossils followed Walker (1987).

Variation in bottom substrate quality was assessed by quantifying the sediment fractions of bulk and coarse (>106 µm) organic matter as weight loss at 550°C (Bengtsson and Enell 1986), and of sand-sized (>106 µm) mineral matter as weight loss at 1,000°C (Digerfeldt 1986). Bulk organic content (%OM) is influenced by local rates of organic decomposition, and its dilution with mineral sediment components. Coarse organic matter (%Coarse OM) is mainly derived from submerged and emergent macrophytes, less from terrestrial vegetation. Sand content (%Coarse MM) is an indicator of substrate stability.

Numerical and statistical analyses

We first carried out gradient analysis on the complete data set of 43 samples from Lake

Naivasha and its satellite basins. Detrended correspondence analysis (DCA; Ter Braak and Prentice 1988) of the chironomid assemblages showed the compositional length of the sampled environmental gradient to exceed two standard deviations, hence unimodal ordination was used to evaluate relationships between chironomid species distribution and selected environmental variables (ter Braak 1986). In this analysis, distance to shore and local water depth served as proxies (correlates) for substrate, food quality, and (primarily in CIC) ambient oxygen regime (see below), three important environmental factors controlling the distribution of chironomid larvae (Brundin 1949; Brinkhurst 1974; Pinder 1995). Salinity (K25, in μS/cm) and direct estimates of substrate quality (%OM, %Coarse OM and %Coarse MM) were also taken into account. Distance to shore was normalised by setting the most distant sample in each basin to 1, and recalculating the remaining distances accordingly. Detrended canonical correspondence analysis (DCCA; ter Braak 1986) with significance testing using 999 unrestricted Monte Carlo permutations (ter Braak and Šmilauer 1998) showed salinity to explain the largest portion of variation in faunal data set (18.1%), followed by the sedimentary contents of coarse organic matter (10.5%), coarse mineral matter (10.0%) and bulk organic matter (8.5%). In DCCA with either distance to shore or water depth as sole constraining variable, these variables significantly explained a modest 5.0 and 3.2% of the faunal variation, respectively. We then analysed faunal gradients in each basin separately, to break the dominant influence of salinity and allow proper focus on relationships between chironomid species distribution and the habitat characteristics controlled by lake morphometry. Short gradient lengths (0.905–1.943 SD) in all three basins (Table 2) indicated that linear ordination methods were appropriate (ter Braak 1995), consequently we used redundancy analysis (RDA) to determine the portion of faunal variance explained by each selected environmental variable; significance of the first ordination axis was assessed as above. Direct and indirect gradient analyses were executed in CANOCO 4.0 (ter Braak and Šmilauer 1998), on squared-root transformed percentage data with down-weighting of rare taxa.

Taxon richness was calculated as (1) the raw number of taxa present, and (2) the number of taxa expected in a sample of 35 fossils (ES35) using Hurlburt's rarefaction method (Magurran 1998) in PRIMER 5.24 (Primer-E Ltd. 2001); 35 is the lowest number of specimens recovered from a sample. Taxa were classified as common or uncommon in a lake basin when their mean frequency exceeded or remained below one specimen per sample, respectively. Taxa with less than 3 occurrences were excluded from numerical analyses, since their distribution is dominated by chance occurrence in samples. Individual species responses to environmental variables, and correlations between environmental variables, were investigated with linear regression techniques (Pearson Product-moment correlation) in Statistica 5.0 (StatSoft Inc. 1998). The degree to which the chironomid species assemblage in individual surface-sediment samples from specific locations are representative for the total (basin-wide mean) chironomid assemblage of a lake basin is calculated as the proportion of the total number of taxa recovered from that lake present in the sample (Heiri 2004). Similarity of individual samples to the total fossil assemblage was estimated using the Bray-Curtis similarity index (Bray and Curtis 1957) and Euclidean distance in PRIMER 5.24 (Primer-E Ltd. 2001).

Results

Relationship of water depth and distance to shore with habitat characteristics

Habitat diversity in each of the basins appears to be overlain by a strong depth gradient, most significantly in Lake Naivasha and Oloidien (Table 1). Organic-matter content (%OM) showed a strong positive correlation with local water depth, whereas coarse organic matter (%Coarse OM) and sand (%Coarse MM) both showed a negative correlation with depth and distance to shore. As a result, fractions of coarse organic matter and sand were also negatively correlated with organic-matter content, resulting in an environmental gradient from stable and relatively coarse-textured, low-organic substrates in shallow water

Table 1 Pearson product correlations between environmental variables in the three study lakes

	Depth	Distance	OM	Coarse OM	CM	Coarse CM	MM
Naivasha							
Depth							
Distance	0.446*						
OM	0.850***	0.406*					
Coarse OM	–0.749***	–0.445*	–0.840***				
CM	–0.130	0.121	0.032	0.053			
Coarse CM	–0.414*	–0.232	–0.556**	0.628***	–0.312		
MM	–0.695***	–0.412*	–0.898***	0.719***	–0.469*	0.628***	
Coarse MM	–0.667***	–0.404*	–0.802***	0.801***	–0.245	0.752***	0.817***
Oloidien							
Depth							
Distance	0.748*						
OM	0.943***	0.899**					
Coarse OM	–0.885***	–0.697	–0.825*				
CM	–0.231	–0.262	–0.119	0.179			
Coarse CM	–0.884***	–0.648	–0.799*	0.981***	0.240		
MM	–0.878**	–0.827*	–0.964***	0.774*	–0.146	0.734*	
Coarse MM	–0.862**	–0.678	–0.828*	0.970***	0.072	0.980***	0.806*
CIC							
Depth							
Distance	0.828*						
OM	0.818*	0.684					
Coarse OM	–0.941**	–0.688	–0.927**				
CM	0.861*	0.695	0.966***	–0.922***			
Coarse CM	–0.801*	–0.582	–0.966***	0.931***	–0.907**		
MM	–0.838*	–0.692	–0.996***	0.932**	–0.985***	0.955**	
Coarse MM	–0.893**	–0.567	–0.899**	0.987***	–0.892**	0.927**	0.903**

to soft organic muds in deeper water. The expected positive relationship between distance to shore and water depth was significant, reflecting a uniform bottom slope in each of the basins.

Faunistics

In Naivasha the 28 surface-sediment samples produced a total of 35 chironomid taxa (Fig. 2a; Table 2), with six taxa (with abundances of 5.1–25.8%) together making up 88.3% of the fauna: *Chironomus formosipennis*, Chironomini larvula type 1, *Procladius brevipetiolatus*, *Dicrotendipes septemmaculatus*, *Psectrocladius viridescens* and *Cladotanytarsus pseudomancus*. Most likely, the abundant Chironomini larvula type 1 (Eggermont and Verschuren 2004a) is here primarily *C. formosipennis*. The eight samples from Oloidien produced a total of 17 taxa (Fig. 2b; Table 2), with four taxa (9.8–32.8%) together making up 86.2% of the local fauna: *P. brevipetiolatus*, *C. pseudomancus*, *Nilodorum brevibucca* and *C. formosipennis*. The eight samples from CIC produced a total of 17 taxa (Fig. 2c; Table 2), with six taxa (10.7–26.9%) together making up 86.8% of the local fauna: *D. septemmaculatus, C. pseudomancus*, *P. viridescens*, Chironomini larvula type 1, *P. brevipetiolatus* and *C. formosipennis*. The three basins are thus distinct in their ranking of dominant taxa (Fig. 2a–c): *C. formosipennis* is the most common taxon in Lake Naivasha, only the fourth and sixth most common in Oloidien and CIC. Summing the percentages of *C. formosipennis* and its probable juveniles Chironomini larvula type 1, this species represents 47.3% of the assembled fauna in Naivasha, versus 10.5% in Oloidien and 22.3% in CIC. *D. septemmaculatus* is with 26.9% the most common species in CIC. The species composition of Lake Oloidien mainly differs from that in the other two basins in the presence of two halophilic taxa (*Microchironomus deribae* and *Kiefferulus disparilis*) alongside high numbers of *P. brevipetiolatus* (32.8%) and *C. pseudomancus* (32.1%).

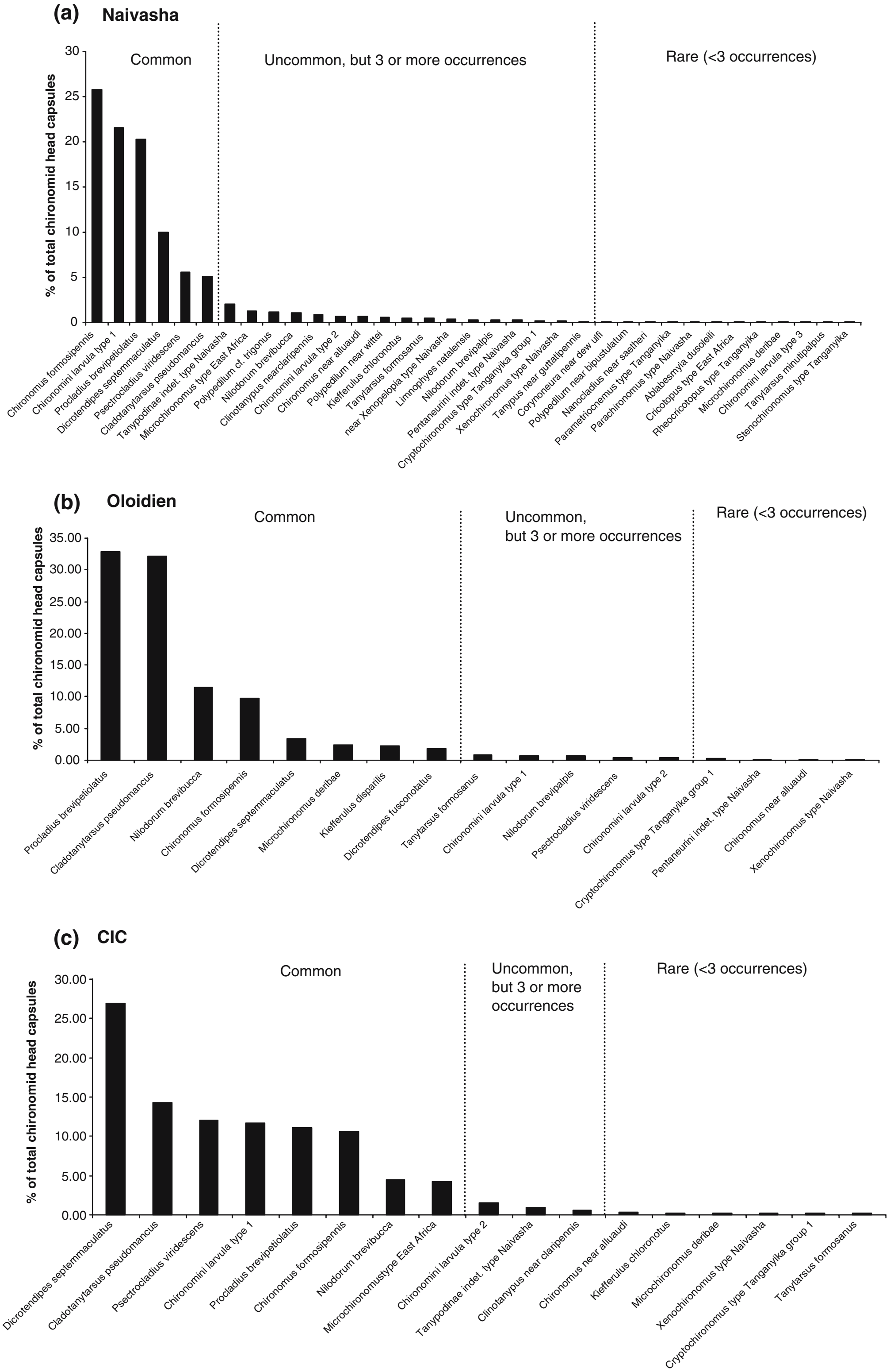

Fig. 2 Species-frequency data for the total (basin-wide mean) chironomid species assemblages in Lake Naivasha (**a**), Oloidien (**b**) and Crescent Island Crater (**c**)

Table 2 Summary statistics and gradient analysis of surface-sediment fossil chironomid assemblages in the three study lakes. Species diversity is expressed as raw taxon richness and as the number of taxa expected in a sample of 35 fossils, ES35; numbers between brackets are standard deviations. Similarity of individual samples with the total (basin-wide mean) subfossil species assemblage of each basin is expressed with values for Bray-Curtis similarity and Euclidean distance, using either common taxa only or (in bold) both common and uncommon taxa

Basin	Naivasha	Oloidien	CIC
# samples	28	8	8
# specimens recovered	2048	733	404
Identified specimens (% of recovered specimens)	98.6	99.6	99.5
Diversity			
# taxa per basin	35	17	17
# taxa per sample	10.4 (4.6)	9.3 (2.5)	10.4 (2.1)
# taxa per sample (% of total taxa within basin)	29.7 (13.0)	54.4 (14.7)	61.3 (12.2)
ES(50) per basin	10.6	8.6	9.4
ES(50) per sample	8.3 (3.2)	7.7 (1.6)	8.2 (1.4)
Similarity index			
Bray-Curtis	68.0 (10.6)–**65.6 (10.2)**	76.5 (9.8)–**73.4 (9.5)**	80.3 (7.6)–**78.8 (8.2)**
Euclidean distance	27.4 (8.2)–**27.9 (8.2)**	25.0 (12.0)–**25.7 (11.8)**	16.3 (6.0)–**16.9 (6.1)**
DCA			
Gradient length (SD)	1.943	1.233	0.905
RDA			
% variance explained by %OM	34.7**	44.5**	26.3
% variance explained by %MM	30.0**	42.8**	27.7
% variance explained by %Coarse OM	35.8**	41.2*	28.7
% variance explained by %Coarse MM	25.7**	41.8**	25.4
% variance explained by Distance to shore	16.8**	45.9**	29.2
% variance explained by Depth	34.2**	36.6*	32.2*

* Significant at the $p = 0.05$ level

** Significant at the $p = 0.01$ level

In Lake Naivasha, 29 of 35 recovered taxa are classified as uncommon or rare (all taxa with on average less than one occurrence per sample); in Oloidien and CIC this proportion is much lower (9 of 17 in both). Although the total number of taxa found in Lake Naivasha (35) was distinctly higher than that recovered from each of its satellite basins (17), the fairly similar number of taxa expected in a random sample of 35 specimens (ES35; Table 2) suggests that the absolute difference in taxonomic diversity is due to the larger combined sample size examined from Naivasha.

Spatial distribution of the chironomid fauna

Results of RDA with each of the environmental variables as the only explanatory variable are presented in Table 2. In Naivasha, all environmental variables explained a significant portion of the variance in the faunal data set. Water depth and direct proxies of substrate quality each explained ~30% or more of the faunal variation, whereas the influence of distance to shore was less (16.8%). In Oloidien, the portion of variation explained was high and significant for the various sediment characteristics (>40%) as well as distance to shore (45.9%) and water depth (36.6%). In CIC, none of the environmental variables except water depth (32.2%) explained a significant portion of variation in the available faunal data set.

Environmental control at the species level

The strong relationship between surface-sediment chironomid assemblages and (proxies for) substrate quality in Lake Naivasha is supported by linear regression analyses, which reveal significant ($p < 0.05$) relationships between the distribution of 17 of 22 (77.3%) analysed taxa and one or more environmental gradients in their bottom habitat (Table 3). This allowed Lake Naivasha chironomids to be sorted in three faunal groups. The first group includes taxa that tend to be more common in offshore organic mud bottoms with little or no coarse plant debris and sand: *C. formosipennis*, Chironomini larvula type 1, *P. brevipetiolatus* and Tanypodinae indet. type Naivasha. This is especially visible in the distribution of these taxa along transect 2T–3T (Fig. 3b). The second group includes 13 taxa that have a negative relationship with water depth, and occur more abundantly on coarsely textured substrates poor in organic matter. Of these, taxa such as *P. viridescens* and *C. pseudomancus* are largely restricted to nearshore shallow-water samples, whereas taxa such as *D. septemmaculatus* and *Chironomus near alluaudi* also occur in offshore samples at slightly greater water depths (Fig. 3a–c). The third group is composed of five uncommon taxa showing no significant relationships with any of the environmental variables. Chironomid concentrations were mostly less than 70 head capsules/g (hc/g) dry sediment, but peaked at 450 hc/g dry sediment in one sample (2T4) from a north-central location (Fig. 3a–c). Considering each transect separately,

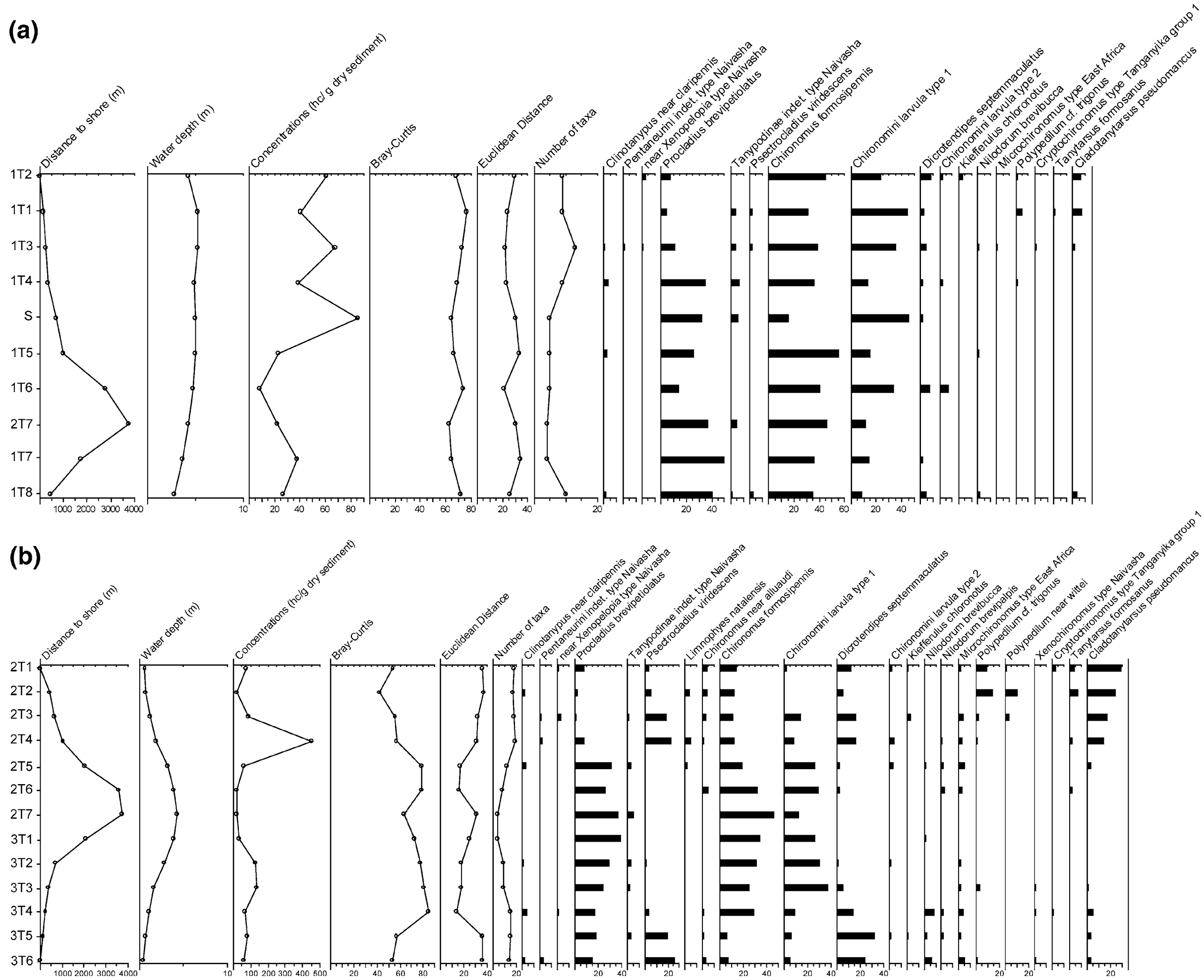

Fig. 3 Distribution and diversity of chironomid taxa in surface-sediment assemblages of Lake Naivasha (**a–c**), Oloidien (**d**) and Crescent Island Crater (**e**) in relation to local water depth and distance to shore. Similarity of the species assemblage in individual transect samples with the total (basin-wide mean) assemblage given as Bray-Curtis similarity index and Euclidian distance. Only taxa with more than three occurrences are shown

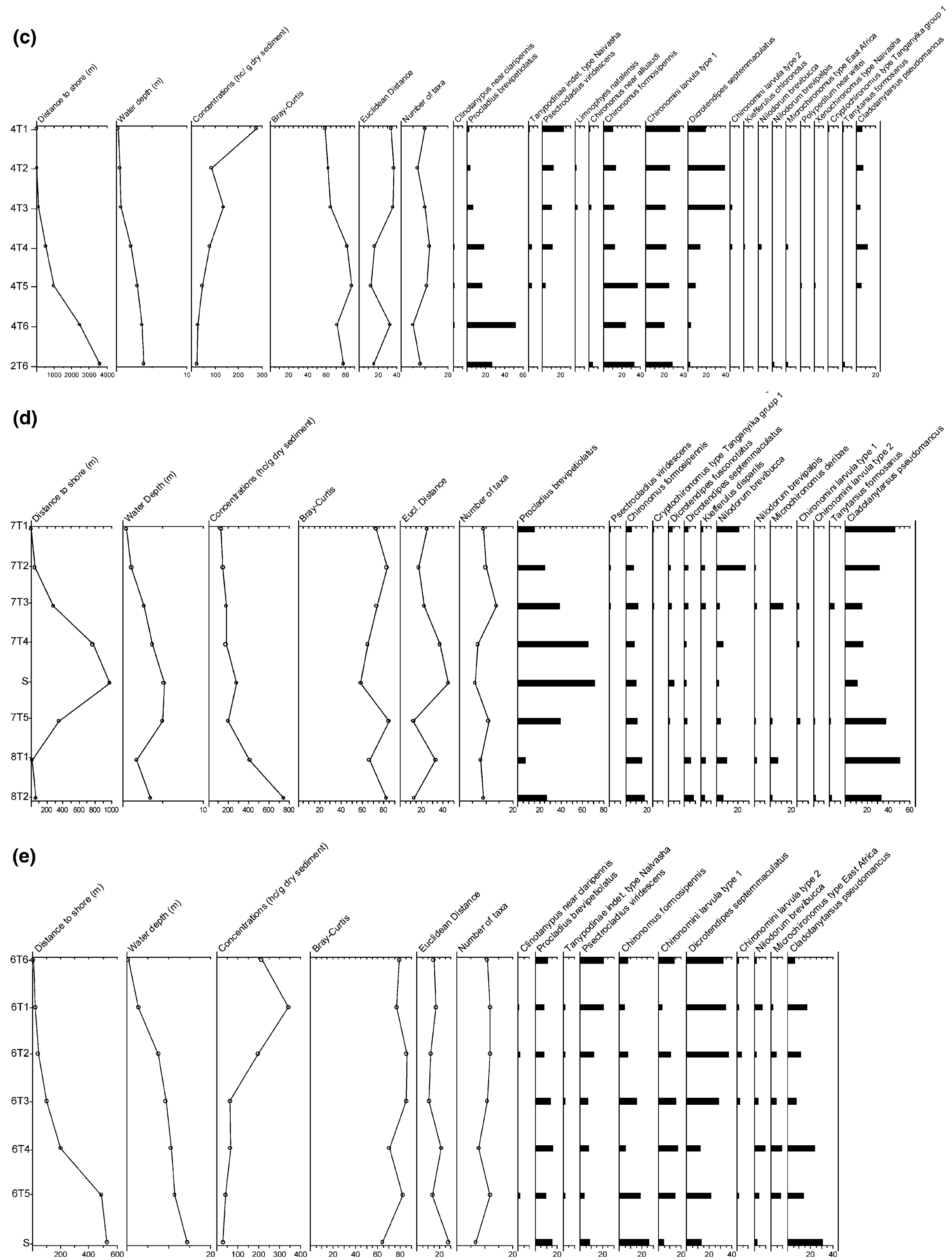

Fig. 3 continued

Table 3 Pearson product correlations between chironomid species abundance in surface-sediment assemblages and selected environmental gradients in the main basin of Lake Naivasha, and rank abundance of individual taxa in the total fossil species assemblage (cf. Fig. 2a)

	Rank abundance	Distance	Depth	OM	Coarse OM	Coarse MM
Group 1						
Procladius brevipetiolatus	3	0.531**	0.487**	0.506**	–0.615***	–0.440*
Chironomus formosipennis	1	0.427*	0.756***	0.719***	–0.629***	–0.549**
Tanypodinae indet. type Naivasha	7	–0.040	0.390*	0.376*	–0.381*	–0.351
Chironomini larvula type 1	2	0.084	0.478**	0.615***	–0.546**	–0.595**
Group 2						
Psectrocladius viridescens	5	–0.411*	–0.712***	–0.622***	0.712**	0.431*
Dicrotendipes septemmaculatus	4	–0.428*	–0.750***	–0.667***	0.646***	0.380*
Cladotanytarsus pseudomancus	6	–0.374*	–0.496**	–0.633***	0.668***	0.740***
Chironomus near *alluaudi*	13	–0.037	–0.447*	–0.609***	0.539**	0.652***
Microchironomus type East Africa	8	–0.081	–0.409*	–0.420*	0.463**	0.397*
Limnophyes natalensis	18	–0.088	–0.305	–0.369*	0.285	0.209
Polypedilum cf. *trigonus*	9	–0.271	–0.241	–0.444*	0.384*	0.598***
Polypedilum near *wittei*	14	–0.119	–0.273	–0.468*	0.260	0.353
Tanytarsus formosanus	16	–0.077	–0.272	–0.441*	0.374*	0.592***
Kiefferulus chloronotus	15	–0.266	–0.244	–0.233	0.486**	0.187
Nilodorum brevibucca	10	–0.243	–0.328	–0.329	0.195	0.377*
Pentaneurini indet. type Naivasha	20	–0.188	–0.169	–0.299	0.428*	0.273
Cryptochironomus type Tanganyika group 1	21	–0.274	–0.279	–0.314	0.463***	0.716***
Group 3						
Clinotanypus near *claripennis*	11	–0.075	0.068	–0.021	–0.175	0.043
Nilodorum brevipalpis	19	0.235	–0.106	0.016	–0.100	0.055
Xenochironomus type *Naivasha*	22	–0.181	–0.253	–0.112	0.045	0.153
Chironomini larvula type 2	12	0.123	0.126	0.073	0.002	0.007
near *Xenopelopia* type Naivasha	17	–0.261	–0.032	–0.026	0.250	0.114

concentrations were generally highest in nearshore samples.

In Lake Oloidien, linear regression analysis revealed significant ($p < 0.05$) environmental control on the subfossil distribution of only five of 14 taxa considered (35.7%; Table 4). Remains of *P. brevipetiolatus* occurred more abundantly at offshore locations, and *K. disparilis*, *C. pseudomancus*, *P. viridescens* and *N. brevibucca* are associated with nearshore environments (Fig. 3d). Surface-sediment distributions of all other taxa failed to show a clear relationship with selected environmental gradients (Table 4), although some taxa (e.g. *Cryptochironomus* type Tanganyika group 1, *Nilodorum brevipalpis*, *M. deribae*) do appear largely restricted to nearshore shallow-water sites (Fig. 3d). Chironomid concentrations were high at the nearshore stations 8T.1 and 8T.2 (411 and 799 hc/g dry sediment, respectively), averaging 215 ± 98 hc/g dry sediment in the other samples ($n = 6$; Fig. 3d).

In CIC, linear regression analysis indicated similarly modest influence of habitat gradients on the distribution of chironomid taxa in surface-sediment assemblages. Only three of the 11 taxa considered (27%) show a significant ($p < 0.05$) relationship with one or more environmental variables (Table 5). As in the main basin of Naivasha, *C. formosipennis* occurred more abundantly on offshore (here deep-water) organic mud bottoms, whereas *P. viridescens* and *D. septemmaculatus* were most common on nearshore (shallow-water) substrates (Fig. 3e). No taxa appear entirely restricted to nearshore or deep-water sites. Chironomid concentrations were distinctly higher at nearshore stations (197–342 hc/g dry sediment) than at deepwater sites (52 ± 16 hc/g dry sediment, $n = 4$; Fig. 5e).

Table 4 Pearson product correlations between chironomid species abundance in surface–sediment assemblages and environmental gradients in Lake Oloidien, and rank abundance of individual taxa in the total fossil species assemblage (cf. Fig. 2b)

	Rank abundance	Distance	Depth	OM	Coarse OM	Coarse MM
Group 1						
Procladius brevipetiolatus	1	0.965***	0.756*	0.901**	–0.787*	–0.796*
Group 2						
Kiefferulus disparilis	7	–0.743*	–0.640	–0.800*	0.420	0.492
Cladotanytarsus pseudomancus	2	–0.797*	–0.557	–0.676	0.779*	0.768*
Psectrocladius viridescens	12	–0.496	–0.793*	–0.629	0.634	0.564
Nilodorum brevibucca	3	–0.579	–0.832*	–0.713*	0.793*	0.777*
Group 3						
Dicrotendipes fusconotatus	8	0.369	0.041	0.275	0.058	0.001
Chironomini larvula type 1	10	0.325	0.515	0.465	–0.582	–0.589
Chironomus formosipennis	4	–0.229	0.268	–0.026	–0.228	–0.179
Cryptochironomus type Tanganyika group 1	14	–0.287	–0.479	–0.378	0.323	0.195
Nilodorum brevipalpis	11	–0.312	–0.195	–0.344	–0.028	0.103
Microchironomus deribae	6	–0.242	–0.144	–0.293	–0.083	–0.002
Chironomini larvula type 2	13	–0.200	0.442	0.217	–0.334	–0.401
Tanytarsus formosanus	9	–0.139	0.079	–0.051	–0.399	–0.425
Dicrotendipes septemmaculatus	5	–0.615	–0.257	–0.498	0.245	0.235

Representation of total (basin-wide mean) fossil assemblage in individual samples

Individual samples in Lake Naivasha contained 4–19 taxa (or 11.4–54.3% of the total number recovered), Oloidien samples 6–14 taxa (35.3–82.4%), and those from CIC 7–12 taxa (41.2–70.6%; Table 2). Figure 4a–e visualize the representativeness of individual samples, i.e. how well the local surface-sediment assemblage along different transects represents the total (basin-wide mean) chironomid assemblage of the basin under consideration, for all taxa with more than 3 occurrences as well as only for the sub-set of common taxa. Clearly, for both groups of taxa offshore samples are less representative of the total chironomid fauna than nearshore samples. The difference is most pronounced in the larger basins, and when both common and uncommon taxa are included: mid-lake samples from Lake Naivasha

Table 5 Pearson product correlations between chironomid species abundance in surface–sediment assemblages and environmental gradients in CIC, and rank abundance of individual taxa in the total fossil species assemblage (cf. Fig. 2c)

	Rank abundance	Depth	Distance	OM	Coarse OM	Coarse MM
Group 1						
Chironomus formosipennis	6	0.723	0.839*	0.501	–0.606	–0.514
Group 2						
Psectrocladius viridescens	3	–0.891**	–0.686	–0.884**	0.956**	0.932**
Dicrotendipes septemmaculatus	1	–0.758*	–0.760*	–0.606	0.623	0.527
Group 3						
Clinotanypus near *claripennis*	11	0.032	0.113	0.247	–0.132	–0.146
Procladius brevipetiolatus	5	0.573	0.386	0.41	–0.51	–0.474
Tanypodinae indet. type Naivasha	10	–0.047	–0.228	–0.057	–0.075	–0.155
Chironomini larvula type 1	4	0.07	–0.074	0.469	–0.328	–0.356
Chironomini larvula type 2	9	–0.401	–0.529	–0.126	0.169	0.06
Nilodorum brevibucca	7	0.072	–0.05	–0.053	0.012	0.016
Microchironomus type East Africa	8	0.421	0.219	0.646	–0.571	–0.586
Cladotanytarsus pseudomancus	2	0.646	0.643	0.32	–0.403	–0.326

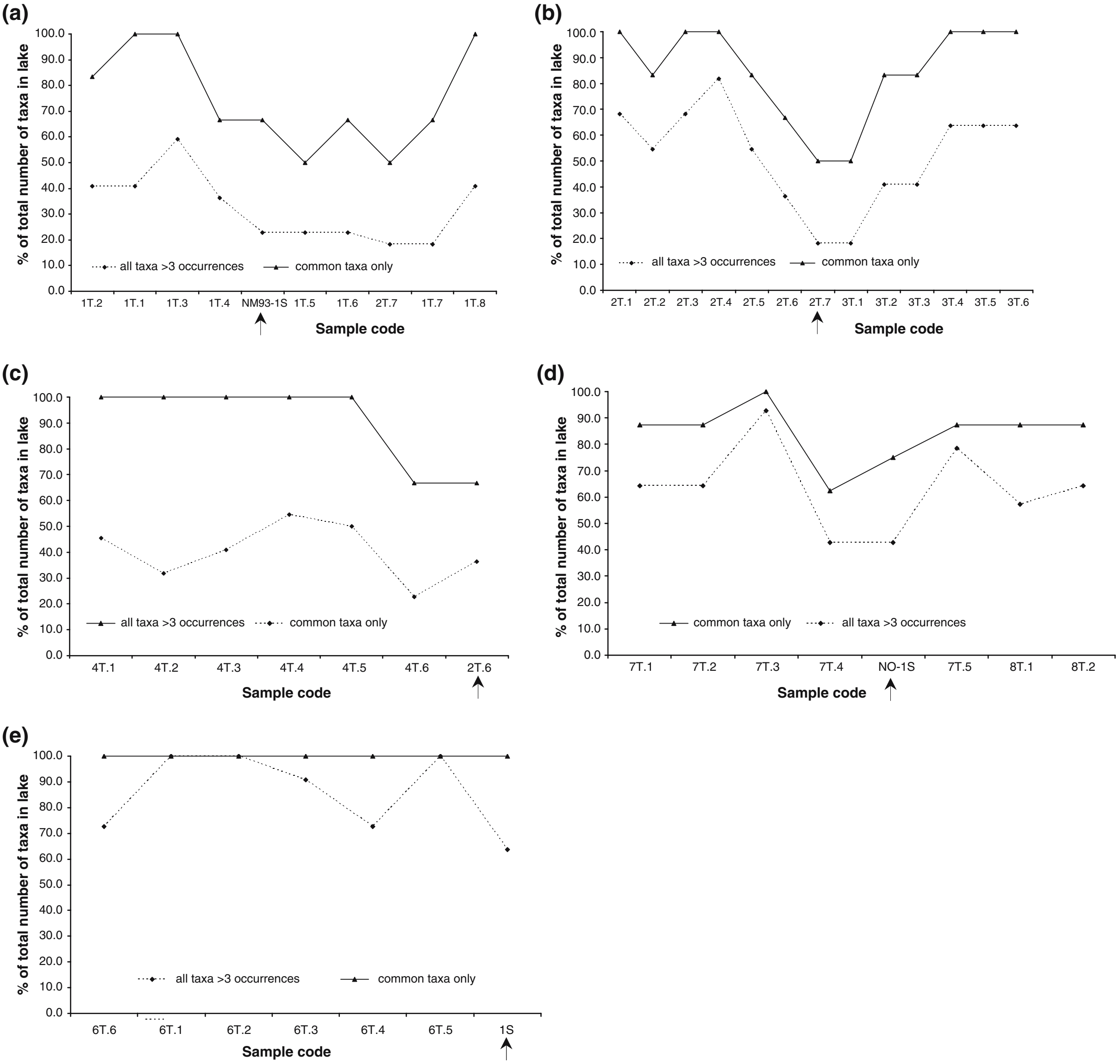

Fig. 4 Representativeness of individual transect samples for the total (basin-wide mean) subfossil chironomid assemblage in Lake Naivasha (**a**–**c**), Oloidien (**d**) and Crescent Island Crater (**e**), expressed as percent raw species richness and calculated both for common taxa only, and for all taxa with more than three occurrences (i.e. both common and uncommon taxa; cf. Fig. 2a–c). *Arrows* indicate the sample recovered from greatest water depth on each transect

contain on average 66.7% of the six common taxa and only 22.7% of the 22 common and uncommon taxa (Figs. 2a, 4a–c); for Oloidien the corresponding values are 75 and 42.9% (Figs. 2b, 4d), and for CIC 100 and 63.6% (Fig. 2c, 4e).

Taxa reaching a higher peak abundance in any one surface-sediment sample also tend to be found in a successively larger fraction of the samples recovered from a basin. This is shown in Fig. 5a–c, where the proportion of samples from which a taxon is recovered is displayed for a range of peak relative abundance thresholds (from 1 to 15%; Heiri 2004). For example, in Naivasha (Fig. 5a) the 25 chironomid taxa reaching an abundance of at least 2% in any one surface-sediment sample are found in 3.5–100% (median

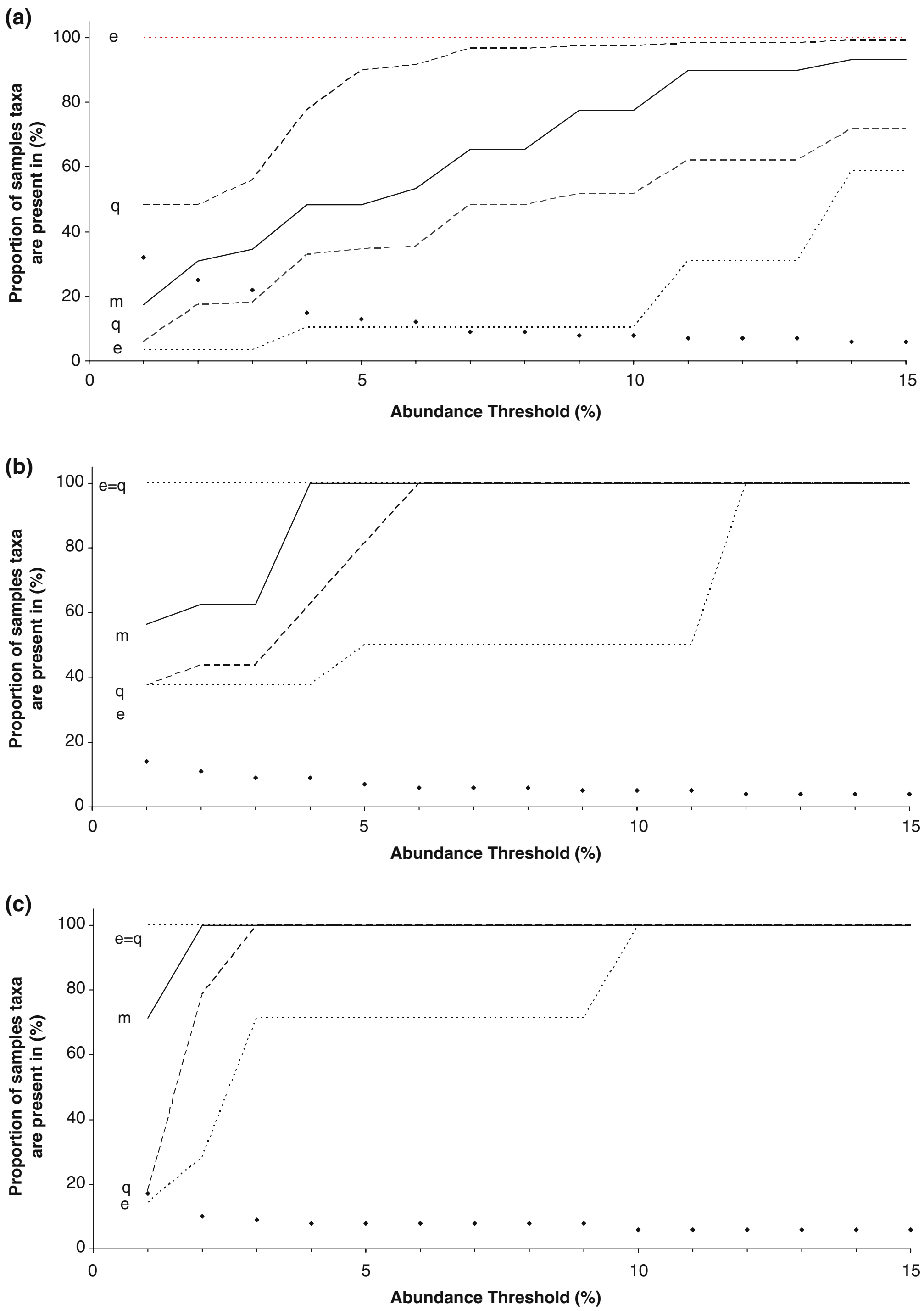

Fig. 5 Representativeness of individual transect samples for the total (basin-wide mean) subfossil chironomid assemblage in Lake Naivasha (**a**), Oloidien (**b**) and Crescent Island Crater (**c**). For all the taxa in a lake reaching a given abundance threshold in any one sample (dots, ranging from 1 to 15%), we plotted the minimum and maximum extremes (*e*), quartiles (*q*) and median (*m*) proportion of samples these taxa are present in Heiri (2004)

31%) of the samples, and even taxa reaching 15% abundance in any one sample are not always found in all samples. In Oloidien (Fig. 5b) the 11 taxa reaching an abundance of 2% in any one surface-sediment sample are found in 37.5–100% (median 62.5%) of the samples, and taxa reaching 12% abundance in any one sample are found in all samples. In CIC (Fig. 5c) the corresponding values are ten taxa, 28.3–100% (median 78.6%), and 10% abundance threshold.

The observation of greater spatial integration in the smaller lake basins is also reflected in the statistical similarity between individual samples within each basin. Both the mean Bray-Curtis similarity index of, and mean Euclidean distance between, individual samples and the basin-wide subfossil assemblage of each lake showed Naivasha samples on average to be less similar to the basin-wide chironomid fauna than Oloidien or CIC samples to their basin-wide means (Table 2). Even though mid-lake samples from Naivasha are less representative of the basin-wide chironomid fauna than nearshore samples (Fig. 3a–e), calculated similarity indices from Naivasha were overall fairly constant throughout the basin. Excluding rare taxa produced similar trends, however with slightly lower similarity values (Table 2).

Discussion

Chironomid concentrations

In all three lake basins, concentrations of chironomid remains were generally highest in surface sediments nearshore. Schmäh (1993) also found this trend along sample transects in the deep, stratified lake Bodensee-Untersee, and attributed it partly to sediment focusing (chironomid remains being diluted by sedimentation rates in the profundal zone) and partly to the depth-related gradient in chironomid production (lower densities and slower growth in the colder, seasonally anoxic hypolimnion). In our lakes, continuous polymixis limits temperature stratification and ensures adequate bottom oxygenation year-round (at least in Naivasha and Oloidien, cf. below), relieving physiological constraints on chironomid production in deeper areas. Hence, lower concentration of chironomid remains in offshore sediments may primarily be a consequence of sediment winnowing nearshore (turbulence prevents settling of the finest sediment particles; Reineck and Singh 1980) and focusing offshore (enhanced sedimentation dilutes the remains of local production). Still, the concentration gradient in Lake Naivasha and its sub-basins is opposite to that observed by Heiri (2004) in small, comparably shallow lakes in southern Norway. There, subfossil concentrations were always higher in the deepest lake areas rather than nearshore, except in one lake with evidence of seasonal bottom anoxia. Thus, in these lakes sediment focusing evidently entrains nearshore chironomid remains to deeper areas in equal or greater proportion to the mineral sediment matrix, and true dilution of remains produced offshore does not occur. Consequently, sediment focusing alone may not suffice to explain the low chironomid concentrations in offshore surface sediments of our study lakes.

Low fossil chironomid concentrations in mid-lake Naivasha sediments (<70 hc/g dry sediment; Fig. 3b) agree with field data from other wind-stressed lakes that document a general negative correlation between living macrobenthos densities and local depth in lakes subject to wind-driven sediment disturbance (Darlington 1977; Wiederholm 1978). At distances less than 500 m from shore in the north-south transect 2T–3T (Fig. 1), concentrations increase to 150 hc/g and more, i.e. comparable with offshore values in the equally shallow but somewhat more sheltered Lake Oloidien (Fig. 3d). Thus, a factor probably contributing to low fossil densities in mid-lake areas of Naivasha is the unfavourable local benthic habitat, specifically the poor support provided by a substrate of flocculent surface muds, and the interference of frequent bottom disturbance with suspension feeding.

Despite excellent wind shelter, fossil chironomid concentrations are also low (<70 hc/g) in water depths ≥9 m in CIC, even at sites only ~100 m from shore (Fig. 3e). Short episodes of bottom hypoxia are known to occur in CIC (DV, personal observation), but this is not likely to significantly influence deepwater secondary production. Although quantitative information is sparse, macrobenthos communities in CIC are known to be quite dense, with 4,000 chironomids m^{-2} (in 1971–1973; Milbrink 1977) compared to 270 m^{-2} in Oloidien (in 1982–1984; Clark et al. 1989). Thus in CIC at least, low fossil concentrations in deepwater surface sediments can in large part be attributed to the diluting effect of very high-recent sedimentation rates: 1.4 cm/year over the past 40 years, versus 0.7 cm/year in Oloidien and 0.8 cm/year in Naivasha (Verschuren 1999).

Taxonomic richness and spatial distribution of the chironomid fauna

The total number of taxa recovered from Lake Naivasha (35) is noticeably higher than that found in its satellite basins (17 in both). A reasonable explanation for this could be that Lake Naivasha, being considerably larger than Oloidien and CIC, offers a greater variety of benthic microhabitat, allowing for establishment of a more diverse chironomid fauna. Comparable ES35 values in all three basins (Table 2) suggest that high-taxon richness in Lake Naivasha is an artifact of larger sample size (2,048 fossils, versus 733 in Oloiden, and 404 in CIC; Table 2). Much of the difference in taxon richness is accounted for by uncommon and rare taxa whose mean frequency is <1 specimen per sample (16 in Naivasha, versus five in Oloidien and three in CIC). Nearshore samples are generally more species rich than their offshore counterparts, reflecting greater diversity in benthic habitat in shallow areas compared to the more uniform mud bottom habitat in deep(er) water.

In all three lake basins, but most significantly in Lake Naivasha and Oloidien, chironomid species distribution in subfossil assemblages showed a strong gradient from shallow nearshore to deeper offshore areas. Living chironomid communities are well known to show distinct shifts in species composition with water depth (especially in deep, seasonally stratified dimictic lakes) through its influence on temperature, oxygen availability and substrate (Brinkhurst 1974; Pinder 1995). In our tropical, warm polymictic study lakes, depth-related faunal shifts primarily reflect the dominant controls of substrate quality and food availability on chironomid composition, rather than oxygen or temperature. Most larval Chironomidae have strong substrate preferences due to their food-gathering strategy, respiration requirements, case-building behaviour, or other life-history characteristics (Pinder 1986; Armitage et al. 1995). The bulk organic-matter content of Lake Naivasha, Oloidien and CIC sediments showed a strong positive correlation with depth, reflecting its slower oxidation (decomposition) in less turbulent deep-water environments (Rowan et al. 1992; Dean 1999). Coarse organic matter and sand both showed a negative correlation with depth and distance to shore, reflecting the preferential removal of fine-grained material in shallow higher-energy environments (Reineck and Singh 1980). As a result, fractions of coarse organic matter (derived from nearshore aquatic macrophytes, and the food of shredding species) and sand were also negatively correlated with bulk organic-matter content (mainly derived from planktonic algae, and the food of engulfers and suspension feeders). Second, different exposure to wind-driven bottom disturbance created an additional near- to offshore gradient in substrate stability, particularly in the main basin of Lake Naivasha. In combination, these result in a strong gradient in larval chironomid habitat from firm and relatively coarse-textured, low-organic substrates in shallow areas nearshore, to soft and unstable organic muds in deeper areas offshore.

In our study, transport of littoral head capsules into the deeper parts of the lake basins is most obvious in CIC, the smallest of all three lake basins. Even though this basin has a quite distinct profundal compartment, none of the taxa appear restricted to the shallower perimeter. In Lake Naivasha, however, several chironomid taxa were confined to the more nearshore (shallower) parts of the lake basin (e.g. near *Xenopelopia* type Naivasha, *P. viridescens* and *C. pseudomancus*). Similarly, in Lake Oloidien, taxa such as *P. viridescens* and *N. brevipalpis* were restricted to nearshore locations.

Auto-ecological information on African chironomids is scarce, however the spatial distribution patterns evident in the surface-sediment assemblages from Naivasha conform with knowledge on modern chironomid ecology. For example, *C. formosipennis*, whose fossil abundance is higher on offshore deep-water organic mud bottoms poor in coarse plant debris and sand, is currently the dominant chironomid on soft mud bottoms of Lake Naivasha (63%) and in the profundal of CIC (50%), and, to a lesser extent in Lake Oloidien (28%; Milbrink 1977; Clark et al. 1989). *D. septemmaculatus*, whose fossil distribution was positively correlated with nearshore shallow-water bottoms rich in coarse organic debris, indeed shows preference for submerged macrophytes in shallow lake waters (Harrison 1987; Kibret and Harrison 1989; Harrison 1993). Other examples include *C. pseudomancus*, whose fossil distribution was very similar to that of *D. septemmaculatus* above. In fact, *C. pseudomancus* has a strong preference for sandy substrates in well-oxygenated but wind-sheltered environments (Verschuren et al. 1997), and in Lake Naivasha it is restricted to nearshore areas with fine to coarse sand; no larvae having been found in soft mud offshore (McLachlan and McLachlan 1971; Hare and Carter 1987; Clark et al. 1989).

Taphonomy and its implications

Chironomid remains are (initially) deposited close to where the larvae live, but sediment erosion and re-deposition transports littoral head capsules into the deeper parts of the lake (Wiederholm 1979; Hofmann 1986; Kansanen 1986; Frey 1988; Brodersen and Lindegaard 1999; Heiri 2004). The extent to which chironomid remains are moved offshore clearly depends upon lake morphometry (Frey 1988) but has not been completely resolved. For example, in her examination of the taxonomic distribution of subfossil chironomids in surficial sediments of the large and deep Bodensee-Untersee, SW-Germany (Z_{max} = 253 m; Z_{mean} = 85 m; surface area = 571 km^2), Schmäh (1993) found that most head capsules in profundal assemblages had been washed in from the littoral zone or from the slope (similarity between profundal and littoral assemblages >70%). Likewise ~80% of fossil heads found in the centre of Lake Washington, USA (Z_{max} = 65 m; Z_{mean} = 39 m; area = 87.6 km^2) originate from the littoral zone (Wiederholm 1979); and mid-lake fossil assemblages of four shallow Danish lakes were most similar (up to 66%) to live chironomid communities in the littoral zone (Brodersen and Lindegaard 1999). Iovino (1975), however, compared extant and fossil chironomid communities in Pretty and Crooked Lakes, IN, USA and concluded that offshore transport of littoral remains was minimal. Similarly, Stark (1976) studied the extent of redistribution of fossil chironomid remains in Elk Lake, MN, USA (Z_{max} = 29.5 m; area = 1.21 km^2), and also concluded that relatively little transport of chironomid head capsules had taken place.

Inshore communities often show a different response to long-term changes than offshore communities (Frey 1988). Since most chironomid-based paleolimnological reconstructions rely on a single mid-lake sediment record, there is consequently the risk that interpretations are biased by redeposition of littoral chironomid taxa in the profundal region (Hofmann 1986, 1988). Within-lake variability of fossil assemblages also contributes to the overall prediction error associated with chironomid-based inference models (Heiri et al. 2003). Hence, assessing whether the chironomid content of a single, centrally located core is representative of the whole lake both in terms of chironomid source communities and accumulation rates within the basin should be a prerequisite to any paleolimnological study, but in practice it has rarely been done (e.g. Schmäh 1993; Heiri 2004). Heiri (2004) studied subfossil chironomids in the surface sediments of mid-lake samples and littoral to deep-water transects of five small and shallow Norwegian lakes. In this study, representativeness of single-core records for the chironomid fauna of a lake was considered with regardto taxon richness (i.e. measured as the proportion of taxa known from a lake, that is found in an individual sediment sample). He concluded that, even though individual transect and mid-lake samples always contained only part of the total local subfossil chironomid fauna, chironomids dominant in any section of the study lake were found in most of the mid-lake samples. These results are clearly supported by our own findings (Figs. 4, 5). However, as various numerical techniques for organism-based quantitative reconstruction essentially use (are sensitive to) percent abundances of taxa (Walker 2001; Eggermont et al. 2006), considering the percent species composition of samples is fundamental to assessing similarity between mid-lake subfossil assemblages and the total (basin-wide) mean chironomid fauna. In this study, nearshore samples always represented the total subfossil assemblage of a basin better than offshore samples. In other words, shallow-water taxa and littoral habitat wereunderrepresented in offshore and mid-lake samples, and spatial integration of fossils through pre-burial transport was nowhere complete. However, when taking only the common taxa into account, the similarity between mid-lake and total subfossil assemblages was still considerably high (66.7% in Naivasha; 75% in Oloidien and 100% in CIC). The observation that samples of the smaller CIC and Oloidien were more representative for (i.e. more similar to) the basin-wide mean assemblage than those of Lake Naivasha can be attributed primarily to the difference in basin morphometry. In the large and shallow Lake Naivasha where bottom dynamics are dominated by wind-driven resuspension and random redistribution of previously deposited sediments (Hilton et al. 1986), frequent mixing and redeposition clearly do not suffice to create uniform chironomid assemblages in lake sediments. In Oloidien and CIC on the other hand, spatial homogeneity of offshore sedimentation and spatial integration of fossils is promoted by a combination of small lake area, strongly ellipsoid (Oloidien) or paraboloid (CIC) bathymetry with steep bottom gradients nearshore, and an essentially flat lake floor (Verschuren 1999). Even though substrate composition in CIC has strong depth dependence (Table 1), pre-burial transport and integration was strong enough to blur the depth (or distance to shore)-related shift in distribution of live chironomid communities.

Limited pre-burial spatial integration of habitat-specific chironomid assemblages in very large and deep lakes has been used for within-lake calibration of environmental gradients (e.g. Verschuren et al 2002; Eggermont and Verschuren 2003), as has been done with other biological proxy indicators (e.g. Mackay et al. 2003). Our results indicate that also in the shallow, wind-stressed Lake Naivasha the near- to offshore gradient in chironomid habitat remains imprinted on subfossil assemblages. Hence, also in shallow fluctuating lakes, given sufficient size, habitat-specific chironomid assemblages can be exploited for within-lake calibration of environmental gradients.

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