

Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa

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Abstract

We report here on the first detailed ostracode stratigraphic record to be obtained from late Holocene sediments of Lake Tanganyika. We analyzed four cores, three from the northern lake region and a fourth from a more southern lake locality, that collectively record ostracode assemblages under a variety of disturbance regimes. These cores provide a stratigraphic record of ostracode abundance and diversity, as well as depositional changes over time periods of decades to millennia. We have investigated the fossil ostracodes in these cores by looking at temporal changes of species diversity and population structure for the species present.

All four cores provided distinct patterns of ostracode diversity and abundance. BUR-1, a northern lake core obtained close to the Ruisizi River delta, yielded a sparse ostracode record. Karonge #3, another northern core from a site that is closely adjacent to a river delta with high sediment loading, yielded almost no ostracodes. The third core 86-DG-14, taken from a somewhat less disturbed area of the lake, suggests that there have been recent changes in ostracode populations. Through most of the lower portion of this core, ostracode abundance is low and species richness is relatively constant. Above 7 cm there is a marked increase in ostracode abundance and a corresponding decrease in species richness, probably signaling the onset of a major community disturbance, perhaps due to human activities. The southernmost core, 86-DG-32, is from a site that is well removed from influent rivers. Ostracode abundance varies erratically throughout the core, whereas species richness is relatively constant and high throughout the core.

The temporal variation evident in ostracode community makeup both within and between the studied cores may be a result of naturally patchy distributions among ostracodes, coupled with local extinctions and recolonizations, or it may reflect inadequate sampling of these high diversity assemblages. In either case, these cores illustrate the potential to obtain high resolution ostracode records from the rich, endemic fauna of Lake Tanganyika that can be used to address questions about the history of community structure and human impacts in this lake.

Introduction

Lake Tanganyika, located in the western branch of the African rift valley, is home to approximately 1400 species of living organisms, of which more than 600 species are endemic (Cohen, 1991; Coulter, 1994).

Among the ostracode crustaceans, approximately 90 species have been described (74 endemic) (Coulter,

1991), and as many as 120 more endemic species remain to be formally described (Cohen, 1994; Martens, 1994). Lake Tanganyika has the second highest species diversity of any lake in the world, after Lake Baikal, Russia. This high diversity may be related to both the 9–12 Ma age of the lake ecosystem (Tiercelin & Mondeguer, 1991; Cohen et al., 1993a) and its complex habitat structure (Cohen et al., 1993b).

Although there have been several studies done on modern Lake Tanganyikan ostracodes and their ecology (e.g., Rome, 1962; Cohen, 1994; Martens, 1994; Cohen et al., 1995), their fossil record has not been investigated. This study examines the recent ostracode stratigraphy and historical biodiversity record found in short cores collected from four different locations around Lake Tanganyika. Our purpose here is to demonstrate the fact that a rich and highly resolved ostracode fossil record can be obtained from Lake Tanganyika. This study also suggests future applications of ostracode paleoecology to questions about ostracode community structure and the history of anthropogenic disturbance as it affects lake communities.

Limnology

Lake Tanganyika is located in the western branch of the East African Rift system. The lake covers an area of 32,600 km², and has a volume of 18,880 km³. Average lake depth is 570 m, and maximum depth is 1470 m. Lake Tanganyika is an open basin, fed by four major rivers (the Malagarasi, Ruzizi, Lugufu, and Lufubu rivers) and numerous smaller rivers, resulting in low salinity and low alkalinity lake waters (conductivity = 670 μScm^{-1} , $A_c = 6.6 \text{ meql}^{-1}$; Cohen et al., 1997a). The lake is anoxic below 100–200 m depth (Hecky et al., 1991), which limits benthos to a 'bathtub ring' around the lake. The substrate around the lake is composed of rock, sand, mud, or a mixture of rock and clastic sediments. Lake waters are productive, but clear. Furthermore, the lake is relatively unpolluted from industry (Vandelannoote et al., in press) but there is a significant discharge of sediments from deforested watersheds (Cohen et al., 1993b).

Description of core localities

This study was based on data obtained from four cores that were collected from Lake Tanganyika (Figure 1). The cores were collected for an unrelated project, but the study cores were chosen from locations that span a range of observable modern patterns of sedimentation disturbance based on their proximity to turbid deltaic inflow. Core BUR-1 was collected from 50 m water depth just offshore from Bujumbura, about 10 km from the Ruzizi River Delta, in northern Burundi, which is adjacent to the areas of highest human population density within the Lake Tanganyikan watershed (> 350 people/km² in Bujumbura in 1990, Republique du

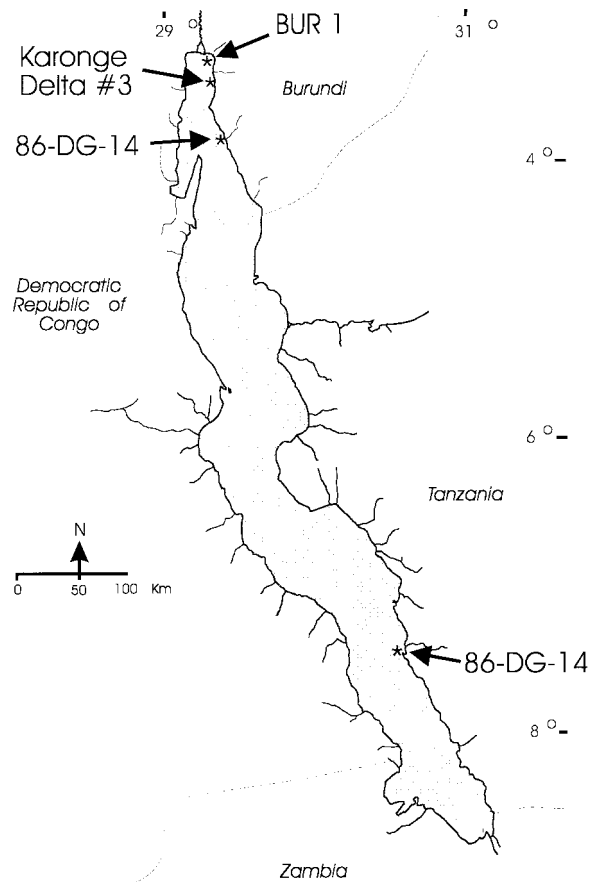


Figure 1. Map of Lake Tanganyika, Africa, showing the locations of core collection sites. Intensity of deforestation is greatest at the northern end of the basin, decreasing in the central and southern regions surrounding the lake.

Burundi, 1990). Karonge Delta Core #3 was collected immediately offshore (~ 0.5 km) from the Karonge Delta, in northern Burundi, from 50 m water depth. The watershed of the Karonge River today is very densely populated by small subsistence agricultural communities. Core 86-DG-14 was collected offshore from central Burundi in the northern part of the lake, in about 60 m water depth. This location is 2.5 km north of the Dama River delta, a densely populated and partially deforested watershed of the northern part of the lake, although a considerably less impacted region than the watersheds near the two northern Burundi core sites. Core 86-DG-32 was collected from the southern region of the lake, near Kipili, Tanzania, from a depth of about 40 m. The core site is approximately 6 km southwest of the nearest delta, the Luamfi River, which drains a relatively undisturbed watershed. This region

has a much lower human population density than the other sites (5 to 10 people/km², Oxford Atlas, 1994), and retains a dense vegetation cover (A.C. personal observation).

Material and methods

The four cores used in this study were collected during different field seasons. Core BUR-1, collected in 1984, is one of 63 cores taken from the Northern Tanganyika basin by the French Project GEORIFT (Tiercelin & Mondeguer, 1991). The GEORIFT cores were collected using a Kullenberg corer using a 7 cm IW PVC core liner. Karonge #3 was collected in 1992 by a joint University of Arizona (U.S.) and University of W. Brittany (France) and Royal Belgian Institute of Natural Sciences expedition, using a 2 m weighted gravity corer (IFREMER type) with a bronze tapered nose cone, leaf-spring core catcher, and a 12 cm IW PVC core liner. Cores 86-DG-14 and 86-DG-32 were taken by a Colorado College (U.S.) expedition in 1986, using a 1 m weighted gravity corer with a bronze tapered nose cone, a leaf-spring core catcher, and an 8 cm IW PVC core liner. All cores were inspected for overpenetration prior to storage (none was evident

based on clear surface water in core liner above core with no evidence of core top resettling), and for evidence of significant sediment deformation (laminae appeared horizontal upon opening and no micro-shearing was evident). Hvorslev (1949) demonstrated that the 'safe sampling length' for simple corers is between 10 to 20 times the inner diameter, and somewhat longer than that for piston-type corers. For longer/thinner cores there is a risk that low shear-strength sedimentary layers will get squeezed aside, and only the high shear-strength ones will be sampled. Since our cores all fall into this range (with the possible exception of the BUR-1 core) this type of artifact is unlikely to be a problem.

Cores BUR-1 and Karonge Delta Core #3 were shipped intact to France and sampled at the sedimentology laboratory at the University of West Brittany, whereas cores 86-DG-14 and 86-DG-32 were opened, logged and sampled in the field at the time of collection. Core BUR-1 (243 cm in length) was sampled at 10 cm intervals (larger sample intervals were necessary when sufficient core material wasn't present) and processed using the same methods as described below. Core BUR-1 was not as ostracode-rich as cores 86-DG-14 and 86-DG-32, thus ostracode counts were variable, depending on the population size of the

Table 1. Summary of core data, including location and environment of collection sites, approximate ages of the cores, and analytical methods used

	Karonge Delta #3	BUR 1	86-DG-14	86-DG-32
Latitude	3 35.5 S	3 24.2 S	3 57.0 S	7 27.3 S
Longitude	29 20.2 E	29 19.2 E	29 25.5 E	30 34.3 E
Water depth of core (m)	50	50	60	40
Adjacent watershed	Karonge River	Ruzizi River	Dama River	Luamfi River
Location of core relative to watershed	Delta	7 km SE of delta	2 km N of delta	8 km S of delta
Local disturbance factors	Near total deforestation	Near total deforestation	Intense deforestation	Very little deforestation
Core length (cm)	116	243	74	92
Estimated age at base	76–85 yrs	post 500 A.D.	> 100–500 yrs	post 500 A.D.
Estimated mean sedimentation rate	1.04 cm yr ⁻¹ to 1988 (from base to 47 cm core depth); 15–20 cm yr ⁻¹ between 1988 and 1992 (upper 47 cm of core) under steady state conditions	3.1–6.5 mm yr ⁻¹ above 142 cm core depth	1.2–2.5 mm yr ⁻¹ above 47 cm core depth	Weak estimate of 0.58–1.22 mm yr ⁻¹ over past 185–385 yrs
Estimated time recorded by core	67–80 yrs	810–1500 yrs	300–500 yrs	< 1500
Features analyzed				
Granulometry	X	X	X	X
Ostracodes		X	X	X
Isotopes ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$)		X	X	X
²¹⁰ Pb	X			

sample, which ranged from 0–360 (see Figure 3a for count sizes). The Karonge Delta #3 core (116 cm in length) was also sampled at variable intervals using the same methods as described below, however very few ostracodes were recovered.

Cores 86-DG-14 (74 cm in length) and 86-DG-32 (92 cm in length) were sampled in 0.5 cm thick slices (approximately 1 g dry weight) at 5 cm intervals. Each core sample, composed of semi-consolidated silt and mud, was then disaggregated using a modification of the USGS freeze-thaw method (Forester, 1991). This method disaggregates the sediments, but leaves the ostracode valves intact. The disaggregated sediments were wet-sieved using U.S. Standard Sieve #100 and 230-mesh sieves, to separate the coarse clastics, plant fragments, and adult ostracodes from the finer sands and juvenile ostracodes (retained by the finer sieve). For this initial study, we counted 300 ostracode valves per sample, and calculated total abundances per g of unsieved sediment, abundance by species, and species richness for each sample. Confidence intervals for this sample size are given in Table 2. Because of the relatively low abundances of ostracode valves per g sediment encountered in these cores, most adult ostracodes in a sample were counted by this technique, although the number of rare taxa encountered suggests that future studies will require larger sample counts. For example, exhaustive counts of all ostracodes in a single sampling horizon (~3,500 individuals) for one sample

from core 86-DG-32 showed that a 300 count picked up about two thirds of the species actually present (Figure 2).

A simple grain size analysis for all cores was based on the relative weight percentage of the sediments separated by each sieve.

The Karonge Delta #3 core was directly dated using ^{210}Pb analysis. ^{210}Pb samples were taken from the Karonge Delta #3 core at 0.5 cm intervals for the upper 20 cm, 5 cm intervals from 20–50 cm, and at 20 cm intervals below that depth. (Total core depth = 116 cm). We used the polonium method of Nittrouer et al. (1979) and McKee et al. (1983) to calculate ^{210}Pb . An advection-diffusion model (Guinasso & Schink, 1975) was used to extract sedimentation information from the down-core distribution of radionuclides associated with particulates.

The other three cores were not directly dated, but correlation of their stable isotope stratigraphy with the late Holocene $\delta^{18}\text{O}$ history known for the lake (Cohen et al., 1997a) provides some additional age and sediment accumulation rate constraints.

Adult specimens of *Mesocyprideis* sp. 2b, *Mecynocypria opaca*, *Candonopsis depressa*, *Gomphocythere* sp. 3, and *Cyprideis* sp. 24 were selected for stable isotope analysis from cores 86-DG-14, BUR-1 and 86-DG-32. At some horizons in BUR-1 and 86-DG-32 these samples were supplemented by mollusc fragments (mostly from the gastropod *Tiphobia horei*). Adhering

Table 2. 95% confidence intervals for a given number of ostracodes (x) collected from a total sample size of 300 ostracodes. From Hamilton (1990)

Number of individuals present for a given species 'n'	Total sample count (all species)	Percentage (P) of total sample that is species 'n'	Lower confidence interval (%) bound (P-1 σ)	Upper confidence interval (%) bound (P+1 σ)
1	300	0.330	0.05	1.90
2	300	0.670	1.80	2.40
3	300	1.000	0.30	2.90
4	300	1.330	0.52	3.38
5	300	1.670	0.71	3.84
6	300	2.000	0.92	4.29
7	300	2.333	1.13	4.74
8	300	2.670	1.36	5.17
9	300	3.000	1.59	5.60
10	300	3.330	1.82	6.03
15	300	5.000	3.05	8.08
20	300	6.670	4.35	10.07
25	300	8.330	5.71	12.01
30	300	10.000	7.09	13.92
35	300	11.670	8.51	15.79
40	300	13.330	9.95	17.65
45	300	15.000	11.40	19.48
50	300	16.670	12.88	21.30

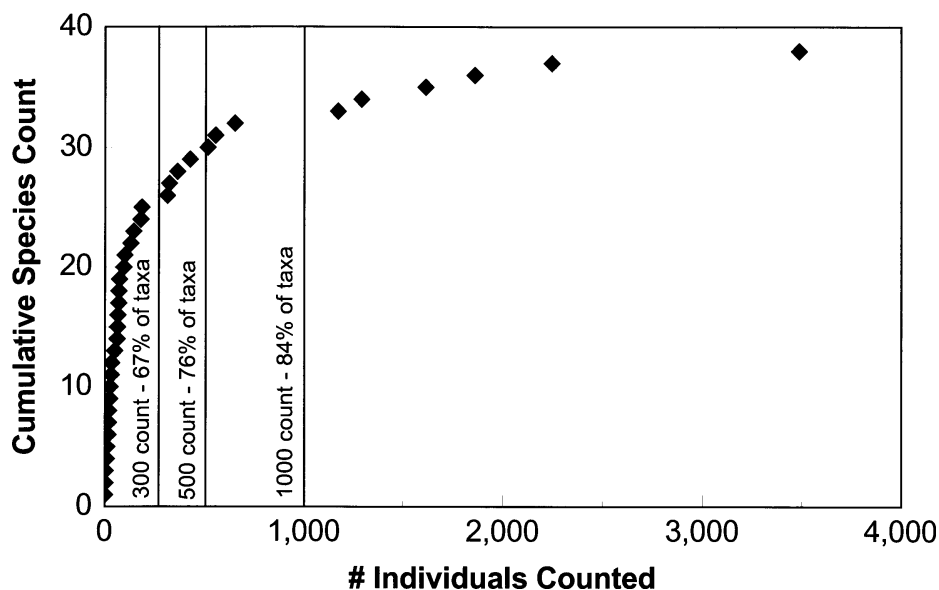


Figure 2. Cumulative species count with the incremental addition of more ostracode individuals from an exhaustively counted sample (86-DG-32, sample P, 72.5–77.5cm downcore). Approximately two thirds of all species present in the 0.5 cm thick stratigraphic horizon were encountered by counting 300 specimens. Continuing the count to 1,000 individuals brought the species enumeration to over 80% of the total, but would have required over 3 times the counting effort.

sediment was removed with a fine (000) brush in 4 × distilled water, or for 86-DG-14, in a 10% solution of hydrogen peroxide followed by a rinse of 4 × distilled water. For core 86-DG-14 we were able to collect at least one specimen for each sample in the upper half of the core. In the lower half of the core, however, adult ostracodes were often absent or too small for stable isotope analysis. For cores BUR-1 and 86-DG-32, the small size of available ostracode fossils necessitated combining several valves of the same species at each horizon into a single sample for analysis. Fossils were analyzed on a Finnigan MAT 251 mass spectrometer paired with a KIEL automated sample preparation device at the University of Michigan Stable Isotope Laboratory. Standard error of results is $\pm 0.08\text{‰}$ for $\delta^{18}\text{O}$, $\pm 0.06\text{‰}$ for $\delta^{13}\text{C}$ based on a replicate analysis of NBS-20, NBS-19, and University of Michigan internal standards.

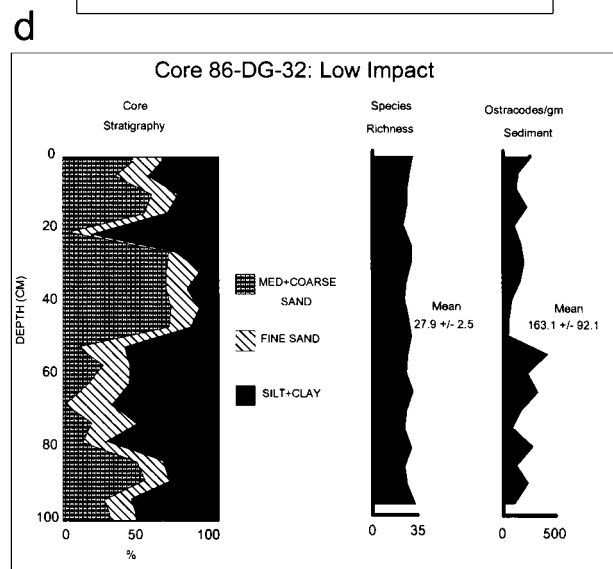
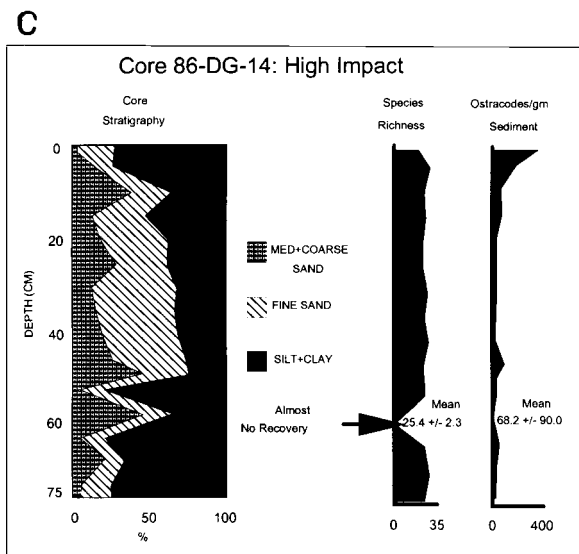
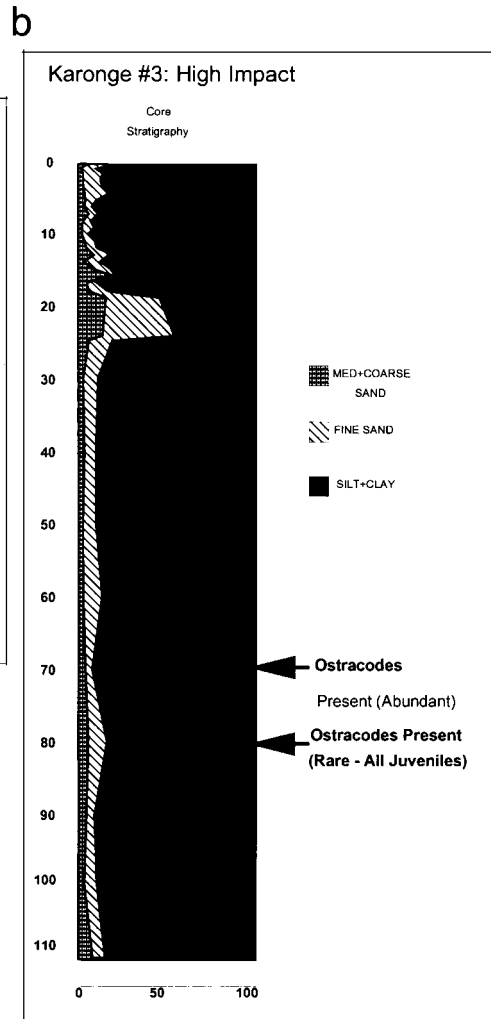
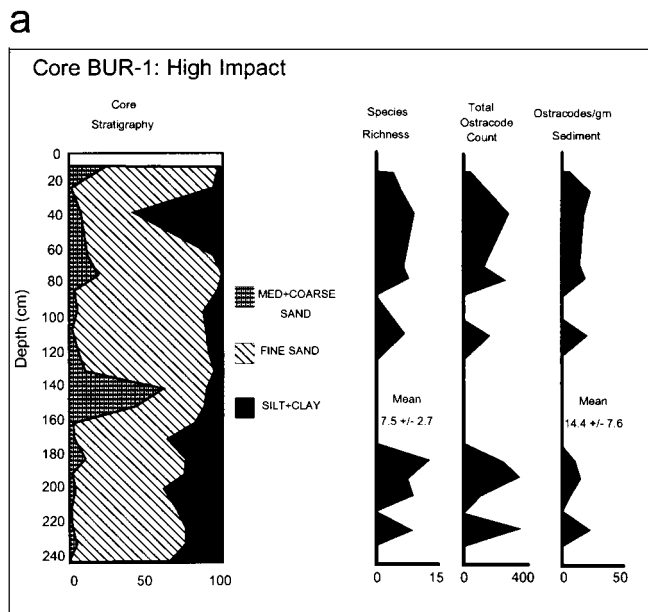
We analyzed the frequency patterns of ostracode species in all of the cores, although, as noted earlier, neither BUR-1 nor Karonge #3 were sufficiently ostracode-rich to allow a complete comparison with the 86-DG-14 and 86-DG-32 cores. We calculated Shannon-Wiener diversity indices (after Krebs, 1972) for samples from the latter two cores, and we calculated faunal similarity through time indices between

stratigraphically adjacent core samples using the Jaccard Index (Valentine, 1973). This index was used to compare overall similarity, as well as to make comparisons between common species (those species making up the most abundant 85% of ostracode individuals from each segment), and between the rare species (those comprising the least abundant 15% of individuals).

Results

Core stratigraphy

Core BUR-1 (Figure 3a) consists of light brown to dark gray, thinly laminated to thick bedded silt to very fine sand that is interbedded with shelly debris in many intervals. The lower portion of BUR-1 (247–172 cm) is dominated by very fine sand and silt and contains abundant gastropods. Above this, the sediments coarsen upwards, with a prominent coarse sand layer at 160 to 142 cm. The upper 123 cm consists of very fine sands with shelly debris throughout. There is a notable silt/clay-rich interval between approximately 30 and 50 cm. Plant material is also found throughout the core, but sponge spicules are absent throughout the core.



The Karonge #3 core (Figure 3b) consists of gray-brown to black, laminated and thinly bedded muds. The core is dominantly silt and clay. From 0–21 cm the core consists of massive muds, underlain by a sandy silt interval between 21 and 27 cm depth. Below 27 cm the sediments are diffusely to well laminated black and gray muds. No sponge spicules are present in this core.

Core 86-DG-14 (Figure 3c) consists of olive to black, thin- to thick-bedded, silty sands that are interbedded with sparse yellowish brown laminae. Bioturbation was not evident in the core. Silty clays in the bottom third of the core abruptly give way to fine sands at ~50 cm depth. Above this the sediment gradually fines upwards. The lower third of the core is dominated by plant debris, whereas the upper two thirds of the core contains a smaller proportion of plant material and a correspondingly greater amount of siliciclastic material. There are notable medium and coarse clastic sandy horizons at 53–58 cm and 47–48 cm core depth. Sponge spicules are absent from the core sediments.

Core 86-DG-32 (Figure 3d) is composed of olive-black silty sands and sandy silts. Apart from occasional laminae, the muds are thick bedded with occasional gastropod (*Tiphobia*, *Neothauma*) shell fragments. Between the base of the core (93 cm) and 47.4 cm, the sediments are dominantly sandy silts and muds. From 47.5 cm up to the top of the core the sediments are generally coarser-grained, silty sands. Plant fragments are uncommon in this core, but there is abundant carbonate silt and sand. Sponge spicules are common.

Problems with age control of cores

Age control for all cores is very limited. Our best age control comes from the ^{210}Pb -dated Karonge Delta #3

Figure 3. Core stratigraphy and overall ostracode stratigraphy. (a): Core BUR-1. Note the sandy interval at approximately 140–157 cm depth in this core, which may be the result of deposition during a lake-level lowstand. This interval lacks ostracodes, and may also correspond to the coarse unit containing few ostracodes in core 86-DG-14; (b): The Karonge Delta #3 core is almost devoid of ostracodes. Only samples at 68 and 78 cm depth contain ostracodes; (c): Core 86-DG-14. Note that in this core there is a decrease in species richness and increase in overall ostracode abundance in the two uppermost sample intervals (0–7 cm depth), which correlates with an increase in mud content in these same samples. A sandy interval at approximately 58 cm depth is almost barren of ostracodes; (d): Core 86-DG-32. There is no obvious relationship between ostracode populations and grain size in this core. A major decrease in ostracode abundance occurs from 57 to 52 cm, coinciding with an abrupt coarsening of sediment.

core (Figure 4). The ^{210}Pb activity profile for this core *increases* downcore to about 47 cm. Below this depth, a normal decay pattern with depth allows a model sediment accumulation rate of 1.04 cm yr^{-1} to be calculated. There are three possible explanations for the inversion of ^{210}Pb decay activity through the upper 47 cm of the core. The most likely explanation of this pattern is a vast increase in sedimentation rate in the upper portion of the core, resulting in progressive sediment dilution of ^{210}Pb . It is possible that the decrease in ^{210}Pb resulted from increased mixing of the sediments due to infaunal organisms. However, the laminated nature of this core suggests that this is unlikely. The level of benthic activity needed to create such mixing is great, and our underwater observations of Lake Tanganyika's macrofauna and box cores show that this magnitude of mixing is uncommon in the deeper parts of the littoral zone. Another possible explanation for the decrease in ^{210}Pb is the slight possibility of remobilization of the ^{210}Pb within the lake sediments, as a result of Fe cycling. In this scenario, Pb is cycled passively with Fe through the sediments because the porewater sulfide content is so low that Fe (and Pb) is mobilized upon reduction and not re-stabilized as FeS. Theoretically, Pb can be released from the particulates and diffused into the overlying water column. This process, however, is rare and unlikely to be responsible for the decreasing ^{210}Pb level in the upper 47 cm of the core. This would require a great diffusive flux or extensive resuspension of the ^{210}Pb to this depth, but because of limitations due to diffusivity and porosity, this scenario is possible only at sites where sediment accumulation rates are less than 0.1 cm yr^{-1} .

Assuming that the ^{210}Pb profile represents a dramatic increase in sedimentation rates in the upper part of the core, it is possible to place age estimates on this curve using a Constant Rate of Supply (CRS) model. The slope of the ^{210}Pb profile below 47 cm yields a sedimentation rate of 1.04 cm yr^{-1} , and given the location of the core site (delta offshore of deforested hillslopes), it is more likely that the sediment accumulation rate has increased in recent years. The most probable explanation for the decrease in ^{210}Pb content in the upper 47 cm is that sediment accumulation rates increased dramatically shortly before 1992.

Because of the analytical uncertainty for ^{210}Pb measurements, we are not able to distinguish between samples whose concentrations differ by 8–12%. Temporal resolution within a sediment core is governed by the half life of ^{210}Pb (22.3 yrs), and an 8–12% change

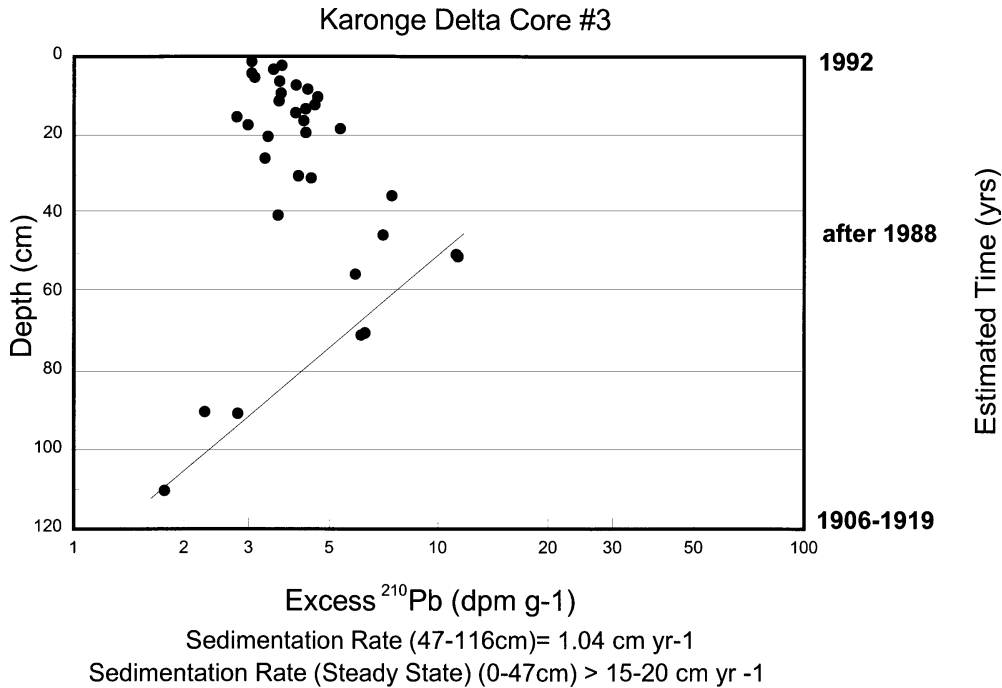


Figure 4. Age control of the Karonge Delta #3 core as determined by ²¹⁰Pb dating. Plot of excess ²¹⁰Pb against depth (left axis) and approximate age in yrs (right axis). The decrease in ²¹⁰Pb content in the upper 47 cm of the core suggests that sediment accumulation rates have increased since before 1992 (the year the core was collected).

in ²¹⁰Pb concentration resulting from exponential decay corresponds to a period of 3–4 yrs. Therefore, the uniform (slightly decreasing) ²¹⁰Pb content in the upper 47 cm of the core indicates that the sediments in this layer accumulated in less than 3–4 yrs, and that the base of the core is approximately 80–82 yrs old. A steady state sedimentation pattern would suggest an accumulation rate of 15–20 cm yr⁻¹, but it is possible that all of the sediment was deposited over a much shorter time interval. If the constant ²¹⁰Pb distribution in the upper 47 cm is the result of rapid sedimentation then a radiogenic isotope with a much shorter half life such as ²³⁴Th (half life = 24 days) is needed to resolve the most recent sedimentation rate.

Age estimates for the remaining cores can only be obtained by making rough estimates of sediment accumulation rates, through lithologic correlations of possible event beds, and through stable isotope correlations with the late Holocene Lake Tanganyika stromatolite record. Tiercelin & Mondeguer (1991) calculated a range of sediment accumulation rates between 0.5 and 3 mm yr⁻¹ for off-shore sites in the northern basin of the lake near the 86-DG-14 and BUR-1 core sites. This range of rates suggests that

Core 86-DG-14 may represent anywhere from 250 to 1500 yrs of sedimentation and that BUR-1 may represent anywhere between 800 and 5000 yrs of accumulation. No radiometrically dated horizons from cores of comparable length from the northern lake basin have yielded evidence of pre- late-Holocene deposits or erosion surfaces. Other data provide additional constraints on the ages of these cores. First, the bases of cores 86-DG-14, BUR-1, and 86-DG-32 all probably postdate 500–600 A.D., based on a comparison of oxygen isotope stratigraphy from these cores (Figure 5) with a $\delta^{18}\text{O}$ record from ¹⁴C-dated fossil stromatolites (Cohen et al., 1997a). Stromatolites from the northern part of the lake that formed prior to 500–600 A.D. are significantly enriched in ¹⁸O ($\delta^{18}\text{O} = +4$ to $+6\text{‰}$ PDB) compared with relatively constant $\delta^{18}\text{O}$ of $+2$ to $+3$ in more recent times. None of the ¹⁸O records of the cores record this shift (Figure 5), and we therefore infer that their bases all postdate 500–600 A.D.

Second, there is a known lake-level fall, determined from shell lag deposits, that occurred between ~1600 and 1800 A.D. (Cohen et al., 1997a) (Figure 5). This lake level low stand may correlate with a coarse sand interval, in which diagnostic littoral ostracode taxa

occur, that is present in both cores BUR 1 (140–160 cm) (Figures 3a and 6) and 86-DG-14 (47–48 cm) (Figures 3c and 7). The coarse interval in core 86-DG-14 contains shallow water ostracodes. Although the coarse horizon in BUR-1 does not contain any ostracodes, a slightly deeper interval (181–193 cm) does contain some shallow to sub-littoral ostracodes. Assuming the correlation of the sandy horizon with the 1600–1800 A.D. low lake stand is correct, these data imply mean sediment accumulation rates above the sandy horizon of 1.2–2.5 mm yr⁻¹ for core 86-DG-14 and 3.1–6.5 mm yr⁻¹ for BUR-1. In the 86-DG-32 core a

possible correlation can be made between a sand interval in this core at 22.5–47.5 cm and the lowstand sandy horizons found in the more northerly cores. If this correlation is correct, it would imply mean sediment accumulation rates at the 86-DG-32 site of 0.58–1.22 mm yr⁻¹ over the past 185–385 yrs. We consider this correlation to be weak, however, given the likelihood that the grain size signal here is a strictly local phenomenon, and due to the absence of littoral ostracodes associated with, or stratigraphically adjacent to, the sandy horizon. Also, the coarse sandy interval in core 86-DG-32 is much thicker than the low stand

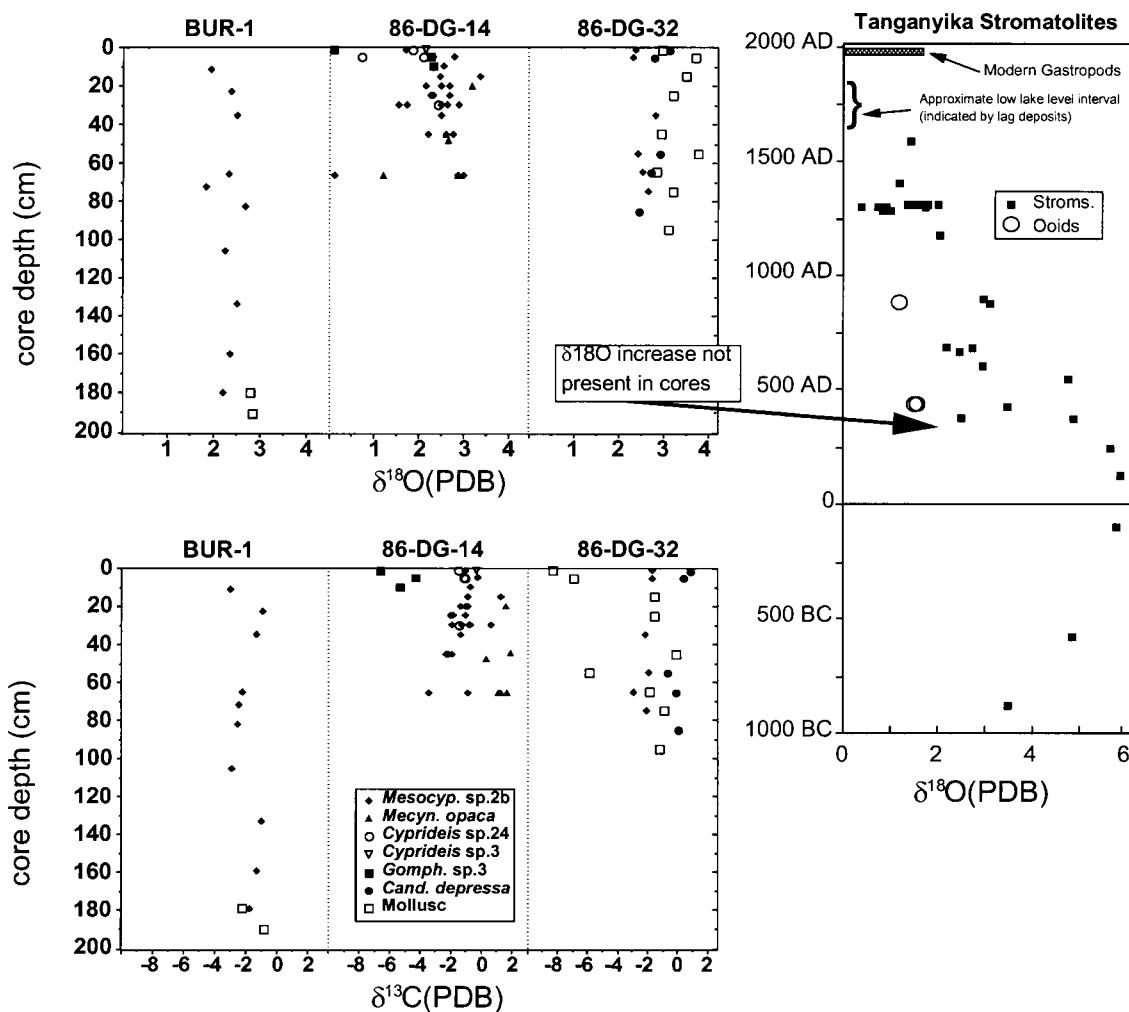


Figure 5. Oxygen and carbon isotope analyses from the three cores. Samples from BUR-1 and 86-DG-32 are from multiple ostracode shells or single mollusc fragments whereas 86-DG-14 data are from single ostracode valves. A comparison of these data to the $\delta^{18}\text{O}$ of fossil stromatolites demonstrates that the base of each core post-dates the return of carbonate $\delta^{18}\text{O}$ values to the modern range of 2–3‰ PDB at approximately 500 A.D. (Lake Tanganyika stromatolite data and associated ^{14}C dates summarized in Cohen et al., 1997a). A prominent sandy horizon with littoral ostracodes recorded in 86-DG-14 at 47–48 cm probably correlates with the ca. 1600–1800 A.D. low lake stand indicated on the stromatolite curve.

sandy intervals in the other two cores, making the correlation less likely.

Ostracode stratigraphy

A diverse ostracode fauna was found in the Lake Tanganyika cores. The fauna consists almost entirely of species endemic to Lake Tanganyika, making comparisons with habitat or depth range for ostracodes from elsewhere in Africa impossible. Many of the species recovered are still undescribed, and their distribution and ecology within Lake Tanganyika are poorly known. Among the 79 taxa encountered in this study, 37 are probably nonswimming species and 42 swimming species. This agrees well with the estimate of K. Martens (pers. comm., 1998) that about 50% of all ostracode taxa in Lake Tanganyika are swimmers (e.g. Cyclopyridinae, including *Mecynocypria* and *Alloocypria* spp.; all Cypridopsinae described to date, including *Cypridopsis*, *Tanganyikacypridopsis* spp. and the Megalocypridinae, e.g. *Tanganyikacypris* spp.). Cytherideidae (e.g. *Cyprideis*, *Tanganyikacythere*, *Archaeocyprideis*, *Mesocyprideis* and *Romecytheridea* spp.), Limnocytheridae (e.g. *Gomphocythere* spp.) and the Candoninae (e.g. *Candonopsis* spp.) comprise the bulk of the nonswimming taxa. Where interpretations can be made concerning habitat range, they are based on a modern distribution database of Lake Tanganyikan ostracodes that is maintained at the University of Arizona. Ostracode species which have not yet been formally described are indicated by a genus name followed by a number or letter (i.e. *Mesocyprideis* sp. 3 or *Gomphocythere* sp. z).

The diversity of ostracodes described in all the cores below must be considered a conservative or low estimate, given the exhaustive count statistics described earlier (Figure 2).

BUR-1 and Karonge #3

As a result of low abundances, the counts for BUR-1 are variable (not equal to 300) (Figure 3a), and these ostracode data cannot be compared statistically to cores 86-DG-14 and 86-DG-32. Ostracode species richness varies between 0 and 13 species ($X = 7.5 \pm 2.7$ for samples where ostracodes occur). Ostracode abundance was very low (0–23.6 valves/g, $X = 14.4 \pm 7.6$ among samples where ostracodes occur) with several barren intervals. These barren intervals are associated with both the coarsest- and finest-grained sediments in the

cores. Ostracode richness is highest in the lower interval of BUR-1, 247–172 cm, including 16 species and 6 genera (2 *Cyprideis* spp., 3 *Mesocyprideis* spp., 3 *Gomphocythere* spp., 1 *Cypridopsis* spp., 5 *Mecynocypria* spp. and 1 *Tanganyikacypris* spp.). Directly above this lower interval is a 20 cm interval of dominantly coarse and medium sand that lacks fossil ostracodes and molluscs. The upper 140 cm is similar in grain size and composition to the lower portion of the core, and its fauna consists mostly of the same species as in the lower portion. This upper interval contains 14 species and 5 genera, marking a 12.5% drop in species richness (2 *Cyprideis* spp., 2 *Mesocyprideis* spp., 1 *Cypridopsis* spp., 5 *Gomphocythere* spp., and 4 *Mecynocypria* spp.). The same species are present in the core below and above the sandy interval, with the exception of *Gomphocythere downingi*, which only occurs in the upper part of the core, and *Tanganyikacypris matthesi* and *Mecynocypria* sp. 33, which only occur in the lower portion of the core (Figure 6).

Ostracodes only occurred in two sample intervals of the Karonge Delta #3 core. At 70–70.5 cm a full 300 individual ostracode sample yielded 17 species. At 80–80.5 cm, 26 juvenile ostracodes were recovered, comprising 8 species (Figure 3b).

86-DG-14

In core 86-DG-14, ostracode abundance is fairly stable and low (0–85 per g of unprocessed sediment, $X = 29.5 \pm 20.03$) from 74–17 cm, then rises gradually from 17–7 cm, and dramatically to > 350 ostracodes/g in the upper 7 cm of the core. With the exception of one barren sandy interval at 53–58 cm, ostracode species richness of core 86-DG-14 is fairly stable (between 24 and 29 species, $X = 25.4 \pm 2.3$) throughout most of the core. However, in the upper 2 cm, the species richness declines abruptly by 31%. This drop in species richness corresponds to an increase in ostracode abundance (ostracodes/g sediment) and a marked decrease in grain size.

Several common species, including *Gomphocythere* sp. 16, *Mesocyprideis* sp. 2b and *Gomphocythere* sp. 3 display an overall upcore increase in frequency (Figure 7). Modern distribution data for the former two species is largely uninformative. They occur erratically on sandy substrates in the lake today at sublittoral-profundal depths (Figure 8). *Gomphocythere* sp. 3 is mostly restricted to profundal environments in the lake today. Other common ostracode species, such as

BUR-1 Ostracodes

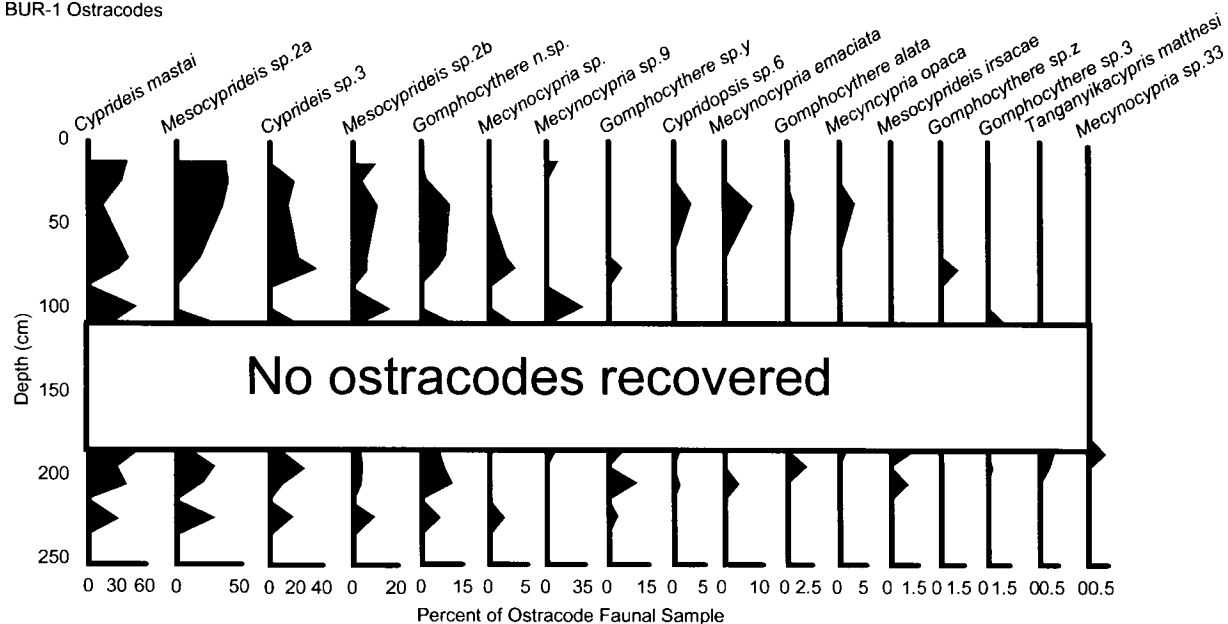


Figure 6. Ostracode stratigraphy of individual species for core BUR-1. Values are the percentage of the total ostracode count for the sample intervals where ostracodes were recovered (variable – see Figure 2a).

Mecynocypria opaca, *Gomphocythere curta*, and *Mecynocypria emaciata*, show an overall decrease upcore (Figure 7). *Mecynocypria opaca* is an extremely abundant species in the modern lake, and occurs most frequently at littoral to sublittoral depths. *Gomphocythere curta* occurs today on firm (rock and sand) substrates at variable water depths. *Mecynocypria emaciata* occurs over a wide range of substrate types and water depths, but is most abundant today at littoral depths on sand and mud bottoms (Figure 8). Several rare species occur at irregular intervals through the core (*Tanganyikacythere burtonensis*, *Romecytheridea tenuisculpta* etc.), whereas many others only occur once through the core.

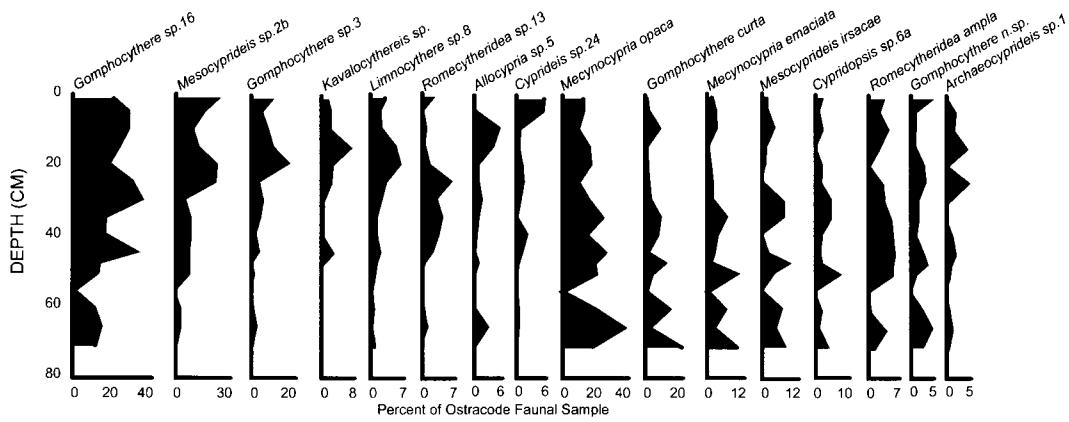
The increase of *Gomphocythere sp. 3* above 50 cm and its subsequent slight decline above 20 cm may reflect slight changes in lake level towards deeper, followed by slightly shallower water depth at the core site. This is also consistent with the interpretation based on the occurrence of the littoral *Cyprideis sp. 3* and the littoral-sublittoral *Mecynocypria opaca*.

86-DG-32

Ostracode abundance in core 86-DG-32 is generally higher than in 86-DG-14. Abundance gradually in-

creases from the base of the core to about 52.5 cm, followed by an abrupt decline, and then followed by a gradual increase up through the rest of the core. There is some fluctuation in ostracode species richness throughout the core, ranging between 24–33 species ($X = 27.9 \pm 2.5$), and this variation shows no distinct pattern. Overall mean species richness for 86-DG-32 is somewhat higher than for 86-DG-14. Many of the common ostracodes in 86-DG-32 are of uniform abundance throughout the core, with no overall increase or decrease. The pattern of occurrence of depth- and substrate-sensitive species primarily suggests shallowing conditions through the core interval (e.g. upcore increases in the littoral-sublittoral *Mecynocypria opaca*, decreases in *Gomphocythere sp. 16*, a sublittoral to profundal species, and the disappearance of *Allocypria sp. 11*, a deep water sand or rock dweller). However, some deep water species, such as *Gomphocythere sp. 3*, show no consistent change through the core, suggesting that other factors, in addition to water depth, are structuring the assemblage. Patterns of rare ostracode occurrences are similar to those of 86-DG-14, with some present throughout the core (*Tanganyikacypridopsis calcarata*, *Cypridopsis bidentata*, *Romecytherideis ampla*), and some at irregular intervals (*Allocypria humilis*, *Candonopsis sp. 2*, *Darwinula stevensoni*).

86-DG-14: Common Ostracode Species



86-DG-14: Rare Ostracode Species

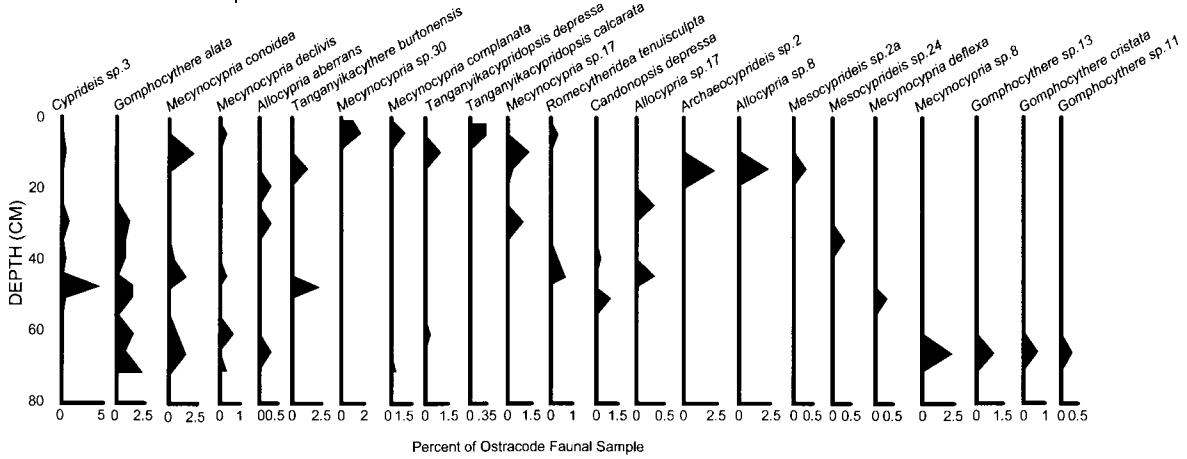


Figure 7. Ostracode stratigraphy of individual species for core 86-DG-14. Values are the percentage of the total ostracode count (300 valves) for the sample interval. The diagrams for the common species have been arranged to show species that display an overall upcore increase on the left, species that show an overall decrease in the center, and those that remain relatively constant or show no consistent trend throughout the core on the right. The diagrams for the rare ostracodes are organized by species which occur only in the upper, middle, or lower portions of the core.

Species diversity/equitability changes over time

We analyzed species diversity and equitability changes within cores 86-DG-14 and 86-DG-32 to determine the variability or stability of faunal composition over the time period (about 300–500 yrs) represented by the cores. Both cores display high and fairly constant levels of species diversity. The slightly higher values observed in 86-DG-32 reflect the greater proportion of rare species, relative to 86-DG-14. A sharp decline in species diversity in the uppermost sample of 86-DG-14 corresponds to the reduced faunal richness of that sample. 86-DG-32 also shows more variable levels of diversity throughout the core with an increase towards the top of the core. Equitability levels are stable

throughout both cores (0.77 ± 0.04 for 86-DG-14 and 0.82 ± 0.03 for 86-DG-32). The Jaccard coefficient of faunal similarity between stratigraphically adjacent samples is significantly lower among rare species than among common ones in core 86-DG-32, and in core 86-DG-14, faunal similarity is more evenly matched between rare and common species. Faunal similarity between adjacent samples for all species is higher in 86-DG-32 than in 86-DG-14. For 86-DG-14, mean variation between all species, common species only, and rare species only is 0.68 ± 0.08 , 0.60 ± 0.18 , and 0.38 ± 0.10 respectively. For core 86-DG-32, the mean variation between all species, common species only, and rare species only is 0.71 ± 0.13 , 0.68 ± 0.14 , and 0.31 ± 0.12 respectively.

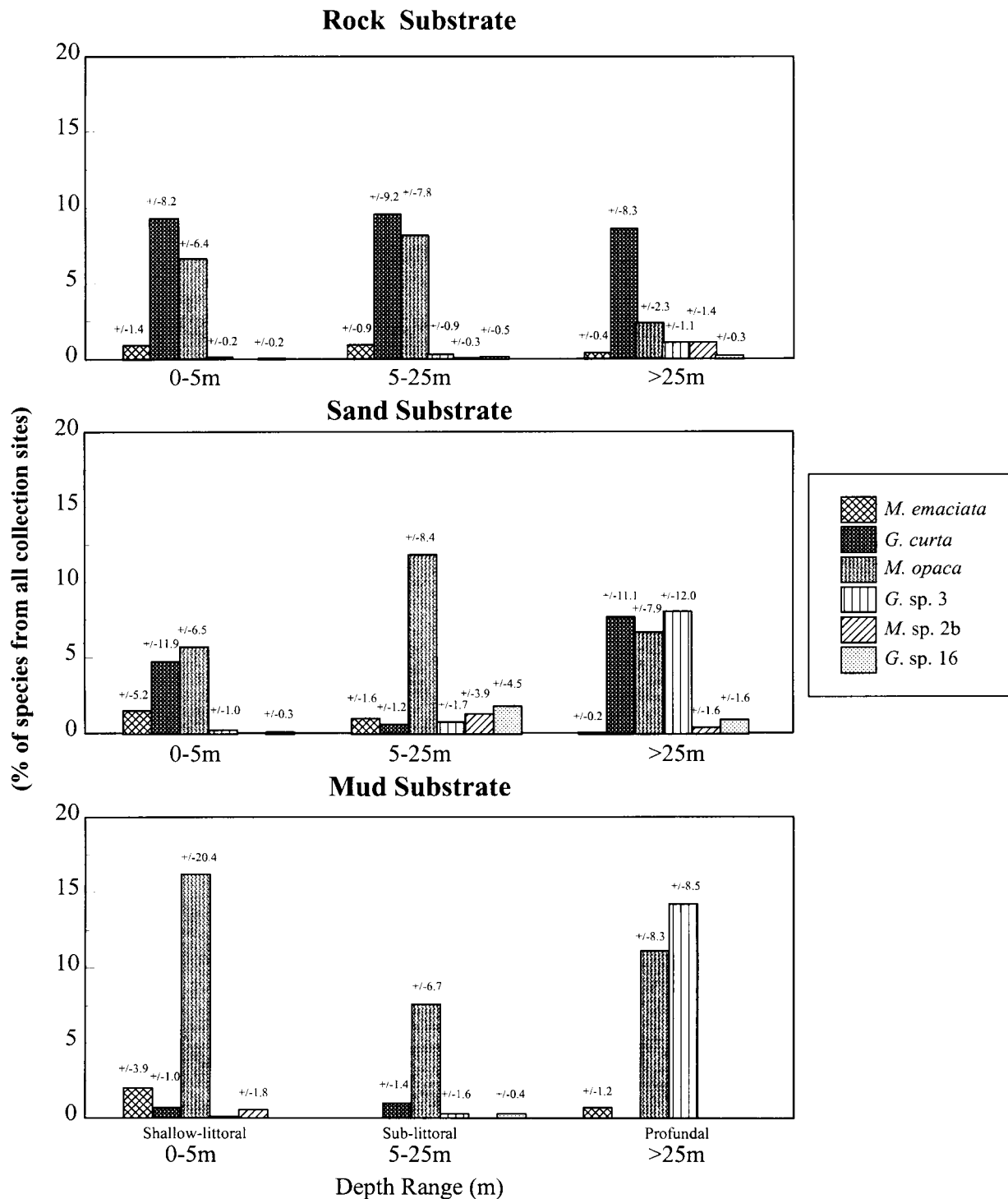
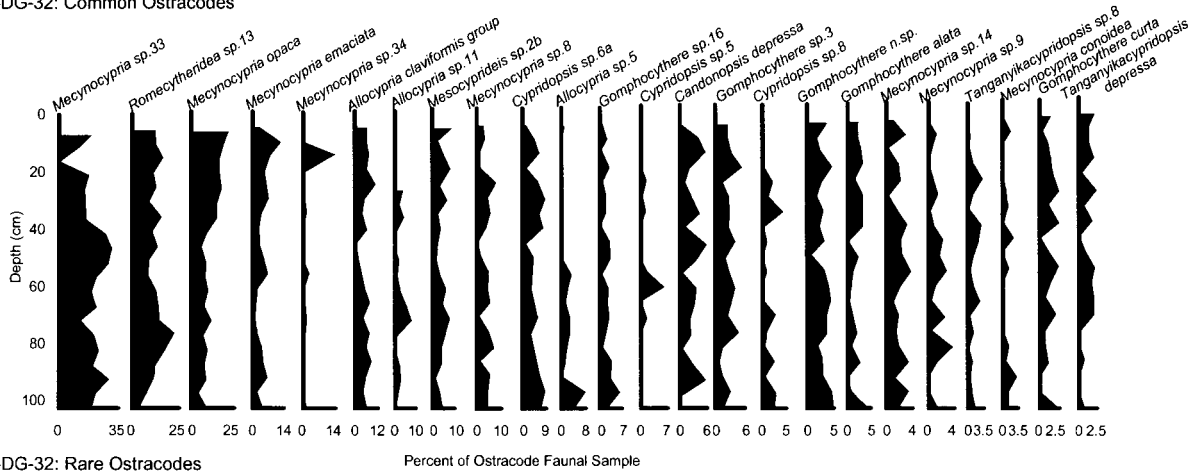


Figure 8. Habitat range of some common modern ostracode species in Lake Tanganyika found in the study cores. Species can be found on rock, sand, and/or mud substrates from shallow littoral to profundal depths. Percentages are the mean percentage (± 1 S.D., shown above the bar) that the species indicated comprises for all ostracode faunal assemblages collected to date in that environmental zone. Data is from Cohen's University of Arizona database of ostracode occurrences in Lake Tanganyika. See text for discussion.

86-DG-32: Common Ostracodes



86-DG-32: Rare Ostracodes

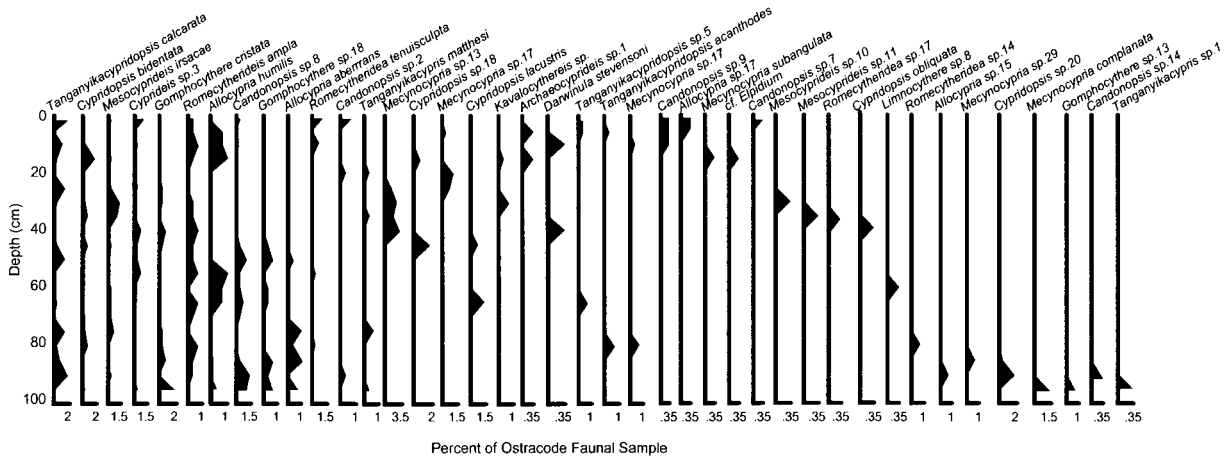


Figure 9. Ostracode stratigraphy of individual species for core 86-DG-32. Values are the percentage of the total ostracode count (300 valves) for the sample interval. The diagrams are organized in a similar fashion to those in Figure 7. This core contains the highest species richness and overall ostracode abundance of all the cores. Note that many of the common ostracodes occur in relatively consistent abundance patterns throughout the core (those which do not disappear/reappear from the record). A few species occur mainly in the middle to lower portions of the core. Rare ostracode occurrences are similar to the occurrence patterns of rare ostracodes in core 86-DG-14 (Figure 6), in which particular species occur in only one portion of the core.

Stable isotope stratigraphy

Stable isotopic analysis of ostracodes from cores 86-DG-14, BUR-1, and 86-DG-32 all demonstrate that little change in $\delta^{18}\text{O}$ of lake waters has occurred at this site over the past 500 yrs (Figure 5). This stability is consistent with earlier analysis of fossil littoral stromatolites that partly cover this same time interval (Cohen et al., 1997a). Consistently more positive $\delta^{18}\text{O}$ values for the mollusc material reflects the difference in $\delta^{18}\text{O}$ fractionation (approximately +0.6‰) between aragonite (gastropods) and calcite (ostracodes) (Tarutani et al., 1969). When this difference is accounted for, the range of values is identical. Among the $\delta^{18}\text{O}$ records

of the cores, the data from 86-DG-32 is the most stable, varying from 2.3 to 3.0‰. The other two cores are more variable, reflecting the influence of river runoff in the area. Interestingly, the single $\delta^{18}\text{O}$ value obtained for the sample at 47–48 cm from core 86-DG-14 (the probable low lake stand horizon) does not suggest a significant change in the evaporative concentration of the lake waters at that time. This may suggest that the lake level fall was a relatively brief event (compared with the lake’s long residence time) and/or that the lake remained hydrologically open through subterranean fissures near the current outlet, although more analyses would strengthen this conclusion.

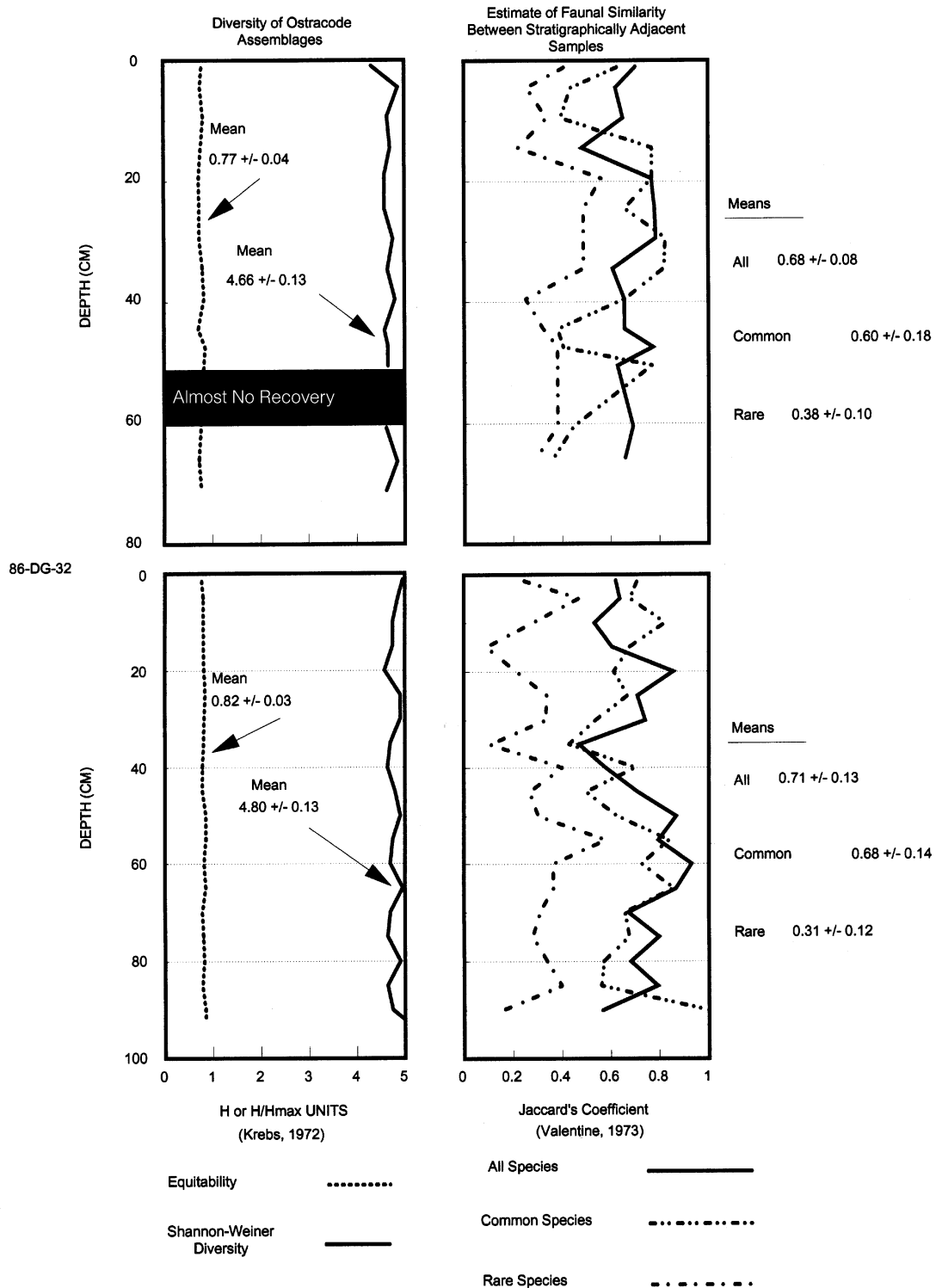


Figure 10. Ostracode species diversity/equitability changes over time in cores 86-DG-14 and 86-DG-32. Both cores display high and fairly constant levels of diversity (except at the top of 86-DG-14 where there is a sharp decline in the species diversity which corresponds to the reduced faunal richness of the sample). Equitability levels are stable throughout both cores.

Discussion

The cores described in this study contain rich fossil ostracode records (with the exception of Karonge #3). Patterns of ostracode variability within each core may reflect such influences as sediment pollution from modern or prehistoric anthropogenic effects, natural disturbances, metapopulation dynamics, or simply insufficient sampling.

There is a general pattern between the four analyzed cores of increasing ostracode abundance and species richness going from Karonge #3 (rare ostracode occurrences) to BUR-1 to 86-DG-14 to 86-DG-32 (Figures 3a to 3d). This ordering also corresponds geographically to current human disturbance levels (from highest to lowest) in terms of probable sediment accumulation rates adjacent to major sediment sources and visible land use degradation. Reduced species richness in heavily disturbed areas may be a reflection of the intolerance of many ostracode species to rapid, repeated or continuous inundation of benthic habitats by extremely turbid water. Alternatively, the abrupt increase in ostracode abundance, which is accompanied by a decline in species richness and reduction in grain size, observed at the top of core 86-DG-14, may be a reflection of locally increased secondary productivity. This interpretation is strengthened by the fine-grained lithology of these uppermost samples and the absence of winnowing or concentration lags of ostracodes or gastropod shells. This local, but abrupt increase in productivity might be the result of enhanced local nutrient discharge into the lake (perhaps from soil nutrient input from the Dama River, but also conceivably from aerosol sources such as cooking fires). Silt and clay-sized soil particles are known to be important vectors for introducing phosphates into lakes, thereby contributing to nutrient loading (Goltermann, 1991). No such core-top change in productivity or species richness is evident in core 86-DG-32 from the less impacted southern Tanzania area. It is interesting to note that sponge spicules were present throughout core 86-DG-32 (the core from the low impact site), but that they are absent from the three cores from the northern, high impact sites. Assuming sponges once lived at the northern lake sites (they are occasionally encountered by SCUBA divers in the area, A.C. pers. observation), the absence of sponge spicules could indicate that sedimentation has impacted the fauna, because sponges are very sensitive to suspended sediment load in turbid waters (Harrison, 1974).

An alternative hypothesis, that the gross patterns of

species richness preserved in these cores results from events that predate modern (post ~1500 AD) human disturbance, cannot be rejected from these core data. No long term trend towards declining diversity was evident in any of the cores. The major decline directly at the top of 86-DG-14 is a poorly recorded event, and possibly could relate to natural fluctuations in community structure. Additional, and more highly resolved sampling is required to address this question. Furthermore, paleogeographic evidence (Lezzar et al., 1996; Cohen et al., 1997b) suggests that low diversity levels observed in northern Burundi rocky habitats may, in part, be a reflection of the young age of those habitats relative to more diverse regions further south. Although our cores are all taken from muddy, not rocky areas, we raise this point to emphasize that a historical explanation for current diversity patterns (predating human impact) cannot be rejected out of hand at this time. However, the rapid acceleration in sediment accumulation rates around heavily deforested watersheds combined with low or zero levels of ostracode diversity in these areas is cause for concern and demonstrates the need for longer duration, high resolution records that span the entire period of intensive land use in this region (several thousand yrs) (Vincens, 1991, 1992).

Ostracode assemblages display substantial variability between stratigraphically adjacent samples in both cores. This intersample variation, averaging 0.68 ± 0.08 in 86-DG-14 and 0.71 ± 0.10 in 86-DG-32 (means for faunal similarity plots between all species), occurs despite the fact that species diversity remains relatively high throughout both cores (except for the pronounced drop at the top of core 86-DG-14) (Figure 10). These facts, coupled with the fact that intersample faunal similarity is even lower among rare species, suggest that local extinctions, recolonizations and reordering of abundance/dominance have been common events in the history of Lake Tanganyikan ostracode communities over the past approximately 500 yrs. Elsewhere, one of us has argued that patterns of vastly different species composition, despite similar diversity levels in spatially adjacent faunal samples from Lake Tanganyika, provide some support for a metapopulation model of ostracode population dynamics (Cohen, 1994). The paleoecological results reported here support this earlier conclusion. This argument suggests that the patterns of ostracode variations throughout the cores reflect the normal fluctuations of species within a community structure with few species capable of achieving long-term competitive dominance. The decrease in species

richness and increase in abundance seen at the top of core 86-DG-14 may reflect these metapopulation dynamics, rather than an anthropogenic signal produced by the effect of deforestation.

Interestingly, the pattern of faunal turnover in BUR-1 is in sharp contrast to 86-DG-14 and 86-DG-32, with little difference among samples even across barren intervals. Only 17 species occur in BUR-1, 16 occur in the lower portion of the core (below the sandy interval), and 14 occur above this interval. One possible explanation of this consistency in population makeup is that the fauna at this highly disturbed site is comprised of only highly eurytopic ostracode species, or species with better capabilities of dispersal across degraded habitat patches (Hansson, 1991). These particular species may be capable of withstanding singular perturbations, such as a lake level fall or recurrent sedimentation disturbance events, by recolonizing the core site habitat once conditions improve. Under these highly disturbed conditions, the pattern of regular faunal overturn and lack of competitive dominance may break down as rarer, less vagile species disappear and a more predictable competitive dominance of a smaller number of eurytopic, easily dispersed species sets in.

There is evidence for anthropogenic impact in the top of core 86-DG-14, but this signal (drop in species diversity and increase in ostracode abundance) is not necessarily the result of sediment pollution impact. The same pattern could be explained by metapopulation community dynamics. The ostracodes in cores 86-DG-14 and 86-DG-32 both display patterns of extinction/recolonization, and the ostracodes in BUR-1 may be displaying a dominance pattern that merely reflects the long-term effects of natural sediment discharge disturbance from the large Ruzizi River. A resolution of this question of human vs. natural perturbations will have to await the analysis of new cores that may provide higher resolution and longer duration stratigraphic records.

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