



## Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IV. Lacustrine paleoecology

Manuel R. Palacios-Fest<sup>1,\*</sup>, Simone R. Alin<sup>2</sup>, Andrew S. Cohen<sup>3</sup>, Brandon Tanner<sup>3</sup> and Heather Heuser<sup>4</sup>

<sup>1</sup>*Terra Nostra, Tucson, AZ 85741, USA;* <sup>2</sup>*School of Oceanography, University of Washington, Seattle, WA 98195, USA;* <sup>3</sup>*Department of Geosciences, University of Arizona, Tucson, AZ 85721, USA;* <sup>4</sup>*College of Forest Resources and Quaternary Research Center, University of Washington, Seattle, WA 98195, USA;* \*Author for correspondence (e-mail: terra\_nostra\_mx@yahoo.com.mx)

Received 10 July 2004; accepted in revised form 15 January 2005

**Key words:** Fish bones, Lake Tanganyika, Molluscs, Ostracodes, Sediment pollution, Sponges

### Abstract

Fossil invertebrates from cores collected in Lake Tanganyika provide a record of probable nearshore ecological response to recent watershed deforestation and sediment erosion in several East African watersheds. We compared paleoecological profiles (primarily from ostracodes) from watersheds spanning a range of sizes and present-day deforestation disturbance levels to understand the timing and magnitude of faunal changes, and their relationship in time to terrestrially-derived disturbance indicators. Profiles from the Lubulungu and Nyasanga/Kahama Rivers (Tanzania) provide a record of faunal variability in watersheds that are currently undisturbed with respect to deforestation. These records indicate continuous faunal turnover through time. However, this pattern of turnover is accompanied by relatively high levels of diversity throughout the record, with no wholesale extinction events. Ostracode taphonomic data and other fossil abundance data from the Lubulungu area provide strong evidence in support of at least two episodes of lower lake levels, associated with episodes of Late Holocene aridity. Records from deltas of disturbed watersheds at the Kabesi River (Tanzania) and those of Northern Burundi all show a combination of profound and abrupt faunal turnover, in some cases accompanied by local extinction and establishment of a few dominant taxa. At the Mwamgongo River delta, fed from a very small, disturbed watershed, species turnover was subtler. In disturbed watershed cores showing abrupt faunal changes the transitions mostly occurred in the late 19th to early 20th centuries, predating the major mid-20th century increase in sediment mass accumulation rates, with the latter only correlated with changing fossil abundance and flux. However, the earlier faunal community changes are contemporaneous with both palynological and geochemical changes in the core profiles indicative of changing land-use patterns. This suggests that lacustrine ecosystem response to deforestation was a two-stage process, with an earlier phase of response to changing quality of sediments or dissolved matter being discharged from the watershed, and a subsequent phase responding to increased quantity of sediment.

### Introduction

Lake Tanganyika, the largest and oldest of the East African rift valley lakes, is a reservoir of

extraordinary lacustrine biodiversity, with over 2000 species of aquatic organisms, at least 700 of which are endemic to that lake (Coulter 1994). Most of this diversity in terms of species richness

and endemism resides in littoral and sublittoral habitats, whereas the pelagic zone is relatively species-poor. The endemic species are dominated by cichlid and noncichlid fishes, molluscs and crustaceans, and are renowned for their morphological, ecological, and behavioral diversity (Coulter 1991; Kawanabe et al. 1997; Rossiter and Kawanabe 2000). Biodiversity and a complex history of diversification in Lake Tanganyika have resulted from the lake's longevity (9–12 million years old) and its complex habitat structure. (Cohen et al. 1993a, 1997; Salzburger et al. 2002).

Prior ecological investigations of Lake Tanganyika have provided abundant evidence linking variations in nearshore benthic community structure and diversity with patterns of anthropogenic activity in adjacent watersheds. The most notable pattern is one of habitat alteration, changing trophic composition, and declining species diversity among fish and invertebrates along portions of the lakeshore adjacent to regions of substantial deforestation (Cohen et al. 1993b; Alin et al. 1999). Lake margin habitats adjacent to areas of extensive deforestation are subject to rapid pulses of sediment erosion, with consequences that may include reduction in habitat heterogeneity from siltation, increased nearshore inputs of soil nutrients, reduction in light penetration, and reduction in the ability of visual predators and fish using color cues for breeding to survive (e.g., Seehausen et al. 1997; Donohue and Irvine 2004). Subtler top down and bottom up effects are also likely consequences of siltation in this lake, for example reductions in biomass specific net productivity as herbivore grazing efficiency declines (O'Reilly 2001) and changes in community structure associated with changing patterns of herbivory and parasitism (Irvine et al. 2000; McIntyre et al. 2005). However, all of these studies have examined variations between disturbed and undisturbed sites over relatively brief intervals, with no records spanning a period when the effects of watershed deforestation were first felt. Our investigation here was intended to address this lack of historical information on patterns of community change through a paleoecological study spanning the most recent episodes of anthropogenic activity in lake-margin areas near selected Lake Tanganyika watersheds. Details of our site selection strategy, sampling locations, coring methods, geochronology, sedimentology, palynology, and stable

isotope studies are provided in companion papers to this one (Cohen et al. 2005a; Dettman et al. 2005; McKee et al. 2005; Msaky et al. 2005; O'Reilly et al. 2005; Palacios-Fest et al. 2005). Here we provide the fossil record of selected, well-preserved aquatic organisms that are commonly encountered in the cores recovered. Our study concentrates on fossil ostracodes, because of both their excellent fossil record in Lake Tanganyika (Alin and Cohen 2003, 2004) and because prior studies (those mentioned above, plus Wells et al. 1999; Alin et al. 2002) suggested that ostracode communities in this lake are sensitive to changes in siltation loads. We also document the abundance of fossil sponge spicules, molluscs, and fish bones in our cores. However, less is currently known about the probable significance of changes in abundance of these fossils and in most cases it was not possible to identify these fossils to the species level because of inadequate taxonomic keys.

In this study, we analyzed the history of ostracode species turnover and diversity from delta platforms adjacent to rivers that have undergone varying levels of deforestation disturbance, all located along the east coast of Lake Tanganyika. The deltas studied are those of the Lubulungu, Kabesi, Nyasanga/Kahama and Mwamgongo Rivers in Tanzania, and the Nyamuseni and Karonge/Kirasa Rivers in Burundi. Core site information is summarized in Cohen et al. (2005a, Tables 1 and 2) and maps of the coring sites are given in Cohen et al. (2005a, Figures 1–5). Geochronology results used in this paper are summarized in McKee et al. (2005). By means of  $^{210}\text{Pb}$  and  $^{14}\text{C}$  geochronology (McKee et al. 2005) and records of varying sediment, pollen and organic matter discharge into the basin (Palacios-Fest et al. 2005; Msaky et al. 2005; O'Reilly et al. 2005), we have documented the timing of disturbance in these watersheds.

Briefly, all coring discussed in this paper was done using a Hedrick-Marrs Multicorer, which is designed to carefully preserve the sediment–water interface and collects four large diameter (10 cm ID) cores of up to 60 cm in length. Core names describing specific samples are followed by letter suffixes (M or R) depending on whether the sample was from the micropaleontology dedicated multicore barrel (M), or the geochronology dedicated barrel (R). We collected two cores from the anthropogenically undisturbed and

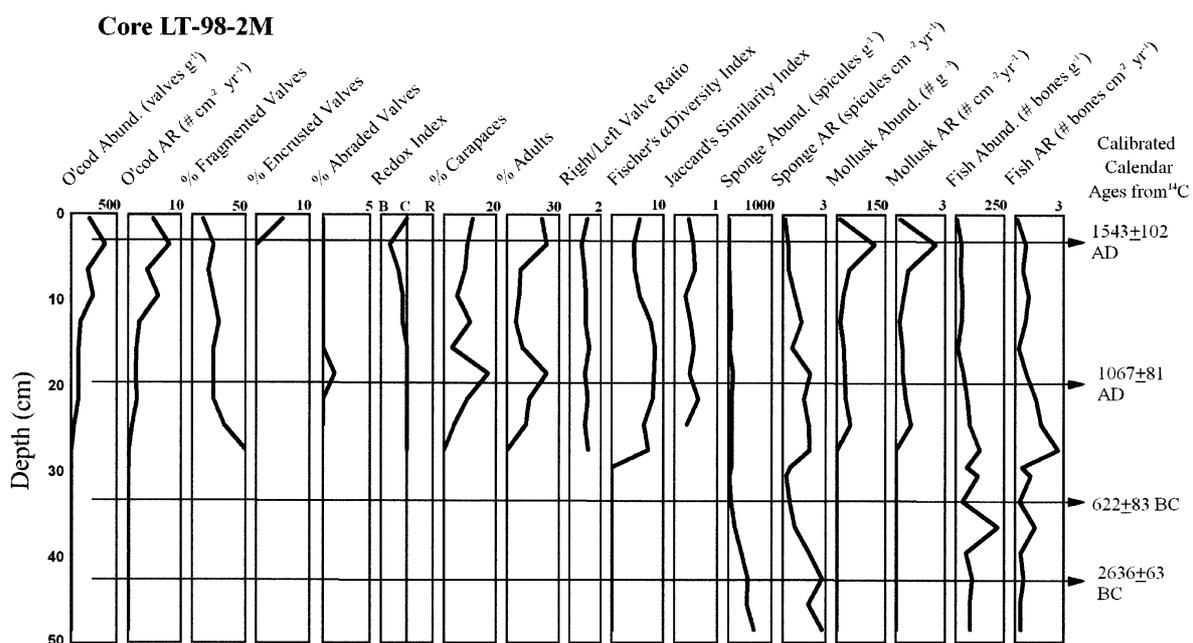


Figure 1. Summary paleoecologic profiles for Core LT-98-2M, central Lubulungu delta, 110 m water depth (currently undisturbed site). Total core length 49 cm (see Cohen et al. 2005a, Figure 2 for location and bathymetric map).

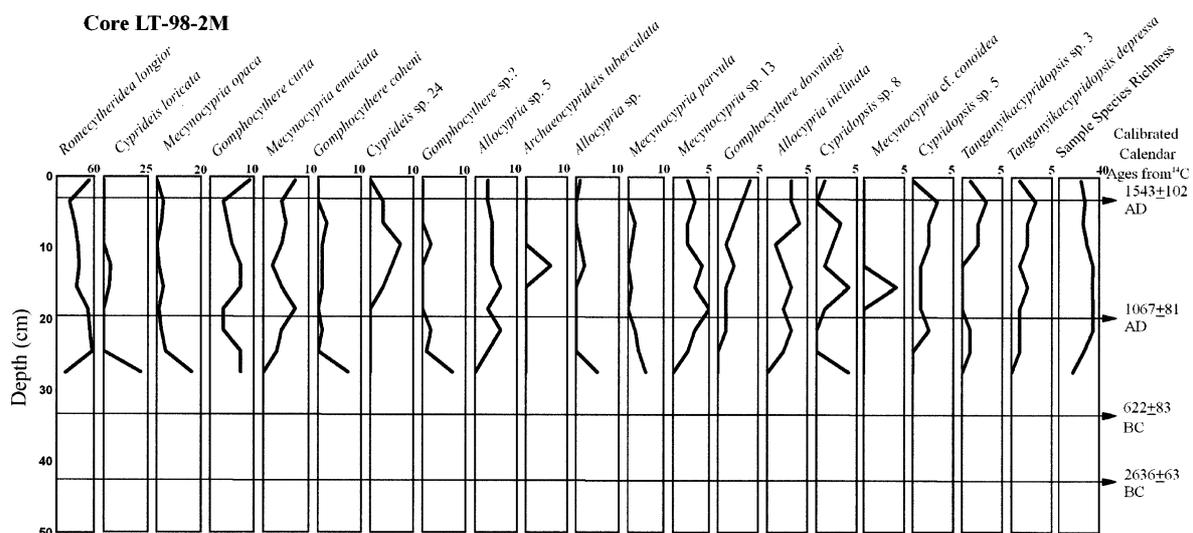


Figure 2. Ostracode biostratigraphic profiles for Core LT-98-2M.

small (50 km<sup>2</sup>) Lubulungu River delta, located in the western Mahale Mountains in what today is Mahale Mountains National Park. These cores, LT-98-2 (110 m water depth) and LT-98-12 (126 m), are from sites within 1-km of each

other, and provide records of background variability in sedimentation and runoff for the period from ~2600 B.C. to 1600 A.D. (~4550–350 B.P.). Very slow sedimentation rates characterize both sites (McKee et al. 2005).

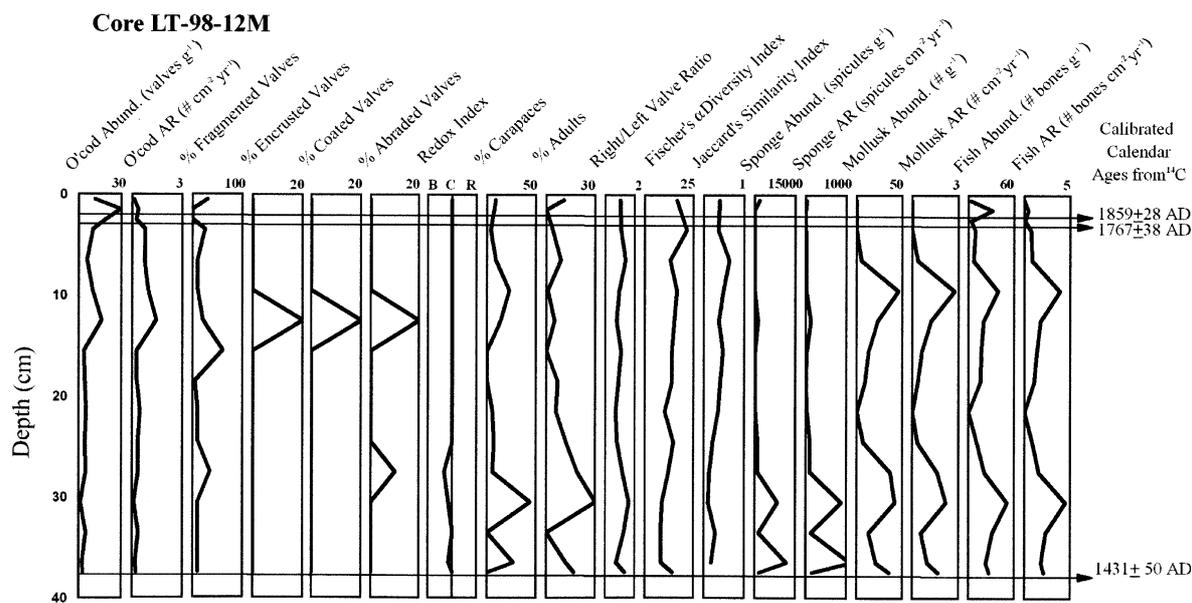


Figure 3. Summary paleoecologic profiles for Core LT-98-12M, central Lubulungu delta, 126 m water depth (currently undisturbed site). Total core length 40 cm (see Cohen et al. 2005a, Figure 2 for location and bathymetric map).

Core LT-98-18 was collected from the Kabesi River delta in 75 m water depth. This 120-km<sup>2</sup> watershed drains the northern flank of the Mahale Mountains, mostly outside of the park boundaries. The watershed is moderately disturbed by subsistence cultivation, mainly in its lower alluvial reach. Core LT-98-18 covers the interval from ~1750 A.D. to modern (McKee et al. 2005, Figures 1 and 7). It provides evidence for a rapid and historically unprecedented 4× rise in sedimentation rates starting in the early 1960s.

Cores LT-98-58 and LT-98-37 record the history of watershed change over the past few centuries for the rift escarpment region of the Tanzanian coast north of the town of Kigoma. The two sites lie on deltas that drain very similar watersheds in all respects except in terms of their history of anthropogenic activity (Alin et al. 2002; Cohen et al. 2005a). LT-98-58 was collected in 76 m water depth in front of the Nyasanga/Kahama watershed, a very small (~7.5 km<sup>2</sup>), steep watershed entirely within Gombe Stream National Park. LT-98-37 was collected in 95 m water depth in front of the Mwamgongo River valley, a very small (7.7 km<sup>2</sup>) watershed in what is today a heavily populated area of villages and subsistence agriculture just north of Gombe Stream National Park. Core LT-98-58 shows little change in sedimentation

rates throughout its ~250 year record (McKee et al. 2005, Figures 2 and 7). By contrast, LT-98-37, which covers the last ~500 years, shows moderate sedimentation rates early in its history, declining to low levels in the 18th–early 19th centuries, and then rising abruptly in the late 19th century and again in the mid-20th century (McKee et al. 2005, Figures 3 and 7; Cohen et al. 2005b, Figure 5).

Cores LT-98-98 (60 m water depth) and LT-98-82 (96 m) were both collected from deltas in front of the highly disturbed Burundian watersheds of the small Nyamuseni Rivers (30 km<sup>2</sup>) and the medium-sized Karonge/Kirasa Rivers (162 km<sup>2</sup> combined) respectively. Exceptionally high sedimentation rates at the LT-98-98 site caused that core to encompass only the past 50 years (McKee et al. 2005, Figures 6 and 7). LT-98-82 covers a considerably longer interval, almost 250 years, and shows the major early 1960s increase in sedimentation rate observed in several of the cores mentioned above (McKee et al. 2005, Figures 4 and 7).

In this study, we will describe the pattern of faunal change inferred for the sublittoral zones of the lake, as observed in the cores mentioned above, and propose probable linkages between the changes we observe and changes in sedimentation patterns.

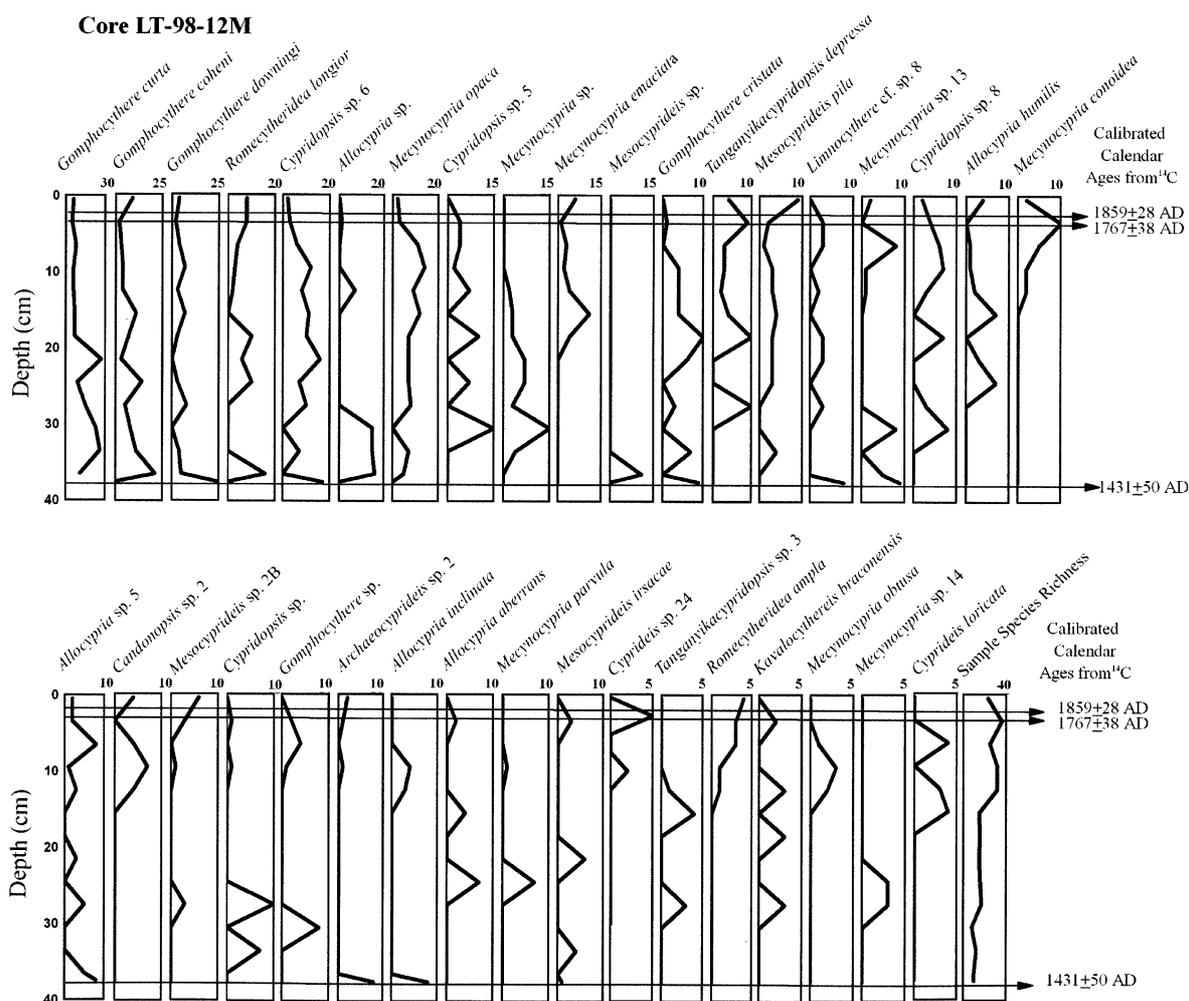


Figure 4. Ostracode biostratigraphic profiles for Core LT-98-12M.

## Methods

### *Ostracode faunal analysis*

Sample splits from chosen cores were analyzed for ostracodes at 3 cm intervals. Ostracodes were disaggregated and separated using the freeze–thaw method of Forester (1991) and then wet sieved, along with other paleontologic samples. Counts of 500 individuals were made from the  $>106\ \mu\text{m}$  sieve fraction. We calculated ostracode abundance as numbers per gram of dry sediment weight, and as accumulation rates (valves accumulated per  $\text{cm}^2$  per year).

Routine micropaleontological analysis on all samples from the sedimentological splits was conducted using a low power stereoscopic

microscope, and all samples were subsequently stored on either micropaleontological slides or in plastic trays. Ostracodes were identified to the species level wherever possible. Species identification was based on publications (e.g., Rome 1962; Martens 1985, 1993, 1997; Wouters 1988; Wouters and Martens 1992, 1994, 1999, 2000, 2001; Park and Martens 2001) and reference collections kept at the Laboratory of Paleolimnology of the University of Arizona. Many species of Tanganyikan ostracodes are endemic and are still undescribed. For these, informal monikers (species numbers) are used, following the collection numbering at the University of Arizona. On all graphs illustrating individual species abundance data, graphs are organized with the most common taxa on the left and increasingly rarer species to the right.

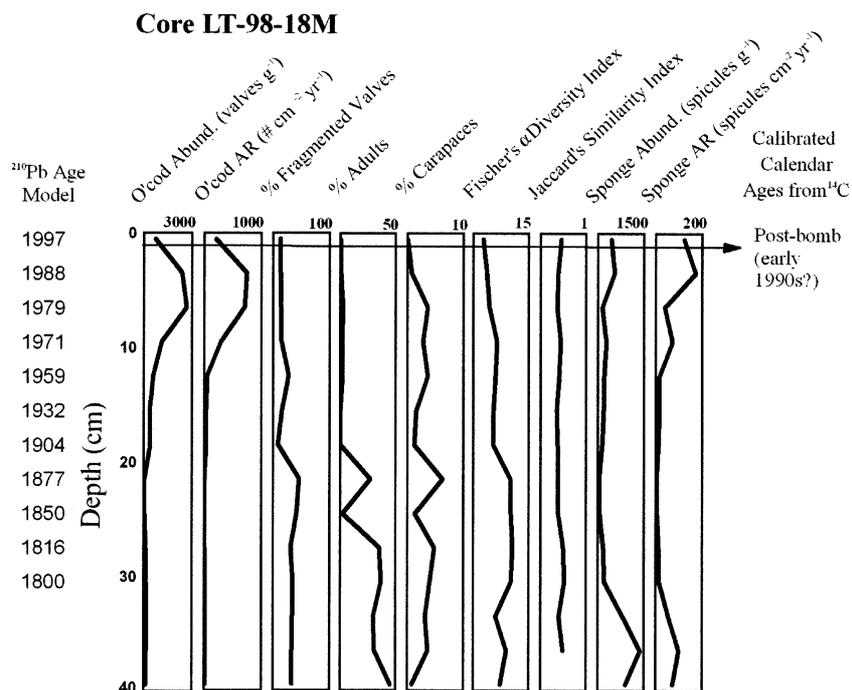


Figure 5. Summary paleoecologic profiles for Core LT-98-18M, Kabesi River delta, 75 m water depth (currently moderately disturbed site). Total core length 42 cm (see Cohen et al. 2005a, Figure 3 for location and bathymetric map).

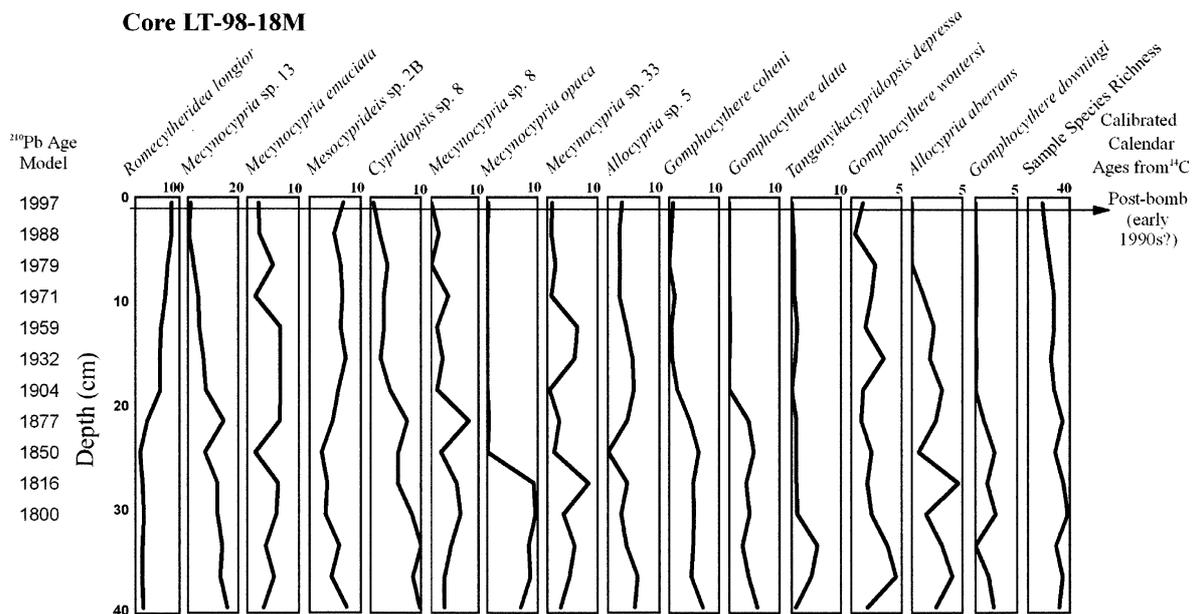


Figure 6. Ostracode biostratigraphic profiles for core LT-98-18M.

Taphonomic indicators of ostracode preservation and adult proportions were tabulated for each stratigraphic interval (some of these variables were

not quantified in core LT-98-18M). These variables can provide clues to reworking of samples, burial environmental conditions, paleo-water

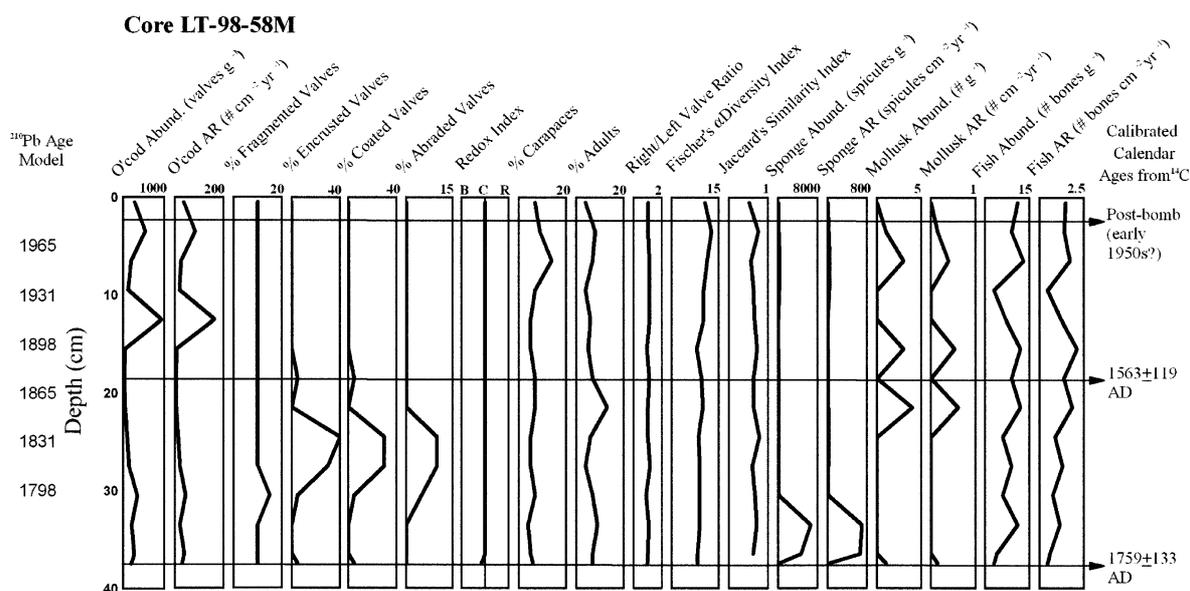


Figure 7. Summary paleoecologic profiles for Core LT-98-58M, Nyasanga/Kahama Rivers delta, 76 m water depth (currently undisturbed site in Gombe Stream National Park). Total core length 39 cm (see Cohen et al. 2005a, Figure 4 for location and bathymetric map).

depth and/or maturation of and ecological stress on the population for % adults (e.g., Brouwers 1988; Whatley 1988; Van Alstine and Cohen 2003a, b). Percentages of fragmented valves, valves coated by calcium carbonate, valves encrusted by materials other than  $\text{CaCO}_3$ , right/left valve ratios (which diverge from 1:1 in shell populations where valves have undergone progressively greater amounts of hydrodynamic sorting) and abraded valves, are all indicative of reworking frequency. Proportions of carapaces (both valves attached) are a function of both reworking and the types of ostracodes present, since some species fall apart more readily than others. We also developed a qualitative redox index, based on the proportions of blackened valves indicative of reducing burial conditions, clear valves from intermediate conditions, or reddened valves from strongly oxidizing conditions.

Three statistical indices of diversity and similarity were used in this study to compare faunal assemblages. Raw sample species richness is simply the number of species encountered per sample, uncorrected for sample size. Although we made routine counts of 500 individual fossils, some samples had very low abundances and 500 counts could not be obtained. Thus the species richness is uncorrected for sample size. Fisher's  $\alpha$  Diversity

Index compensates for variations in sample size for the purpose of comparing diversity in samples of different sizes, and is expressed by Equation (1):

$$\alpha = \frac{N(1-x)}{x}, \quad (1)$$

where  $x$  is estimated by iterating the following term (Equation (2)):

$$\frac{S}{N} = \left[ \frac{1-x}{x} \right] [-\ln(1-x)], \quad (2)$$

where  $S$  is the number of species in the sample and  $N$  the total number of specimens. In the vast majority of cases in this study species richness and diversity are highly correlated.

The Jaccard's Similarity Index is used to compare faunal similarity between pairs of samples (in this case, stratigraphically adjacent samples) (Equation (3)):

$$C_j = \frac{C}{S_1 + S_2 - C}, \quad (3)$$

where  $C$  is the number of species common to both samples and  $S_1$  and  $S_2$  are the total number of species in each sample. We used Jaccard's Index to identify overall faunal similarity through core sequences and times of rapid faunal overturn. In

addition, correspondence and cluster analyses using XLSTAT® were conducted on every core to establish species associations to be used as environmental indicators.

#### *Other paleontological analyses*

In addition to ostracodes and pollen (discussed in the companion paper by Msaky et al. 2005), other fossils that were routinely collected in 106  $\mu\text{m}$  or coarser sieved samples were counted and tabulated. These include fish bones, mollusc fragments and sponge spicules. Little work has been done to date to determine the paleoecological significance of total sponge, mollusc, and fish bone counts in Lake Tanganyika, so this attempt should be viewed as exploratory in nature. Sponges are filter feeders known to be sensitive in stream ecosystems to high levels of turbidity. Several endemic species of both erect and encrusting sponges are known from Lake Tanganyika, although little is known of their ecology in detail. In principle, the abundance of their siliceous spicules (skeletal elements) might reflect turbidity and ecological impact on benthic filter feeding communities. However, we have no information on the preservational (taphonomic) controls of transport and resuspension that may affect local abundance in sediment cores. Furthermore, sponges are extremely abundant on the undersurfaces of rocks today in northern Burundi, where sedimentation rates are high, suggesting that other factors, such as grazing intensity, may be more important than turbidity *per se* in regulating sponge density in Lake Tanganyika.

Tanganyikan molluscs also display high degrees of endemism, although the range of trophic guilds occupied by these species is much wider than the sponges. Most gastropod species encountered as fossils in sub-wave base cores are detritus feeders, and all of the species encountered are likely to be derived from soft-bottomed habitats. Tanganyikan bivalves are filter feeders, but are comparatively rare in these cores. A total abundance of mollusc fragments, normalized for sediment accumulation rate (most are not preserved as whole shells) may then be indicative of secondary productivity in the detritus feeder food web. Again taphonomic constraints limit our ability to

interpret these data, although prior investigations do provide some guidelines (Cohen 1989).

Disarticulated fish bones are common fossils in core materials from Lake Tanganyika. Fish bones encountered in offshore samples such as our cores represent, are likely to sample the relatively simple pelagic fish community (two species of clupeid 'sardines', and four species of predatory *Lates*). Additionally, deep benthic cichlids may be represented in these samples, although they are likely to be impossible to identify to the species level from disarticulated bones. One interesting observation we have made in many surface and core samples is an inverse correlation between the abundance of fish and ostracode skeletal material, suggesting that factors that favor ostracode (detritus feeder) production may be inimical to fish bone accumulation. However, whether this represents a biological, taphonomic, or mixed phenomenon is unknown.

Because of uncertainties in identifications, no attempt was made to identify these materials by species. However, the material has been retained and, for the molluscs at least, such identifications could be done easily in the future. All three groups are enumerated as both abundance per gram dry weight of samples, and as accumulation rates.

## **Results**

### *Paleontologic records by core*

Stratigraphies of summary ostracode data (including taphonomic features), sponge spicule counts, and fish bone counts, and estimated accumulation rates are given in Figures 1, 3, 5, 7, 9, 11, and 13. Profiles for individual ostracode species are given in Figures 2, 4, 6, 8, 10, 12, and 14, with each figure organized with the more common taxa on the left. Profiles for rare species are not illustrated, although total species richness (given in the last column on the right of each abundance profile) includes the tally of these taxa.

### *Ostracodes*

Ostracode abundance varies greatly within and between cores ( $< 10^1$  to  $> 10^4 \text{ gm}^{-1}$ ). A hallmark feature of all of the cores however is the very high

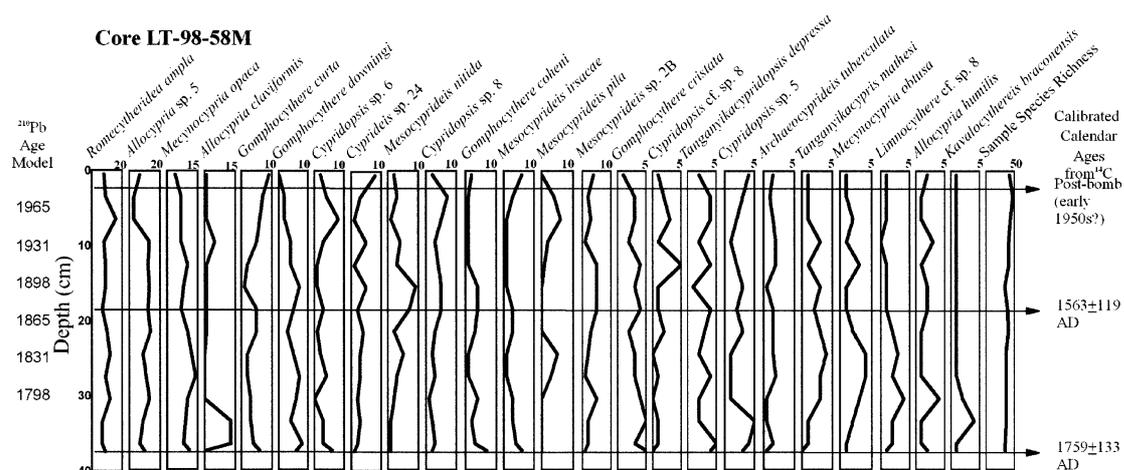


Figure 8. Ostracode biostratigraphic profiles for Core LT-98-58M.

levels of species richness and diversity encountered. Typically, we found 25–35 species in each 500-count sample, consistent with very high levels of ostracode species richness encountered in prior paleoecological studies of Lake Tanganyika cores (Wells et al. 1999; Alin et al. 2002). Some exceptional samples had as many as 50 species. Most samples include large proportions of very rare species, and almost all taxa encountered were species, or in many cases genera that are endemic to Lake Tanganyika. These high levels of ostracode diversity and endemism found in core samples are typical for the modern Lake Tanganyika crustacean, mollusc and fish fauna noted earlier (Coulter 1991). Another unifying feature of the cores studied is the high degree of faunal overturn between samples, marked by the relatively low Jaccard indices of similarity between stratigraphically adjacent samples. This pattern is also consistent with prior paleoecological observations of rapid community turnover and patchy ostracode species distribution in both space and time in Lake Tanganyika (Cohen 2000).

In core LT-98-2M (Figure 1), from offshore of the small watershed, low disturbance Lubulungu River, total ostracode abundance is low to moderate ( $< 500 \text{ g}^{-1}$ ), and is generally positively correlated with decreased grain size and increased TOC (Palacios-Fest et al. 2005, Figure 2). Ostracodes are absent in the lower 21 cm of the core (49–28 cm), prior to  $\sim 0$ –100 A.D. The lower barren zone is marked by low total organic carbon (TOC) content and coarser grain size. This

absence, as well as the absence of other calcareous fossils and very low mid-Holocene total inorganic carbon (TIC) values, has been observed in contemporaneous core records from various parts of the lake and probably relates to a shallowing of the lake-wide carbonate compensation depth, or alternatively a lakewide shift to calcium carbonate saturation in the epilimnion. Numbers per gram gradually increase upwards from zero at 28 cm, a short distance above the sedimentologic change (see Figure 1 in Palacios-Fest et al. 2005), to near the surface (3–4 cm, mid 16th century) where they decline slightly. Based on interpolated sedimentation rates alone ( $\text{mm yr}^{-1}$ ), this gradual initial increase in ostracode abundance lags the initial increase in fine detrital sediment by about 750 years, but corresponds very closely with a secondary fining event that eliminated almost all sand input, and also corresponds with initial increases in TIC and charcoal abundance.

Ostracode species richness ranges from 14 to 34 species per sample, with 47 species in total occurring throughout core LT-98-2M. Twenty species occur in abundances of  $> 5\%$  in at least one sample (Figure 2), with the remainder occurring periodically or rarely in the record. *Romecytheridea longior*, represented in this core largely by juveniles, is the dominant species and its proportional abundance therefore is negatively correlated with the cumulative abundance of all other taxa. This species is widely distributed in Lake Tanganyika, where it occupies a broad range of habitats. Several common or fairly common species display

upcore abundance increases (*Gomphocythere downingi*, and possibly *Mecynocyprina emaciata*, *Tanganyikacypridopsis depressa*, and *Tanganyikacypridopsis* sp. 3), whereas others decline upcore (*Mecynocyprina opaca*, *Mecynocyprina parvula*, *Mesocyprideis loricata*, *Gomphocythere* sp., and *Alloocyprina* sp. 5, and possibly *Gomphocythere coheni*). None of these fluctuations in individual species abundances show strong correlations with individual measured sedimentologic variables.

Ostracode diversity (Fisher's- $\alpha$  diversity index) shows high and relatively constant diversity from the first appearance of ostracodes to about 13 cm from the surface. Above this, diversity decreases upcore, associated with the disappearance of numerous rare taxa. This change corresponds approximately in time with the onset of increased charcoal abundance and inferred watershed aridification in the 13th century A.D. (see Palacios-Fest et al. 2005, Figure 2). Jaccard's similarity index between adjacent samples is low throughout the core (0.25–0.56) with no apparent trends, indicating substantial faunal turnover between sampling intervals. This largely reflects patchy occurrences of rare taxa, although some common species (e.g., *Cyprideis loricata*, *Mecynocyprina opaca*, *Archaeocyprideis tuberculata*, *Cypridopsis* sp. 8) also show this pattern of erratic appearance and disappearance.

Seven taphonomic features are recorded for ostracodes: fragmentation, encrustation, abrasion, redox index, % carapaces, % adults, and the right/left valve ratios (Figure 1). Fragmentation is low throughout the core and decreases upwards, indicating that ostracode populations have not been heavily damaged or sorted by wave activity. Abrasion is minimal throughout the core, and there is no obvious right/left valve bias, suggesting little transport. Diagenetic features like encrustation are rare, and the redox index is low, implying that there are no significant burial effects on the valves. The low proportion of carapaces probably reflects simple-post-mortem disarticulation (most Tanganyikan species have weak hinges on their valves). Low adult ratios suggest that few individuals are maturing, typical of deep-water, stressed habitats like this core site and all others in the study. The presence of some encrusted valves and higher proportions of adults and carapaces both in the 11th century, and again near the top of the core (mid-16th century) is indicative of somewhat

shallower water, consistent with both the LT-98-12M ostracode record discussed below and the charcoal records from both LT-98-12M and 2M. All of these data suggest somewhat drier conditions at this time, consistent with earlier interpretations of the Lake Tanganyika paleoclimate record (Alin and Cohen 2003).

Core LT-98-12M, also from the Lubulungu River delta, is marked throughout by very low ostracode abundance and flux (Figure 3). This difference from nearby core LT-98-2M is probably a result of the greater water depths of core LT-98-12M (126 m vs. 110 m), placing core LT-98-12M very close to the depth of oxygen depletion, where both ostracodes and molluscs are typically absent. Differences may also be attributed to variations in water depths for the different intervals represented by these two cores. A notable upcore increase in ostracode abundance occurs at about 13 cm, above which ostracode abundance remains relatively higher. This rising abundance in the late 17th century A.D. would be consistent with somewhat shallower water conditions and increased aridity, corresponding with an increase in charcoal abundance in the same core (Palacios-Fest et al. 2005).

Ostracode species richness ranges from 8 to 36 species per sample, with at least 46 species encountered throughout core LT-98-12M. In part, the very low abundance of ostracode fossils in the lower portion of the core, which precluded full 500 counts for all of the LT-98-12M samples, accounts for the upcore increase in species richness. However, there is a long-term rise in sample-size corrected diversity, which is not an artifact of unequal sampling. Although the species present in this core are largely similar to those of LT-98-2M, there are large differences in abundance patterns through time for individual taxa between the two cores. This pattern is typical of the ostracode community structure observed in paleoecological records from anthropogenically undisturbed localities in Lake Tanganyika, with their combination of extremely high diversity and extremely patchy distributions of individual species (Cohen 2000). An extraordinary 36 ostracode species occur at frequencies of  $\geq 5\%$  in at least one sample (Figure 4). Unlike LT-98-2M, no single species dominates most of the core; at various horizons *Gomphocythere curta*, *G. coheni*, *G. downingi*, *Romecytheridea longior*, *Cypridopsis* sp. 6, *Alloocyprina* sp., and *Mecynocyprina*

*opaca* dominate specific samples, but each is also rare or absent at other horizons. *Gomphocythere* species collectively decline upcore, particularly the abundant *G. curta*. Species showing marked upcore increases include *Mesocyprideis pila*, *Romecytheridea ampla*, *Mesocyprideis* sp. 2B, and possibly *Candonopsis* sp. 2 and *Mecynocypria conoidea*. The latter three species appear abruptly in the core at 15.5 cm (mid-17th century A.D.), a point of major assemblage changes (many species peak here and subsequently decline) and overall rise in ostracode abundance. Both upcore declines and increases, as well as the overall upcore increase in abundance and species richness, correspond with upcore changes in sedimentology (increase in coarser sediment, slight decrease in TOC, and rising charcoal frequency – see Palacios-Fest et al. 2005, Figure 4).

Fisher's  $\alpha$  diversity is higher at LT-98-12M than in the LT-98-2M core, particularly notable since the total abundance of ostracodes was so low at the former site. Diversity rises gradually throughout the core. The Jaccard's Index is very low (0.2–0.4) in the lower part of the core, indicative of a combination of extreme faunal turnover and the small populations encountered in these samples, but increases in parallel with diversity upcore, although even near the core top species turnover is quite rapid.

Ostracode taphonomic features in LT-98-12M are similar to those found in LT-98-2M, indicating good preservation of a highly stressed population, with relatively minor *post-mortem* reworking of valves (Figure 3). Abundance spikes of broken, encrusted, coated, and abraded valves in the mid-16th, late 17th-early 18th and (for fragmented valves) late 18th centuries are consistent with other indications of shallower water and more arid conditions at those times. The timing of these low lake stand, arid events suggested by this study is slightly earlier than Alin and Cohen (2003) inferred in their study, a discrepancy that is the result of age model uncertainties and new radiometric age dating. Aside from valve fragmentation there are no other indications of a late 18th–early 19th century low lake stand is evident in this core, although this event is recorded in the taphonomic data from other cores discussed below. However the sampling resolution of LT-98-12M is not good in that period and it is likely that the event has been simply missed in sampling.

Ostracode abundance in core LT-98-18M (Kabesi River delta-medium sized, moderate disturbance delta) is highly variable, with relatively low levels in the lower part of the core (18th–19th centuries), giving way to slowly increasing values in the late 19th to early 20th century, and a rapid rise starting in the early 1960s (Figure 5). The latter change was coincident with a significant increase in sedimentation rate and charcoal flux (Palacios-Fest et al. 2005, Figure 6). Diversity and species richness decline gradually upcore, with many species declining after 1900 (Figures 5 and 6). Jaccard's Index of similarity is relatively constant and moderately low (0.3–0.5) throughout the core, indicating substantial faunal turnover. A remarkable change in diversity and community structure occurs in core LT-98-18M between the late 19th century and 1960, marked by the rising dominance by *Romecytheridea longior*, at the expense of most other previously common species, some of which locally become extinct. Notably, this change in dominance is accompanied by a vastly greater proportion of unfragmented juveniles among *R. longior* populations. There are two possible explanations for such a fossil population. Our preferred explanation (because of its consistency with other factors considered in the discussion section), is that they may have floated and have been rafted offshore in very large numbers. Alive, this species is most common on shallow mud bottoms, and the valves show little sign of breakage (a probable outcome of traction or bed-load transport). The observed assemblage change would then represent the offshore accumulation of light, easily transported juvenile valves that were derived from abundant and increasing nearshore benthic production. Alternatively, large proportions of monospecific juveniles may represent ecological stress on a community, with many species disappearing and individuals of the dominant species incapable of maturing to the adult phase. Regardless of which explanation is correct (or both may have been operative), the processes must have been occurring through a time interval, starting in the early 20th century and intensifying in the early 1960s, when community structure was becoming simplified through some disturbance factor.

Core LT-98-58M, from the low disturbance, small watershed, Nyasanga/Kahama River delta, displays moderately high but erratic abundance of

ostracodes through the core. As in cores LT-98-2M, 12M, and 18M, periods of rising ostracode accumulation rates are contemporaneous with periods of rising charcoal accumulation rates (Figure 7; also see Palacios-Fest et al. 2005, Figure 8). Ostracode accumulation rates mirrored the raw abundance curve, as sedimentation rates were relatively constant throughout the core. Abundances and accumulation rates were high in the early interval (before the early 1800s), then declined significantly throughout the 19th century and then rose, albeit erratically, in the 20th century. Species richness is highest in this core of all cores presented here (range: 33–47 species per sample), and shows a small increase over time, particularly since the early 20th century. Jaccard Index values were surprisingly high throughout this core (0.52–0.78), indicative of substantial community stability in terms of species presence/absence. Jaccard results from this locality stand in contrast to both other low impact sites investigated in this study, and to earlier work (Cohen 2000), which had suggested that substantial faunal turnover is commonly coupled with high diversity at low impact sites.

The continuity of species occurrences (presence/absence) in core LT-98-58M notwithstanding, the abundance of individual species changes markedly upcore, with very little if any correlation with measured sedimentologic variables (Figure 8; also see Palacios-Fest et al. 2005, Figure 8). This core is notable for its evenness in species abundance distribution, with fewer very rare species and more relatively common ones than most other cores. The absence of dominance by any given species is also evident in the relatively low proportions found among all common ostracode species. Some species show long-term trends in abundance, for example upcore increases in *Gomphocythere curta* and *Cypridopsis* sp. 8, and declines in *Gomphocythere downingi*, *Mecynocypria opaca*, and, since the early 19th century, *Mecynocypria obtusa* and *Tanganyikacypris matthesi*. Significant dominance changes, associated with the aforementioned increases and decreases in ostracode abundance, occur in the late 19th or early 20th century. For most other species, the general pattern is one of erratic fluctuations.

Taphonomic data indicate that the ostracode accumulations are probably life-assemblages (Figure 7). Fragmentation is low and constant

throughout the core, and there is a 1:1 ratio of right:left valves throughout the core. Abraded valves (always >10%) are only recorded between 33 and 21 cm, consistent with a known decline in lake level in the late 18th to early 19th centuries. This pattern, along with increased levels of fragmented, encrusted or coated valves, all indicative of increased reworking is observed during this time interval in several cores as well (LT-98-18M, LT-98-37M and LT-98-82M). The low percentages of fragmentation and abrasion throughout the remainder of LT-98-58M both indicate *in situ* deposition. Diagenetic features like encrustation, coating, and redox alteration are minor and sporadic, indicating that the absence of post-depositional effects despite the relatively high total concentration of CaCO<sub>3</sub> in the core. The brief interval of abundant CaCO<sub>3</sub> encrustation in the early 19th century corresponds with generally higher rates of TIC accumulation at that time, consistent with known lower lake levels and therefore shallower water depths of the time (Alin and Cohen 2003). The low percentages of adults are reflective of the generally oxygen-stressed, deep-water environment of the core site.

Ostracode abundance in core LT-98-37M (Mwamgongo River delta, high disturbance, small watershed area) declines dramatically from very high levels prior to the mid-19th century, remaining relatively stable thereafter, with a second drop in the uppermost sample (Figure 9). Ostracode accumulation rate estimates also show the post early 19th century decline, but rise slightly in the late 19th century. Both ostracode abundance and accumulation rate changes are correlated with changes in % sand, TOC MAR, and less strongly with TIC MAR and charcoal MAR (Palacios-Fest et al. 2005, Figure 10). This relationship may be indicative of the changing quality of organic matter being delivered to detritus feeders from the watershed. As with the other northern Tanzanian area core, species richness is very high (typically 35–40 species per sample), and Fisher's  $\alpha$  diversity index is high and constant throughout the core. Jaccard's Index values (0.51–0.76) indicate comparatively high levels of faunal similarity between samples throughout the core, similar to LT-98-58M. However, Alin et al. (2002), in a detrended correspondence analysis of ostracode assemblages from this site, which, unlike the Jaccard Index, is sensitive to proportional changes in dominance of

various species, observed a significant assemblage shift after the 1930s. This was in contrast with their analysis of the LT-98-58M core (undisturbed Nyasanga/Kahama site), which showed no such temporal shift.

Several species decline through the core interval (notably *Alloocypria* sp. 5, *Cypridopsis* spp. 5 and 6, and *Gomphocythere cristata*) (Figure 10). Several unillustrated species, including *Candonopsis* sp. 11, *Tanganyikacypridopsis* sp. 3 and *Limnocythere* sp. 8 disappear entirely from the core record between the late 19th and early 20th century. Over the past 100 years other species show increases, including *Gomphocythere downingi*, *Archaeocyprideis tuberculata*, *Alloocypria inclinata*, *Alloocypria reniformis*, and *Romecytheridea longior*. Modern distributional data for the latter species in Lake Tanganyika suggest it is a good indicator of human disturbance and increasing silt loading. This species shows a marked rise in the uppermost samples (post-1950s) at this site. Jaccard Indices are moderately high throughout most of the core (0.53–0.76) with no strong trends evident throughout the core.

Taphonomic studies of LT-98-37M ostracodes show low and constant degrees of fragmentation throughout the core (Figure 9). Lack of abrasion is consistent with low fragmentation, suggesting *in situ* deposition. Features indicative of diagenetic

alteration like encrustation and coating are also uncommon (redox conditions were not recorded), indicating that post-depositional burial effects are minimal despite the relatively high concentration of  $\text{CaCO}_3$  throughout most of the core. Low percentages of adults are again consistent with deep-water stress.

Core LT-98-98M, from the Nyamuseni River delta (extremely highly disturbed, small watershed) of the northern Burundi coast, was nearly barren of ostracodes (Figure 11). Two samples at the top of the core from the 1990s contained low abundances of valves, and correspond with the simultaneous appearance of other rare benthos and fish, although the fossil appearances are uncorrelated with any measured sedimentologic variable changes. Apparently the sample site became briefly inhabitable for benthos in the late 1990s at what had, for the previous 30 years, been an extremely inhospitable environment. Both of the upper samples contained low diversity assemblages, dominated by a small number of species, although the species richness of the surface sample was significantly higher than the lower ostracode-bearing sample (3.5 cm downcore) (Figure 12). The Jaccard Index is very low comparing the two samples in which ostracodes were found, in part reflecting the extremely low diversity encountered in the lower, ostracode-bearing sample. The

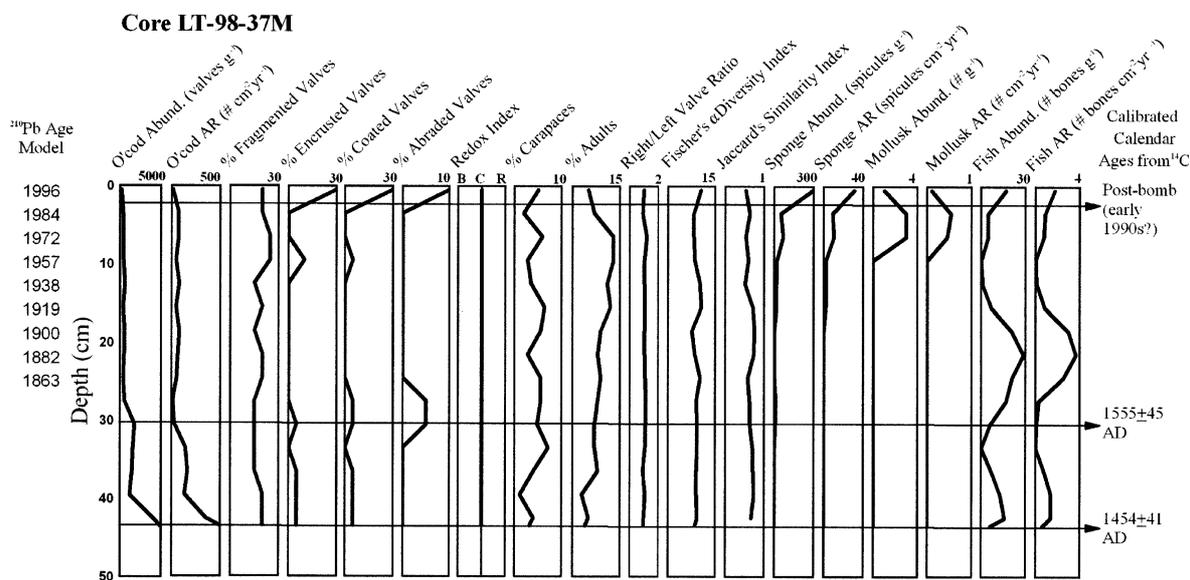


Figure 9. Summary paleoecologic profiles for Core LT-98-37M, Mwamgongo River delta, 76 m water depth (currently highly disturbed site). Total core length 45 cm (see Cohen et al. 2005a, Figure 4 for location and bathymetric map).

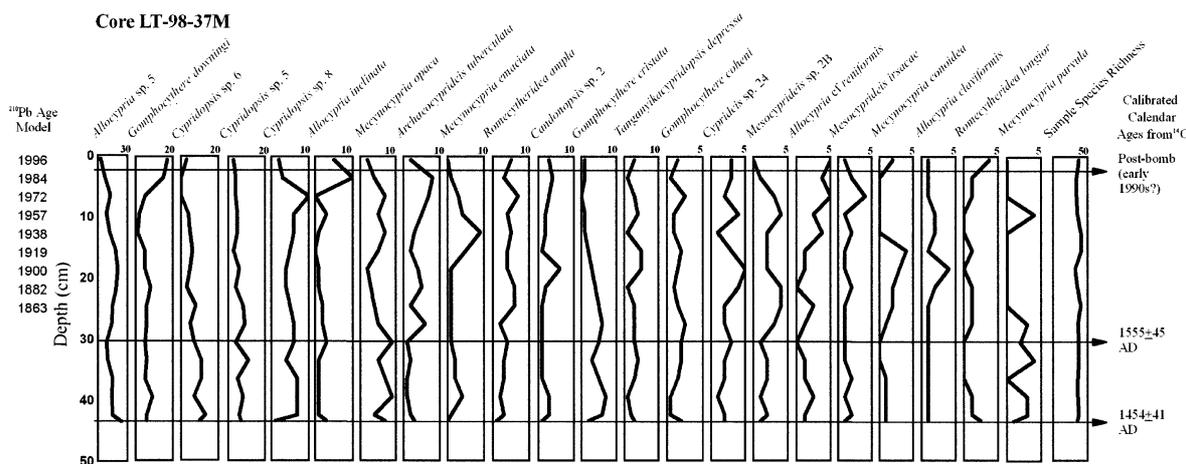


Figure 10. Ostracode biostratigraphic profiles for Core LT-98-37M.

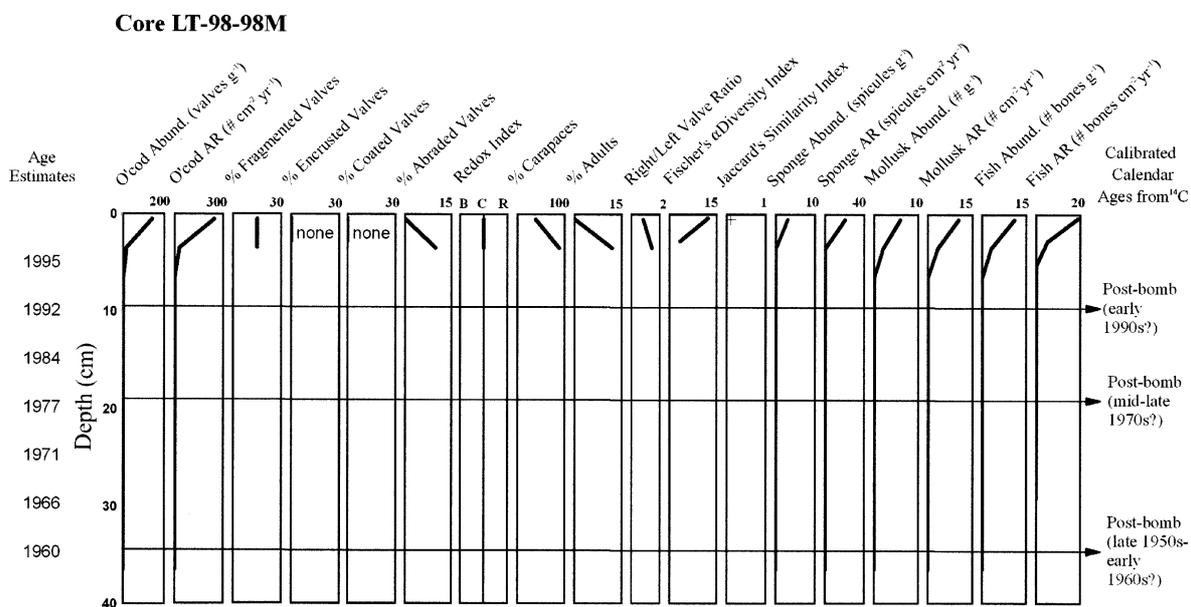


Figure 11. Summary paleoecologic profiles for Core LT-98-98M, Nyamusenyi River delta, 60 m water depth (currently very highly disturbed site). Total core length 37 cm (see Cohen et al. 2005a, Figure 5 for location and bathymetric map).

Jaccard Index is very sensitive to unequal diversity levels between samples.

Taphonomic features of the LT-98-98M samples are substantially different from other cores, with abundant carapaces and adults recorded in one sample, though not the other (Figure 11). Fragmentation and abrasion ratios are both low suggesting the assemblage was not significantly reworked. The difference in adult and carapace abundance between this core and those from other sites can probably be attributed to the core site's

relatively shallow depth (60 m) compared with the other more oxygen-stressed core localities.

Core LT-98-82M (Karonge/Kirasa River delta, medium sized watershed, extremely high disturbance), like the other extremely high disturbance site core from northern Burundi, has few ostracodes, and the upper 25 cm (i.e., post-1860s) is barren (Figure 13). Because the number of individuals encountered was so low, species richness cannot be directly compared with the Tanzanian cores. Jaccard Similarity Indices are very low

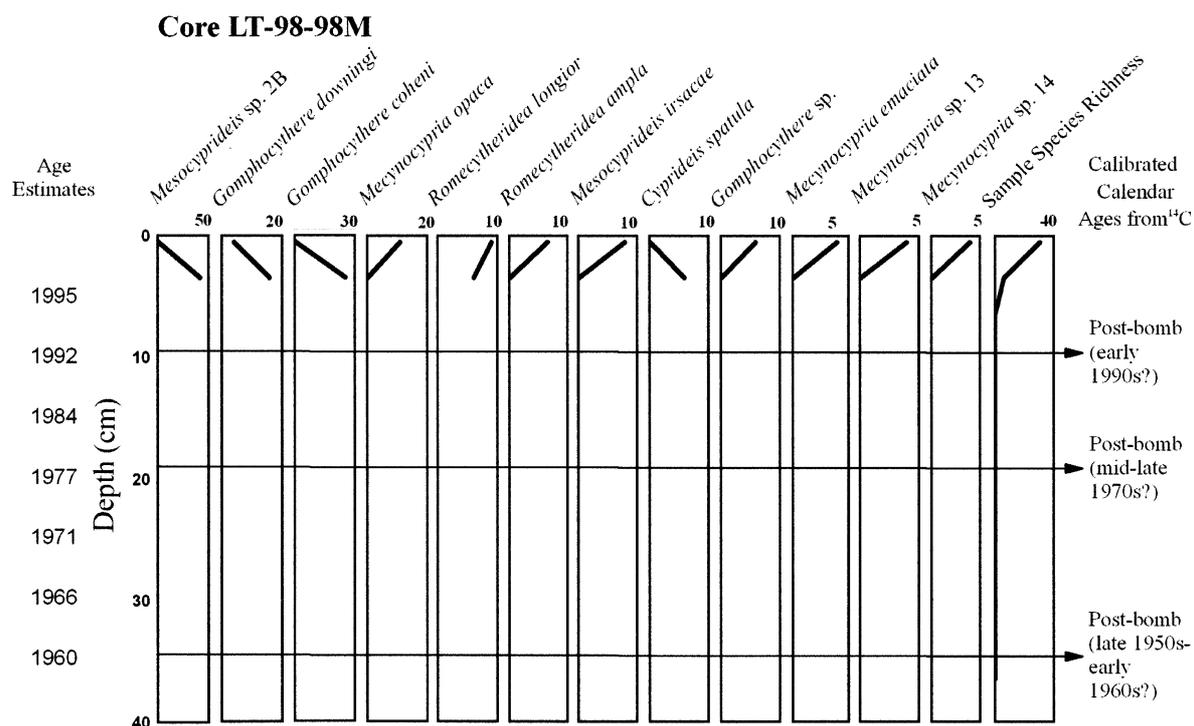


Figure 12. Ostracode biostratigraphic profiles for core LT-98-98M.

throughout the core (0.07–0.48), indicating substantial turnover, although their significance is limited by small and variable fossil population sizes. A small number of species dominate these lower core samples, with erratic abundances, as in other cores (Figure 14). Percentages of fragmented, encrusted, coated and abraded valves are all relatively high in comparison with other cores, and right/left valve ratios are erratic. In the 1820–1840s interval these values are high enough to suggest that the assemblage may have been significantly transported and/or reworked from older deposits.

Comparison of stratigraphic profiles for the four core sites where upcore sedimentation rate increases are evident (LT-98-18M, LT-98-37M, LT-98-98M, and LT-98-82M) suggests that a small group of relatively common species persists (and perhaps thrives) under relatively high sediment accumulation rate conditions. Listed from apparently most tolerant, these include *Romecytheridea longior*, *Mesocyprideis* sp. 2B, *Gomphocythere coheni*, *Mecynocypria opaca*, *Mesocyprideis irsacae*, and *Gomphocythere downingi*. However, the complete disappearance of ostracodes from the

LT-98-82M record after the mid-19th century, and their near-total absence in the 20th century record of LT-98-98M suggests that, for at least the past 130 years, the northern Burundi coastal areas have been inhospitable environments for ostracode populations. Attempts to generalize about species that are intolerant to high sediment accumulation rates are confounded by both geographic range variability among species and the general patchiness of rare ostracode species observed around Lake Tanganyika (Cohen 2000).

#### *Molluscs*

Mollusc fossils throughout the cores are primarily fragments that cannot be identified to species. In those rare cases where fragments are large enough to identify, the species present invariably belong to the deepwater detritivore group of endemic gastropods, including *Paramelania iridescens* and *Tiphobia horei*, and less commonly, *Neothauma tanganyicense*.

Mollusc fossils in core LT-98-2M are absent in the lower part of the core (consistent with

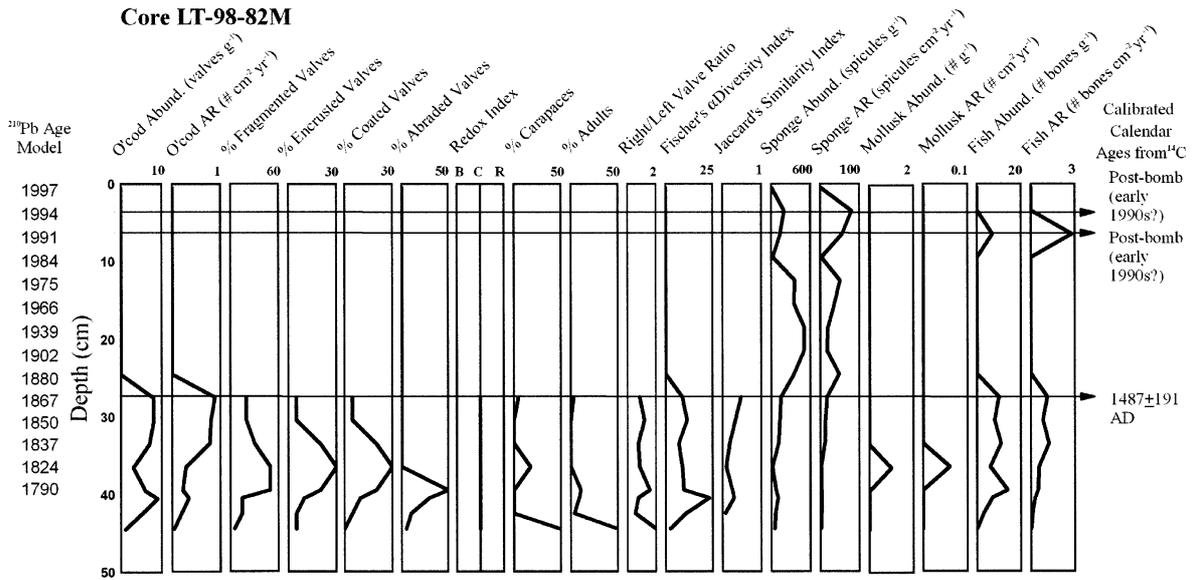


Figure 13. Summary paleoecologic profiles for Core LT-98-82M, Karonge/Kirasa River delta, 96 m water depth (currently very highly disturbed site). Total core length 46 cm (see Cohen et al. 2005a, Figure 5 for location and bathymetric map).

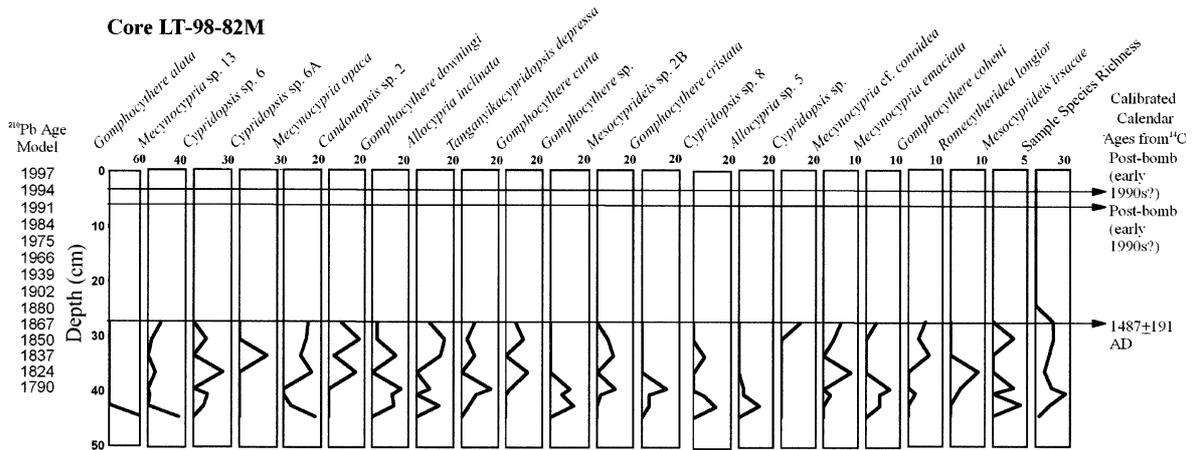


Figure 14. Ostracode biostratigraphic profiles for core LT-98-82M.

ostracodes) (Figure 1). They first appear at about 25 cm (~400–600 A.D., or somewhat after the first ostracodes) and then remain at moderate levels of abundance until ~1500 A.D., when they increase dramatically. These peaks in abundance and subsequent declines may be correlative with the mollusc abundance peak at about 30 cm downcore in LT-98-12M (Figure 3). Both cores have considerably higher mollusc abundance on average than any other cores studied. Greater abundances of molluscs in the mid-16th and mid-18th centuries are consistent with either shallower water (i.e.

more arid) or deeper mixing conditions (windier and/or cooler) at those times, which would have made this part of the lake more habitable for gastropods.

No mollusc abundance data are available for core LT-98-18M. In both Gombe area cores (LT-98-58M, Figure 7; and LT-98-37M, Figure 9) molluscs are rare and occur only sporadically through the cores (none were accumulating in the LT-98-37M site prior to the 1950s). Molluscs were almost entirely absent from cores LT-98-98M and LT-98-82M (Figures 11 and 13, respectively).

## Sponges

No keys exist to identify spicules of the nine species of sponges found in Lake Tanganyika, and therefore data are presented only as total abundance. Spicule abundance varied greatly both among and within cores, from 0 to  $>10^4 \text{ g}^{-1}$ .

In LT-98-2M, spicule abundance varies inversely with grain size, total organic matter, charcoal, as well as the abundance of all other benthic invertebrates throughout the core (see Palacios-Fest et al. 2005, Figures 1 and 2). Two periods of declining abundance are evident in the core. An initial, major decrease started after  $\sim 2600$  B.C., and a further pronounced decline occurred after the 12th–13th century A.D. These intervals are also mirrored in spicule accumulation rate changes, except that an abrupt increase in accumulation rates occurred about 0–100 A.D., simultaneous with the first occurrences of calcareous fossils in the core. Spicule abundance, both in numbers per gram and as accumulation rates, is generally much higher in the younger part of the Lubulungu delta record preserved in LT-98-12M (Figure 3) than in the LT-98-2M. LT-98-12M displays higher spicule abundance in the late 15th to early 16th century, followed by a sharp decline in the mid-later 16th century. Both spicule abundance and accumulation rates remain relatively low in LT-98-12M from the 16th century until the present. At the intermediate disturbance site core LT-98-18M, spicule abundance is intermediate between the other Mahale area cores, and shows less variability through the core interval (Figure 5). An upcore decline at the base of the core is followed by slowly increasing abundance and accumulation rate above  $\sim 21.5$  cm (late 19th century), and a rapid increase in spicule flux after the 1960s. The timing of spicule change is synchronous with rising ostracode abundances and declining ostracode diversity.

The Gombe area core spicule records provide an interesting comparison with the Mahale cores and with each other (Figures 7 and 9). LT-98-58M, the low disturbance site adjacent to Gombe Stream National Park, displays very high levels of spicule abundance in several samples near the bottom of the core (late 18th century), followed by very low abundances and accumulation rates up to the present. In contrast, at the high disturbance, Mwamgongo site, core LT-98-37M had very low

spicule counts throughout most of the lower portion of the core. Very few spicules were found in the lower portion (prior to the 20th century). However, abundances gradually increase after the early 20th century. Then, spicule abundance increases rapidly after the early 1960s, simultaneous with rising sedimentation rates and soil nutrient discharge (see Palacios-Fest et al. 2005, Figure 10 and O'Reilly et al. 2005, Figure 2).

Spicule abundance patterns from the two very high disturbance site cores from Burundi were also surprising. As with other fossils, LT-98-98M is almost completely barren of spicules, appearing in very low abundance only in the uppermost sample (Figure 11). However, spicules were moderately abundant in LT-98-82M (Figure 13). As with the other disturbed site cores previously discussed (LT-98-18M and LT-98-37M), the timing of this increase (beginning in the early 19th century) corresponds with a general increase in watershed soil erosion and sediment accumulation rate, and a decline in both ostracodes and fish fossils, suggesting a possible causal linkage between terrestrial processes and lake ecological change. The direction of change for the sponges, generally more abundant with increasing erosion disturbance, was unexpected, given the commonly held notion that sponge abundance is strongly correlated with low levels of siltation. However, casual observation of littoral rock surfaces in many highly disturbed littoral areas of the Northern Burundi coastline shows that sponges are extremely common on the undersides of rocks in this region today in all but the most disturbed and turbid localities. One possible explanation is that sponge abundance is more strongly linked to top-down effects of grazing pressure than directly to sedimentation loading *per se*. Changing food web structure associated with siltation appears to have significantly reduced the numbers and diversity of littoral cichlid grazers in disturbed sites (Alin et al. 1999; McIntyre et al. 2005). This reduction in grazing intensity may have actually released sponge growth rates from intensive top-down cropping, allowing more sponge biocover and higher rates of spicule production. It may be significant in this regard that higher spicule abundance in core LT-98-12M in the 15th century also correlates with times of increased watershed fires as indicated by charcoal records.

### *Fish*

Fossil fish bones occur at abundances of  $0\text{--}10^2\text{ gm}^{-1}$  in most core material examined, often varying erratically between stratigraphically adjacent samples. At present these bones cannot be identified to family. Fish bones were most abundant in the low disturbance Lubulungu River cores (LT-98-2M and LT-98-12M, Figures 1 and 3), and moderately abundant in the two Gombe area cores (LT-98-58M and LT-98-37M). Fish bones in LT-98-12M almost perfectly mirror the abundance record of molluscs, again supporting the notion of multiple lowered lake levels (more nearshore conditions) during the mid-16th and mid-18th centuries. In contrast, the very high disturbance site cores from Burundi (LT-98-82M and LT-98-98M) suggest very low abundance (or absence) of fish fossil accumulation through much of the core intervals. In LT-98-82M, fish fossils disappear from the record after the 1860s (except for one very recent sample), simultaneous with other indications of disturbance.

### **Discussion**

The lacustrine paleoecological records from Lake Tanganyika deltas discussed here document recent (late Holocene) changes in invertebrate and fish faunas. The most significant indicators of environmental change in the lake were ostracodes. Notable changes in ostracode diversity, species richness and assemblage structure at presently disturbed sites, as well as sponge abundance correlate with profound changes in sediment input rates and sediment composition. Long-term intersite differences between the faunas of deltas of presently disturbed and undisturbed watersheds also argue strongly for an important role for sediment accumulation rates in structuring Lake Tanganyika's littoral and benthic communities. However, major changes in ostracode species composition and diversity observed in some presently disturbed sites began in the late 19th century, well before we observe the major mid-20th century mass sediment accumulation rate increases at the same sites. Both abundance and taphonomic data are probably influenced by variations in lake levels over the study interval.

Two possible scenarios can be proposed to explain the variations in timing of changing

community structure between disturbed sites. First, invertebrate faunal diversity declines in presently sediment impacted regions may have been the result of some completely different forcing factor, perhaps unrelated to human activities. In this scenario, the correlation between presently impacted sites and faunal diversity decline is either a coincidence, or is the result of some broader range of human activity, which is indirectly correlated with land-use activity and subsequent soil erosion. The alternative explanation, which we favor, is that diversity declines are linked to changing soil erosion patterns, but that other factors aside from mere quantity of discharged sediment may be affecting invertebrate diversity in these areas. Most likely this would have involved an initial change in the composition of river-discharged effluent (both suspended and dissolved load) associated with deforestation and the onset of village growth, grazing and subsistence agriculture on steep slopes. Our primary line of evidence supporting the latter interpretation comes from the fact that, whereas the 19th to early 20th century invertebrate faunal diversity declines in both the Kabesi and northern Burundi sites precede the mid-20th century rise in mass sediment accumulation rate, they precisely correspond to palynological indications of changing vegetational cover related to disturbance (Msaky et al. 2005). Furthermore, at disturbed sites in northern Tanzania and Burundi, changes in nitrogen isotopes indicative of increased soil N discharge are evident starting by the late 19th to early 20th century interval of rapid invertebrate faunal change (O'Reilly et al. 2005), much earlier than the widespread early 1960s increase in sediment mass accumulation rates.

Lacustrine invertebrate community change at impacted sites may have occurred through a two-step process. The initiation of deforestation, largely a late 19th to early 20th century phenomenon in the central-northern Tanzanian portions of the Lake Tanganyika catchment (somewhat earlier in northernmost Tanzania and Burundi), was marked by rapid changes in soil composition and organic matter discharge to the lake. Ostracode community shifts coincided with these changes and may have been sensitive to them as a result of the changing quality of organic detritus, or indirectly from the consequent effects of increased nutrient loading or dissolved organic matter on the

nearshore ecosystem. However, this early phase did not result in massive increases in mass sediment discharge, because, as explained by McKee et al. (2005), much of this sediment volume was sequestered during this period as subaerial alluvium. Only in the mid-20th century, coincident with a period of anomalously high rainfall, flooding, and lake highstands were the large volumes of sediment stored in river valleys and alluvial plains discharged into the lake. Although ostracode communities had already undergone major changes in composition by this point in time, there was a significant increase in flux or numbers of individuals, possibly the result of rising mid-20th century benthic secondary productivity.

The records from cores LT-98-12M, LT-98-2M and LT-98-58M, all offshore from currently forested sites, make clear that ostracode faunal variability also responds to nonanthropogenic limnologic changes, probably driven by changing Late Holocene climate, in ways that are sometimes similar to those observed in the late 19th/20th century records of the moderately to highly disturbed sites. For example, under moderate and increasing sediment loading, ostracode abundance and flux actually rise, perhaps the result of increasing food availability from terrestrial detritus. This pattern is observed associated with 20th century anthropogenic changes (e.g., LT-98-18M), but also in the increasing sediment and charcoal input associated with the drought and higher fire frequency of the Little Ice Age. All sites studied display substantial species turnover within sites and broad variability in species composition among sites, even for contemporaneous samples collected in close proximity. Ostracode taphonomy data and sponge, mollusc and fish abundance data from LT-98-12M provides strong evidence for the occurrence of important low lake stands and probable aridity during several periods between the late 15th to early 19th centuries.

The major declines in ostracode species diversity, or in some cases, total absence of fossil fauna, observed in the moderately disturbed site of the Kabesi River (LT-98-18M) and the very highly disturbed sites of northern Burundi (LT-98-82M and LT-98-98M), are unparalleled in the 'natural disturbance experiments.' Declining diversity is also frequently accompanied by changes in the age structure of ostracode fossil populations, with increasing representation of juveniles and fewer

adults. The disturbed but very small Mwangongo River site (LT-98-37M), shows major faunal overturn associated with late 19th/20th century anthropogenic disturbance, but does not show the marked decline in overall diversity evident from both the other highly disturbed sites discussed here and those described by Wells et al. (1999). This suggests that disturbance thresholds from siltation impacts on lacustrine organisms are linked to the size of the adjacent watershed. Small watersheds like the Mwangongo River, especially where they discharge onto steep sublacustrine lake margins, may simply be incapable of delivering sufficient sediment to completely eliminate invertebrate populations, although sedimentation impacts may still substantially alter community structure.

Some of our results were unexpected. The observation that sponge spicule abundance is quite high at disturbed sites, and in fact seems to rise coincident with increasing sedimentation rates is counterintuitive, given the common association of freshwater sponges with nonturbid conditions. Most likely, changes in the fossil assemblages we observe through intervals of increasing sedimentation disturbance reflect both direct physical and chemical impacts, as well as indirect effects from trophic interactions, particularly top-down effects of selective foraging and/or grazing. For some groups, such as sponges, a reduction in the intensity of the normally very strong grazing pressure by benthic cichlid fishes as a result of siltation, may actually enhance growth in appropriate habitats, such as the crevices and overhangs of otherwise heavily silted habitats, where sponges are quite common today. A full analysis of the significance of these spicule data can only occur once we have a more complete understanding of the taphonomic conditions surrounding spicule accumulation and abundance patterns in modern lakes.

### Acknowledgements

We thank the United Nations Development Programme's Lake Tanganyika Biodiversity Project for providing the bulk of the financing for this research. Additional student project support came from the US National Science Foundation (NSF Grant #s EAR 9510033 and ATM 9619458). We especially thank Drs. Andy Menz, Graeme

Patterson and Kelly West of the LTBP for all of their gracious support at all stages of this project, and the crew of the *R/V Tanganyika Explorer* for their tireless efforts on our behalf during the coring cruise. We gratefully acknowledge the Tanzanian Council for Scientific Research (COSTECH), the Tanzanian Fisheries Research Institute (TAFIRI), and the University of Burundi, for their support of this research program. We are in debt with Dr. Sarah E. Metcalfe and an unknown reviewer for their insightful comments during the peer-review process. This is contribution #167 of the International Decade of East African Lakes (IDEAL).

## References

- Alin S.R. and Cohen A.S. 2003. Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth. *Palaeogeog. Palaeoclim. Palaeoecol.* 199: 31–49.
- Alin S.R. and Cohen A.S. 2004. The live, the dead, and the very dead: translating live ostracod assemblages into the fossil record in Lake Tanganyika, East Africa. *Paleobiology* 30: 44–81.
- Alin S.R., Cohen A.S., Bills R., Gashagaza M.M., Michel E., Tiercelin J.J., Martens K., Coveliers P., Mboko S.K., West K., Soreghan M.J., Kimbadi S. and Ntakimazi G. 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika. *Conserv. Biol.* 13: 1–7.
- Alin S.R., O'Reilly C.M., Cohen A.S., Dettman D., Palacios-Fest M.R. and McKee B. 2002. Effects of land-use change on aquatic biodiversity: a view from the paleorecords at Lake Tanganyika, East Africa. *Geology* 30: 1143–1146.
- Brouwers E.M. 1988. Sediment transport detected from the analysis of ostracod population structure. In: De Deckker P., Colin J.-P. and Peypouquet J.P. (eds), *Ostracoda in the Earth Sciences*. Elsevier Publishers, Amsterdam, pp. 231–244.
- Cohen A.S. 1989. The taphonomy of gastropod shell accumulations in large lakes: an example from Lake Tanganyika, Africa. *Paleobiology* 15: 26–45.
- Cohen A.S. 2000. Linking spatial and temporal changes in the diversity structure of ancient lakes: examples from the ostracod ecology and paleoecology of Lake Tanganyika. In: Rossiter A. and Kawanabe H. (eds), *Ancient Lakes: Biodiversity, Ecology and Evolution*. Adv. in Ecol. Res., Vol. 31. Academic Press, San Diego, CA, pp. 521–537.
- Cohen A.S., Palacios-Fest M.R., McGill J., Swarzenski P., Verschuren D., Sinyinza R., Songori T., Kakagozo B., Syampila M., O'Reilly C.M. and Alin S.R. 2005a. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: I. An introduction to the project. *J. Paleolimnol.* 34: 1–18.
- Cohen A.S., Palacios-Fest M.R., Msaky E.S., Alin S.R., McKee B., O'Reilly C.M., Dettman D.L., Nkotagu H.H. and Lezzar K.E. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IX. Summary of paleorecords of environmental change and catchment deforestation at Lake Tanganyika and impacts on the Lake Tanganyika ecosystem. *J. Paleolimnol.* 34: 125–145.
- Cohen A.S., Soreghan M.J. and Scholz C. 1993a. Estimating the age of formation of lakes: an example from Lake Tanganyika, East African rift system. *Geology* 21: 511–514.
- Cohen A.S., Bills R., Cocquyt C. and Caljon A.G. 1993b. The impact of sediment pollution on biodiversity in Lake Tanganyika. *Conserv. Biol.* 7: 667–677.
- Cohen A.S., Talbot M.R., Awramik S.M., Dettman D.L. and Abell P. 1997. Lake level and paleoenvironmental history of Lake Tanganyika, Africa, as inferred from late Holocene and modern stromatolites. *Geol. Soc. Am. Bull.* 109: 444–460.
- Coulter G.W. 1991. *Lake Tanganyika and its Life*. Oxford University Press, Oxford, United Kingdom, 354 pp.
- Coulter G.W. 1994. Lake Tanganyika. In: Martens K.B., Goddeeris B. and Coulter G.W. (eds), *Speciation in Ancient Lakes*. Arch. Hydrobiol. Beih. Ergebn. Limnol., Vol. 44, pp. 13–18.
- Dettman D., Palacios-Fest M.R. and Nkotagu H.H. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VII. Carbonate isotope geochemistry as a record of riverine runoff. *J. Paleolimnol.* 34: 93–105.
- Donohue I. and Irvine K. 2004. Seasonal patterns of sediment loading and benthic invertebrate community dynamics in Lake Tanganyika, Africa. *Freshwater Biol.* 49: 320–331.
- Forester R.M. 1991. Ostracod assemblages from springs in the western United States: implications for paleohydrology. *Mem. Entom. Soc. Canada* 155: 181–201.
- Irvine K., Donohue I., Verheyen E., Sinyinza R. and Taylor M. 2000. Special study on sediment discharge and its consequences: impacts of sedimentation on biota. UNDP-GEF Lake Tanganyika Biodiversity Project Document Tech. Rep. 9. <http://www.ltbp.org/FTP/SSS9.PDF>.
- Kawanabe H., Hori M. and Nagoshi M. (eds) 1997. *Fish Communities in Lake Tanganyika*. Kyoto University Press, 298 pp.
- Martens K. 1985. *Tanganyikacypridopsis* gen. N. (Crustacea, Ostracoda) from Lake Tanganyika. *Zool. Scripta* 14: 221–230.
- Martens K. 1993. On the taxonomy and zoogeography of the genus *Gomphocythere* SARS, 1924 (Crustacea, Ostracoda) with a description of a new species from the Nahal Dan (Israel). *Belgian J. Zool.* 123: 39–54.
- Martens K. 1997. Recent non-marine Ostracoda. Lake Tanganyika Biodiversity Project – Workshop, Kigoma, Tanzania, 13 pp.
- McIntyre P., Michel E., France K., Rivers A., Hakizimana P. and Cohen A.S. 2005. Individual and assemblage-level effects of anthropogenic sedimentation on snails in Lake Tanganyika. *Conserv. Biol.* 19: 1–11.
- McKee B., Cohen A.S., Dettman D.L., Palacios-Fest M.R., Alin S.R., Ntungumburanye and G. 2005. Paleolimnological investigations of anthropogenic change in Lake Tanganyika: II. Geochronologies and mass sedimentation rates based on  $^{14}\text{C}$  and  $^{210}\text{Pb}$  data. *J. Paleolimnol.* 34: 19–29.
- Msaky E.S., Livingstone D. and Davis O.K. 2005. Paleolimnological investigations of anthropogenic change in Lake Tanganyika: V. Palynological evidence for deforestation and increased erosion. *J. Paleolimnol.* 34: 73–83.
- O'Reilly C.M. 2001. The effects of land use change on littoral zone dynamics of Lake Tanganyika, East Africa. Ph.D. diss. University of Arizona, 144 pp.

- O'Reilly C.M., Dettman D.L. and Cohen A.S. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VI. Geochemical indicators from lacustrine organic matter. *J. Paleolimnol.* 34: 85–91.
- Palacios-Fest M.R., Cohen A.S., Lezzar K.E., Nahimana L. and Tanner B.M. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: III. Physical stratigraphy and charcoal analysis. *J. Paleolimnol.* 34: 31–49.
- Park L.E. and Martens K. 2001. Four new species of *Gomphocythere* from Lake Tanganyika, East Africa (Crustacea, Ostracoda). *Hydrobiologia* 450: 129–147.
- Rome D.R. 1962. Resultats Scientifiques: Exploration Hydrobiologique du Lac Tanganyika (1946–1947). Les Ostracodes, vol. III, Fasc 8. Institut Royal des Sciences Naturelles de Belgique, 305 pp.
- Rossiter A. and Kawanabe H. 2000. Ancient Lakes: Biodiversity, Ecology and Evolution, Adv. In Ecol. Res., Vol. 31. Academic Press, 624 pp.
- Salzburger W., Meyer A., Baric S., Verheyen E. and Sturmbauer C. 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African Haplochromine cichlid fish faunas. *Syst. Biol.* 51: 113–135.
- Seehausen O., van Alphen J.J.M. and Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808–1811.
- Van Alstine J.M. and Cohen A.S. 2003a. Nyanza Project research on the relationship of ostracode abundance and taphonomy to environmental variables on the Luiche Delta Platform, Lake Tanganyika. Amer. Soc. Limnol. Oceanogr. Ann mtg., Salt Lake City, UT, abstr. w/prog., 132 pp.
- Van Alstine J.M. and Cohen A.S. 2003b. Relationship of ostracode abundance and taphonomy to environmental variables on the Luiche Delta Platform, Lake Tanganyika (Nyanza Project 2001). 3rd Int. Limnogeol. Congress, Tucson, AZ, abstr. w/prog., 303 pp.
- Wells T.M., Cohen A.S., Park L.E., Dettman D.L. and McKee B.A. 1999. Ostracode stratigraphy and paleoecology from surficial sediments of Lake Tanganyika, Africa. *J. Paleolimnol.* 22: 259–276.
- Whatley R.C. 1988. Population structure of ostracods: some general principles for the recognition of palaeoenvironments. In: De Deckker P., Colin J.-P. and Peypouquet J.P. (eds), *Ostracoda in the Earth Sciences*. Elsevier Publishers, Amsterdam, pp. 2245–2256.
- Wouters K. 1988. On *Romecytheridea ampla* Wouters sp. Nov. *Stereo-Atlas of Ostracod Shells* 15: 101–106.
- Wouters K. and Martens K. 1992. Contribution to the knowledge of Tanganyika cytheraceans, with the description of *Mesocyprideis* nom. Nov. (Crustacea, Ostracoda). *Bull. Inst. Roy. Sci. Nat. Belgique* 62: 159–166.
- Wouters K. and Martens K. 1994. Contribution to the knowledge of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika, with the description of three new species. *Bull. Inst. Roy. Sci. Nat. Belgique* 64: 111–128.
- Wouters K. and Martens K. 1999. Four new species of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika. *Bull. Inst. Roy. Sci. Nat. Belgique* 69: 67–82.
- Wouters K. and Martens K. 2000. On the taxonomic position of the genera *Archaeocyprideis* and *Kavalocythereis* of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika in Lake Tanganyika (East Africa) with the first description of the appendages. *Bull. Inst. Roy. Sci. Nat. Belgique* 70: 207–216.
- Wouters K. and Martens K. 2001. On the *Cyprideis* species flock (Crustacea, Ostracoda) in Lake Tanganyika, with the description of four new species. *Hydrobiologia* 450: 111–127.