Journal of Paleolimnology (2005) 34: 125–145
DOI 10.1007/s10933-005-2422-4

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

Andrew S. Cohen[1,*], Manuel R. Palacios-Fest[2], Emma S. Msaky[3], Simone R. Alin[4], Brent McKee[5], Catherine M. O'Reilly[6], David L. Dettman[1], Hudson Nkotagu[7] and Kiram E. Lezzar[1]

*[1]Department of Geosciences, University of Arizona, Tucson, AZ 85721 USA; [2]Terra Nostra, Tucson, AZ 85741, USA; [3]Tanzania Petroleum Development Corporation, Dar es Salaam, Tanzania; [4]School of Oceanography, University of Washington, Seattle, WA 98195, USA; [5]Department of Geology, Tulane University, New Orleans, LA 70118, USA; [6]Environmental Science Program, Vassar College, Poughkeepsie, NY 12604 USA; [7]Department of Geology, University of Dar es Salaam, Dar es Salaam, Tanzania; *Author for correspondence (e-mail: acohen@geo.arizona.edu)*

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

Key words: Deforestation, East Africa, Lake level, Lake Tanganyika, Late Holocene, Soil erosion

Abstract

Paleorecords from multiple indicators of environmental change provide evidence for the interactions between climate, human alteration of watersheds and lake ecosystem processes at Lake Tanganyika, Africa, a lake renowned for its extraordinary biodiversity, endemism and fisheries. This paper synthesizes geochronology, sedimentology, paleoecology, geochemistry and hydrology studies comparing the history of deltaic deposits from watersheds of various sizes and deforestation disturbance levels along the eastern coast of the lake in Tanzania and Burundi. Intersite differences are related to climate change, differences in the histories of forested vs. deforested watersheds, differences related to regional patterns of deforestation, and differences related to interactions of deforestation and climate effects. Climate change is linked to variations in sediment accumulation rates, charcoal accumulation, lake level and water chemistry, especially during the arid-humid fluctuations of the latter part of the Little Ice Age. Differences between forested and deforested watersheds are manifested by major increases in sediment accumulation rates in the latter (outside the range of climatically driven variability and for the last ~40 years unprecedented in comparison with other records from the lake in the late Holocene), differences in eroded sediment and watershed stream composition, and compositional or diversity trends in lake faunal communities related to sediment inundation. Variability in regional patterns of deforestation is illustrated by the timing of transitions from numerous sedimentologic, paleoecologic and geochemical indicators. These data suggest that extensive watershed deforestation occurred as early as the late-18th to the early-19th centuries in the northern part of the Lake Tanganyika catchment, in the late-19th to early-20th centuries in the northern parts of modern-day Tanzania, and in the mid-20th century in central Tanzania. Rapid increases in sediment and charcoal accumulation rates, palynological and lake faunal changes occurred in the early-1960s. We interpret this to be the result of greatly enhanced flushing of sediments in previously deforested watersheds triggered by extraordinary rainfall in 1961/62. Regional differences in deforestation histories

can be understood in light of the very different cultural and demographic histories of the northern and central parts of the lake shoreline. Incursion of slaving and ivory caravans from the Indian Ocean to the central coast of Lake Tanganyika by the early-19th century, with their attendant diseases, reduced human and elephant populations and therefore maintained forest cover in this region through the late-19th to early-20th centuries. In contrast, the northeastern portion of the lakeshore did not experience the effects of the caravan trades and consequently experienced high human population densities and widespread deforestation much earlier. These studies demonstrate the importance of paleolimnological data for making informed risk assessments of the potential effects of watershed deforestation on long-term lake ecosystem response in the Lake Tanganyika catchment. Differences in sediment yield and lake floor distribution of that yield, linked to factors such as watershed size, slope, and sediment retention, must be accounted for in management plans for both human occupation of currently forested watersheds and the development of future underwater reserves.

Introduction

The comparison of paleoenvironmental records obtained from various parts of a large lake basin provides an excellent means of differentiating local vs. regional external processes impacting the lake's ecosystem, as well as differentiating local vs. lake-wide responses to those perturbations. In these papers published in this issue of the Journal of Paleolimnology we have used specific sedimentologic, geochemical and paleoecologic indicators in Lake Tanganyika (31°8′–8°47′ S, 29°05′–31°18′ E, 772 masl) to examine changing conditions of climate and watershed land use during the Late Holocene (Cohen et al. 2005; Dettman et al. 2005; McKee et al. 2005; Msaky et al. 2005; Nkotagu 2005; O'Reilly et al. 2005; Palacios-Fest et al. 2005a, b). Details of coring location and watershed characteristics are given in Cohen et al. (2005). Briefly, Lake Tanganyika is the largest and deepest of the East African rift valley lakes. The lake houses an extraordinary endemic ecosystem, with over 1500 species of organisms at least 600 of which are endemic to this lake, the product of $\sim$10 million years of lacustrine evolution (Coulter 1991; Cohen et al. 1993a). It is also an extraordinary natural resource for the region as a result of its very large and productive fishery, and as a source of freshwater. Concerns about various environmental threats to this ecosystem began to accumulate in the early 1990s (e.g., Cohen 1991; Lowe-McConnell et al. 1992; Cohen et al. 1996), and were a major motivating factor behind the development of the United Nations Development Programme/Global Environmental Facility's Lake Tanganyika Biodiversity Project (LTBP) in the mid 1990s (www.ltbp.org). One of the major threats to be assessed by the LTBP was the impact of deforestation and consequent soil erosion on the Lake Tanganyika catchment and ecosystem. The work reported in this special issue and summarized in this paper represents the paleolimnological and some of the hydrological investigations associated with the LTBP research program, as well as continuing investigations of the Nyanza Project funded by the National Science Foundation (US) and LTBP, an interdisciplinary research training program for American and African students on tropical lakes. For these papers we conducted an extensive study involving coring and modern process studies over several field seasons to gather paleorecords of late Holocene environmental change in various parts of Lake Tanganyika.

These records each provide evidence for profound changes in both the watershed of the lake and the lake ecosystem itself during the late Holocene. In this summary paper we present a synthesis of these changes, both spatially and temporally, in order to better understand the relationship between terrestrial and lacustrine environmental changes at Lake Tanganyika.

Intra-site comparisons between data sets

Our synthesis consists of initially comparing the results from each core site across data sets and then examining these sites in the context of both watershed- and regional-scale changes in human demography and catchment disturbance. For a summary of core site latitudes, longitudes, water depth and delta characteristics see the introductory paper in this issue (Cohen et al. 2005, Tables 1 and 2, Figures 1–5). Core site summaries are presented from south to north, with an indication for each of the present-day level of disturbance from deforestation impacts within their respective watersheds. We compare key data sets from each of the individual indicator studies discussed in detail elsewhere in this issue with each other to infer the absolute chronologies of depositional events. These are displayed against our most current understanding of lake-level fluctuations in Lake Tanganyika, compiled from prior sources (Evert 1980; Cohen et al. 1997; Alin and Cohen 2003 and Van Alstine and Cohen 2003) as well as results from this study.

Cores LT-98-2M (6.1653° S, 29.7060° E) and LT-98-12M (6.1655° S, 29.7178° E). Lubulungu River, W. Mahale Mountains, central Tanzanian coast (low disturbance watershed) (Figures 1 and 2)

Cores LT-98-2M and 12M (collected in 110 m and 126 m water depth, respectively) collectively provide us with our longest-duration record, extending back to the mid-Holocene. Although it was not our original intention to investigate deltaic records prior to the last few hundred years, the results from core LT-98-2M are nonetheless interesting because they provide information on landscape variability in the Mahale region long before to the modern situation, and serve as a basis of comparison for the levels of variability observed in our late-19th and 20th-century records. Age models for both cores are weaker than at most other sites as a result of the extremely slow and probably pulsed rates of sedimentation encountered here (McKee et al. 2005).

Core LT-98-2M is characterized by extremely slow sediment accumulation rates overall, although those rates increase markedly upcore (McKee et al. 2005). Between ~600 and 700 B.C., sedimentation at the core site shifted abruptly to finer muds. This initial fining was associated with increasing total organic and inorganic carbon accumulation rates, and a decline in arboreal pollen, especially high-elevation conifers. Around the 1st century B.C. charcoal concentration and

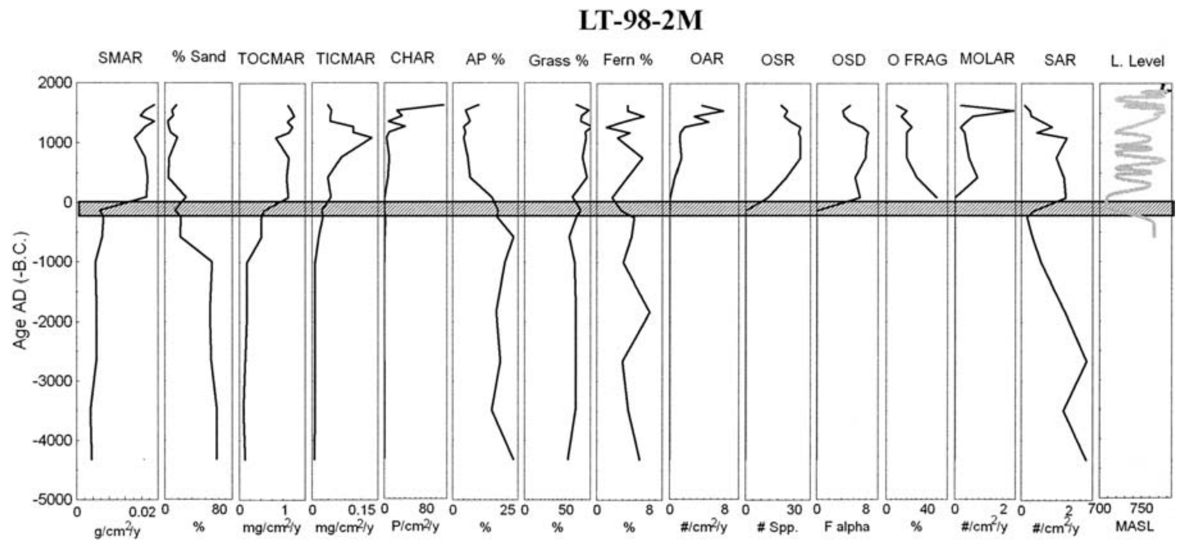

Figure 1. Composite chronology for key paleoenvironmental variables from core LT-98-2M (Lubulungu River delta, western Mahale Mountains, central Tanzania, undisturbed watershed). SMAR = Sediment mass accumulation rate. TOC MAR = total organic carbon mass accumulation rate. TIC MAR = total inorganic carbon mass accumulation rate. CHAR = charcoal accumulation rate (expressed as particles (P)/cm^2 /yr. AP% = percent arboreal pollen. OAR = ostracode valve accumulation rate. OSR = ostracode species richness. OSD = ostracode species diversity (Fisher's alpha). OFRAG = % ostracode valves fragmented. MOLAR = mollusc shell (bivalves + gastropods) accumulation rate. SAR = sponge spicule accumulation rate. Cross-hatched zone marks time of initial supersaturation of $CaCO_3$, increased aridification, rising charcoal, and sediment accumulation rates. The lake level curves for Figures 1–7 incorporate inferences of paleo-lake levels from this study, Cohen et al. (1997) and Alin and Cohen (2003), and historical data from Evert (1980) and NASA satellite altimetry data for the post 1980 period (Birkett et al. 1999). Inferred paleo-lake levels are shown in gray lines and should be treated as qualitative estimates, whereas instrumentally measured levels are shown in black lines.

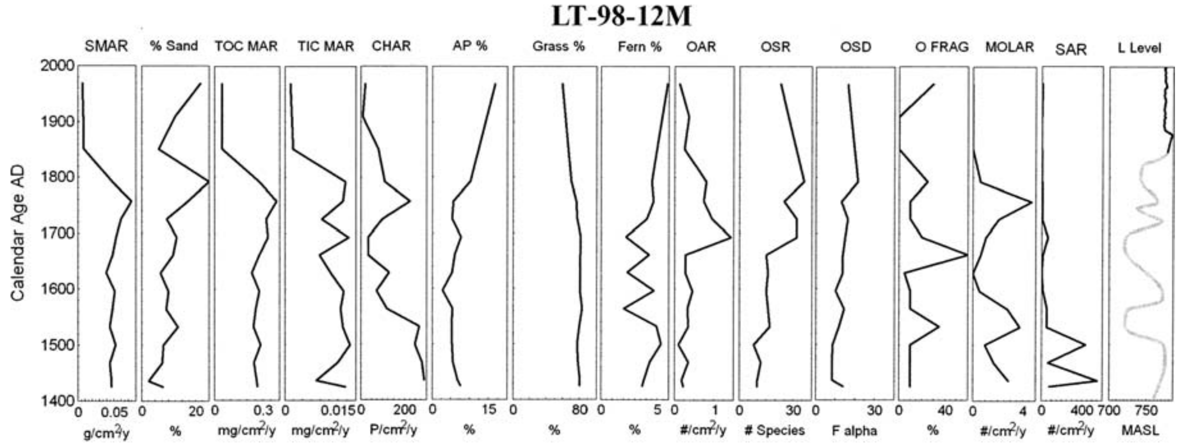

Figure 2. Composite chronology for key paleoenvironmental variables from core LT-98-12M (Lubulungu River delta, western Mahale Mountains, central Tanzania, undisturbed watershed). Abbreviations as in Figure 1.

accumulation rates in the core begin to rise appreciably, concurrent with increasing sediment accumulation rates (Palacios-Fest et al. 2005a). Benthic calcareous fossils (ostracodes and gastropods) make their initial appearance in the record, and sponge spicules also display an abrupt increase at this time (Palacios-Fest et al. 2005b). Multiple core records that cover this time interval from other locations in Lake Tanganyika also show this rise in preservation of calcareous skeletal material and calcium carbonate content in general (e.g., Alin and Cohen 2003). This indicates that the abrupt appearance of calcareous fossils is most likely a consequence of a deepening of the carbonate compensation depth throughout the lake, resulting from some combination of increased carbonate production and decreased dissolution. The very low levels of carbonate in all mid-late Holocene cores prior to this time suggest that about this time the concentration of calcium carbonate, and probably all other dissolved solids, underwent a marked increase. Taken in combination with other terrestrial data (charcoal, pollen, sediment accumulation rates), our data points toward a major aridification event at this time, consistent with earlier interpretations (Alin and Cohen 2003).

Siliciclastic sand input was greatly reduced after about 400–500 A.D., by which time the sediment at the core site was almost completely comprised of fines. Arboreal pollen concentrations stabilized at relatively low levels at this same time, following a long period of decline. Carbonate and ostracode accumulation rates began to rise at this time as well, corresponding to the overflow of Lake Kivu into the Lake Tanganyika basin from the north (Haberyan and Hecky 1987; Cohen et al. 1997). Currently, Lake Kivu (1°34′–2°31′ S, 28°49′–29°21′ E, 1460 masl, 2700 km^2 area) provides a major source of dissolved solids to the lake, which probably account for the rapid rise in ostracode abundances and total inorganic carbon (TIC) preservation starting in about the 5th century A.D. Palynologic records from the highlands north of Lake Tanganyika point towards substantially wetter conditions after ~720 A.D. (Jolly and Bonnefille 1992), and rising lake levels for Lake Tanganyika (note declining ostracode fragmentation since approximately the 1st century B.C.) also suggest increased water availability after about the late-6th century A.D., consistent with other lake records to the north (Alin and Cohen 2003). However, the terrestrial record from LT-98-2M does not reflect this change, with low arboreal pollen concentrations and rising (although low) charcoal concentrations. It is likely that wetter conditions prevailed north of Tanganyika, including those within the high-elevation catchment of upstream Lake Kivu and the northern Burundi highlands, but that this trend was absent or at least subdued further south in the Mahale Mountains region.

TIC accumulation rates peaked and then rapidly declined after ~1100 A.D., probably corresponding to decreasing solute inputs (especially Mg and Ca) from Lake Kivu at that time, consistent with both a decrease in lake level and drier regional paleoclimatic records to the north (Alin and Cohen 2003). There is little change in pollen profiles through the interval from about the 6th to 12th century A.D., again indicating greater climatic instability north of Tanganyika than in the Mahale region over this time period (Msaky et al. 2005). However, a major rise in charcoal MARs beginning in about the early-13th century signals that drier conditions had arrived in the central Lake Tanganyika catchment by that time. Rising proportions of adults and carapaces at this time also point toward declining lake levels (Palacios-Fest et al. 2005b).

From about the 13th to 15th centuries charcoal flux in LT-98-2M declined slightly and more evergreen forest pollen is evident, suggesting wetter conditions. Declines in ostracode diversity during this time, along with increasing abundance of deep-water species such as *Gomphocythere downingi*, are consistent with earlier suggestions of higher lake levels during this interval (Alin and Cohen 2003).

The records from LT-98-2M and LT-98-12M overlap slightly in the 15–16th centuries A.D. and are generally coherent over this time interval, with differences that can be attributed to slightly different depositional settings and water depths. LT-98-2M shows an extraordinary rise in charcoal accumulation rate in about the early 16th century, and while this rise is not captured in the basal part of the LT-98-12M record, charcoal accumulation rates are at their maximal level for this core during the same time interval (Palacios-Fest et al. 2005a). High charcoal accumulation rates in approximately the early-16th century are closely followed by evidence of lowered lake levels by about the mid-16th Century in the form of ostracode taphonomic indicators, and increasing mollusk and fish fossil abundances at the core site (Palacios-Fest et al. 2005b). The interval between the 16th and 18th century provides evidence for several discrete episodes of low lake levels and aridity, notably in about the early-mid 18th century, generally consistent with earlier interpretations of low stands and aridity for the Lake Tanganyika during the latter part of the Little Ice Age (Alin and Cohen 2003).

After about the late-18th century the core LT-98-12M record demonstrates a major decline in sediment accumulation rates on the Lubulungu delta, which persists to the present. This is accompanied by a long-term upcore increase in the abundance of arboreal pollen, low elevation euphorbs and herbs (Msaky et al. 2005). In contrast, the abrupt 20th century increases in fern spores encountered in most other cores is not evident in this currently protected watershed. The combination of a long- term rise in arboreal pollen, declining sediment and charcoal accumulation rates, and indications of deeper water conditions after the 18th century are all consistent with the timing of termination of Little Ice Age aridity and the probable progressive reforestation of this region as rainfall increased. Numerous high-elevation areas of the Mahale Mountains National Park that are not above thermal tree line, and which receive abundant precipitation, but are currently barren of trees, also indicate earlier extensive burns.

Core LT-98-18M (5.9768° S, 29.8167° E). Kabesi River, N. Mahale Mountains, central Tanzanian coast (moderate disturbance watershed) (Figure 3)

Core LT-98-18M, collected in 75 m water depth, provides one of our most compelling records of environmental change in the Lake Tanganyika catchment. An excellent age model is available for this core, and the profile shows coherent and interpretable patterns of change, particularly over the past century (McKee et al. 2005). Charcoal accumulation rates show a gradual decline from high values during the late-18th century (the arid, latter Little Ice Age) through to about the 1960s, when they rise again dramatically (Palacios-Fest et al. 2005a). Palynologic records show an abrupt decline in grass pollen and increases in arboreal pollen (especially low-elevation euphorbs and high-elevation trees), fern spores and composites (Msaky et al. 2005). The transition begins in about the late-19th century and accelerates greatly after the early-1960s.

Similar timing of change is indicated in many records from this core. Ostracode abundance starts to increase in about the late-19th century and increases rapidly after $\sim$1961, as does sponge abundance (Palacios-Fest et al. 2005b). The ostracode record shows a major decline in diversity and an increase in assemblage dominance by well-preserved juveniles of *Romecytheridea longior*, a relatively shallow water, muddy-bottom and

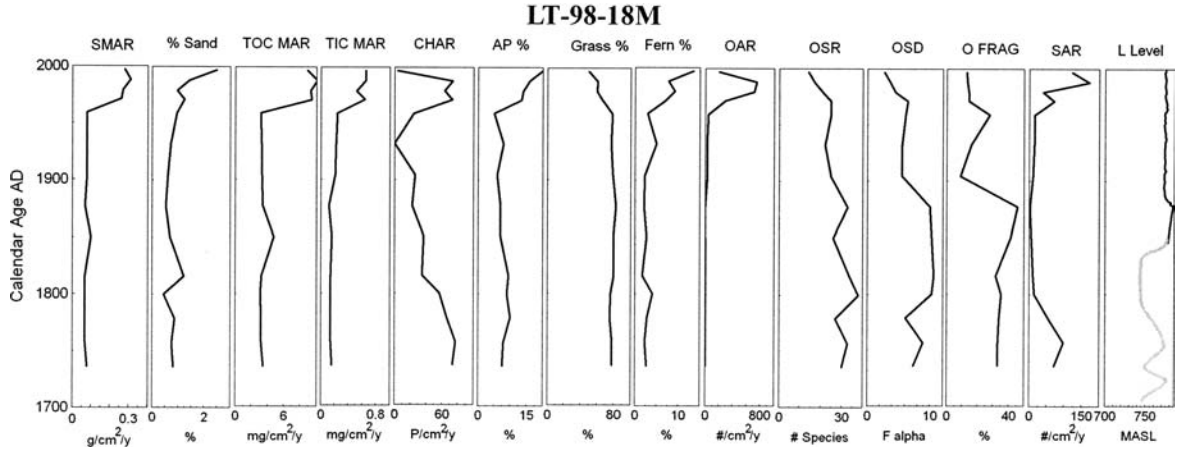

Figure 3. Composite chronology for key paleoenvironmental variables from core LT-98-18M (Kabesi River delta, northern Mahale Mountains, central Tanzania, moderately disturbed watershed). Abbreviations as in Figure 1.

sedimentation-tolerant species. Although sediment accumulation rates do not show any significant change in the late-19th century, they triple in ~1961. Increasing sediment accumulation rates at that time suggest that both TOC and TIC fluxes must have increased to maintain their constant proportionality.

The ~1961 increase in sediment accumulation rates, TOC and TIC accumulation rates, accumulation rates of *Romecytheridea longior* ostracodes and sponge spicules are all consistent with indications of less evaporative fractionation from groundwater residence in stable isotope records (Dettman et al. 2005). Meanwhile coarse sediment input suggests an increase in the efficiency with which shallow-water sediment (both suspended and bed load) was transported offshore to the core site. There are at least two reasons why such increased transport might have occurred. First, total discharge of water plus sediment may have increased. Alternatively, the position of the predominant distributary channel outlet may have changed, making the core site more proximal to it. Earthen-work drainage diversions for irrigation purposes can be observed on the lower Kabesi and new outlet channels are constructed periodically. However interviews with local residents indicate that such features were constructed more recently than the early 1960s, making the second explanation less likely.

The correspondence of the lake signals with the palynologic record, as well as our approximate hydrologic modeling from stable isotope data, provides strong support for a total discharge explanation. Work by Nkotagu (2005) and Dettman et al. (2005) suggests that decreased forest and woodland cover within the Lake Tanganyika catchment is likely to be accompanied by increased hydrologic discharge and reduced groundwater infiltration, as overland impediments to flow are removed from the landscape. Early indications of this change may date from the late-19th century, when palynologic changes first appear, and benthic detritivores first begin to increase in abundance. However, the largest changes clearly date from about the early-1960s.

Core LT-98-58M (4.6883° S., 29.6167° E) Nyasanga/Kahama Rivers, Gombe Stream National Park, northern Tanzania (low disturbance watershed) (Figure 4)

Core LT-98-58M, collected in 76 m of water, records a ~300 year history adjacent to Gombe Stream National Park (McKee et al. 2005). Terrestrial indicators show the previously discussed grass-arboreal pollen conversion starting in about the 18th century and accelerating in about the mid-20th century. Rapidly increasing fern abundances and declining grass pollen appear after about the early-mid 20th century, along with rising abundance of both low-elevation (*Acacia*) and high-elevation (*Podocarpus*) trees (Msaky et al. 2005). Extremely abundant charcoal occurs throughout the core, with the highest values in about the late-18th to early-19th and the mid- to late-20th century sediments (Palacios-Fest et al. 2005a). In contrast to these indications of terrestrial disturbance, there is no indication of concurrent sedimentologic change or change in sediment accumulation rates since about the mid 18th century. Inorganic carbon MARs peak in about the late-18th to early-19th and mid- to late-20th centuries, whereas TOC accumulation rates and coarse sediments show no pronounced changes (Palacios-Fest et al. 2005b). Low but somewhat variable $\delta^{15}N$ values on bulk organic matter persist through the entire core record at this site, indicating an unimpacted nutrient source for lake phytoplankton rather than soil nitrogen or sewage (O'Reilly et al. 2005).

Benthic invertebrate diversity is very high throughout this core (Palacios-Fest et al. 2005b). Interestingly, periods of rising ostracode abundance parallel periods of rising charcoal accumulation. Multivariate analysis of ostracode community structure from LT-98-58M shows no directional trend towards a disturbance-tolerant fauna (Alin et al. 2002). Ostracode taphonomic indicators (especially carbonate coatings), along with charcoal and sponge spicule records, are consistent with lowered lake levels and aridity in the late-18th to early-19th centuries, which are a reflection of widespread East African aridity at this time (Nicholson 1998; Verschuren et al. 2000; Alin and Cohen 2003). For later parts of the record, the pollen and charcoal changes we observe (Msaky et al. 2005; Palacios-Fest et al. 2005a) do not closely match any known climatic trends. Given that pollen and charcoal are easily transported, it is more likely that they reflect the regional pattern of changing land use in northern Tanzania and southern Burundi during the 19th and 20th centuries, rather than providing a watershed-scale signal. This is perhaps not surprising, given the small size of the Nyasanga and Kahama drainages. A flat sediment accumulation rate curve and nitrogen isotopes in bulk organic matter from this area are also consistent with an absence of major soil erosion pulses from the Nyasanga/Kahama watershed during the late-19th to the 20th centuries (O'Reilly et al. 2005). The only terrestrial indicators that may be attributable to local changes within Gombe Stream National Park following the establishment of watershed protection policies in the mid-20th century is the apparent increase in woodland tree pollen dating from this time. Possible evidence for this comes from the records of *Brachystegia* and *Acacia*, which occur in the park today as large, mid-elevation (1200–1400 m) trees and low elevation (775–950 m) thickets, respectively (Clutton-Brock and Gillett 1979). No evidence exists in the pollen records to confirm the conversion of low-elevation woodland to canopy forest that has been observed in recent decades in the protected park areas (A. Collins pers. comm. 1999).

Core LT-98-37M (4.6227° S, 29.6332° E). Mwamgongo River, Gombe area, northernmost Tanzania (high disturbance watershed) (Figure 5)

This core, collected in 95 m water depth, provides a ~500 year record of a region that, for most of its history, was probably quite similar to the LT-98-58M core Nyasanga/Kahama area several kilometers to the south. Contrasts between the two

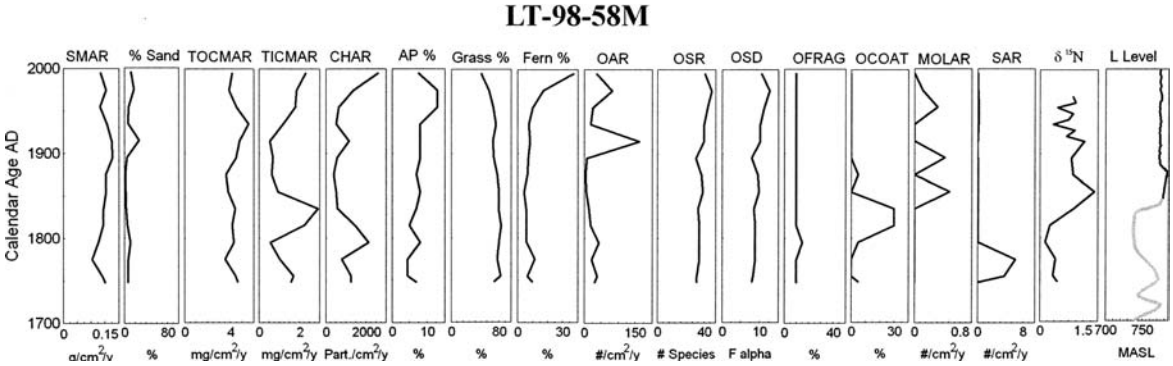

Figure 4. Composite chronology for key paleoenvironmental variables from core LT-98-58M (Nyasanga/Kahama River delta, Gombe Stream National Park, northern Tanzania, undisturbed watershed). Abbreviations as in Figure 1.

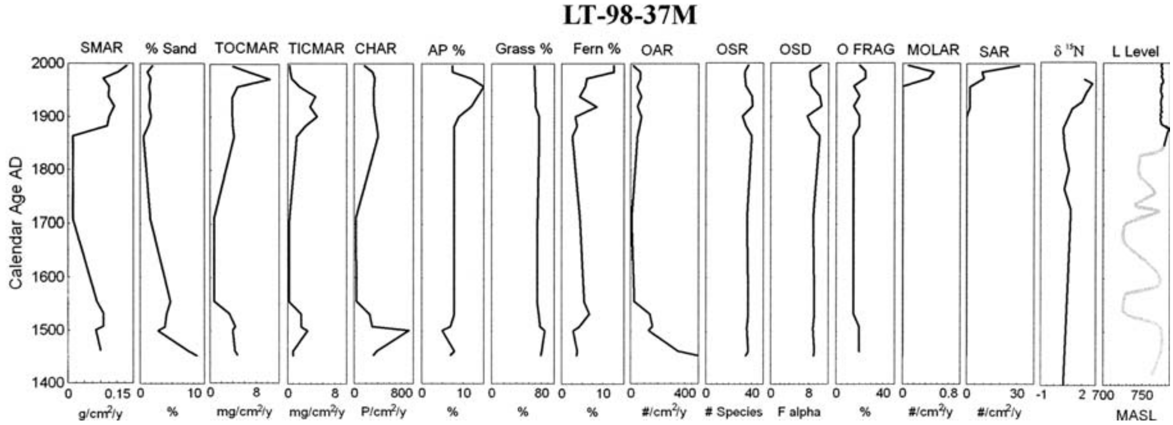

Figure 5. Composite chronology for key paleoenvironmental variables from core LT-98-37M (Mwamgongo River delta, northern Tanzania, highly disturbed watershed). Abbreviations as in Figure 1.

sites are therefore of considerable interest (e.g., Alin et al. 2002). The Mwamgongo watershed lies just outside of the Gombe Stream National Park boundary. The Nyasanga/Kahama watershed has undergone afforestation starting in the 1950s and has a relatively small human population of national park personnel, families and visitors today, whereas Mwamgongo has continued to be a site of increasing population density over the same time.

Sediment accumulation rates in LT-98-37M show a gradual decline from about the 15–18th centuries, accompanied by a gradual decline in grain size (McKee et al. 2005; Palacios-Fest et al. 2005a). This was followed by low sediment accumulation rates until about the mid-19th century. At that time, sediment accumulation rates rise dramatically, accompanied by a slight increase in grain size. A secondary rise in accumulation rates occurred in about the early-1960s. Late-20th century sediment in the core also changes in appearance. There is an abrupt switch from older greenish-brown muds to younger reddish brown clays, the latter reminiscent of eroded lateritic soils. This terrigenous sediment change is contemporaneous with an abrupt decline in TIC (from previously high carbonate input), both of which suggest terrestrial forcing of sedimentologic changes. The prominent color change was observed in multiple cores from this delta (Cohen et al. 2005; Palacios-Fest et al. 2005a). The pattern is not observed in cores from undisturbed deltas at similar depths, ruling out simple redox transitions as a likely explanation. Charcoal and TOC accumulation rate profiles are similar to those of TIC, with peaks in about the early 16th century and increasing again about the mid 19th century (Palacios-Fest et al. 2005a). Surprisingly, absolute charcoal accumulation rates are lower than for the currently undisturbed Nyasanga/Kahama delta. This difference is most likely a consequence of differences in particle delivery and current conditions at this site.

The pattern of palynological change in LT-98-37M is quite similar to LT-98-58M, with a gradual, long-term decline in grass pollen starting in about the late-18th to early-19th centuries (Msaky et al. 2005). The decline accelerates in about the late-19th and early-20th centuries, simultaneous with rapidly rising proportions of fern spores and tree pollen. These changes are largely synchronous with more positive δ^{15}N isotopic values (O'Reilly et al. 2005) and sediment accumulation rates (McKee et al. 2005) and are consistent with the hypothesis that major changes in watershed vegetation were linked to rising soil erosion rates. The somewhat earlier rise in charcoal accumulation rates shows that extensive burning starting in approximately the mid-19th century preceded this increase in soil denudation rates.

The benthic faunal response at the Mwamgongo site is similar in notable ways to the LT-98-18M (Kabesi River) site discussed previously, although the changes occur much earlier at Mwamgongo. Pronounced faunal changes do occur starting in about the early-20th century, notably as a shift in the ostracode community towards dominance by sediment disturbance taxa (Alin et al. 2002). This is indicated by the rising abundances of species such as *Romecytheridea longior* discussed previously. Ostracode diversity remains high through this upper interval. This may indicate that overall community disturbance is regulated or dampened by the combination of small watershed area and steep slopes prevailing in the Mwamgongo area. Sponge spicule accumulation rates also rise gradually after about the early-20th century and rapidly in the early-1960s. As explained in Palacios-Fest et al. (2005b) sponges today are extremely common in highly disturbed areas such as the Burundian littoral region, apparently the result of reduced predation rates by reduced predator populations. One aspect of the LT-98-37M record that differs markedly from the Kabesi record is the high and relatively constant ostracode diversity observed at this site throughout the past ~500 years. In this respect the record is quite similar to its undisturbed neighbor, LT-98-58M. The smaller watersheds and steeper littoral zones of the two Northern Tanzanian sites may render their benthic faunas less susceptible to the smothering effects of sedimentation pulses on benthic habitats (e.g., Donohue et al. 2003). In this regard, it is significant that even during the maximum disturbance period of the late-20th century, the absolute sediment accumulation rates of both LT-98-37M and LT-98-58M are considerably lower than those of the moderately disturbed but much larger watershed of the Kabesi River delta, with strong implications for the very highly disturbed and larger drainages of Burundi.

Core LT-98-98M (3.6193° S, 29.3402° E). Nyamuseni River, northern Burundi, (very high disturbance watershed) (Figure 6)

Core LT-98-98M, collected in 61 m water depth, represents a brief record of environmental change, covering only the past approximately 40–50 years. Sedimentation at this site has been characterized by extremely rapid accumulation rates throughout its history, suggesting that land disturbance predates the base of the core record (consistent with the LT-98-82M record discussed below). Based on the shape of the ^{210}Pb profile, combined with the ultramodern (i.e., post-bomb) ^{14}C dating, sedimentation also appears to have been pulsed or episodic at this site, and may in fact involve a series of large, rapid events, each depositing several cm of sediment (McKee et al. 2005). Episodes of rapid increase date from both the ~early-1960s and the ~early-1990s, the latter consistent with earlier data from northern Burundi (Wells et al. 1999).

The core is characterized by very high TOC and TIC accumulation rates throughout its duration in comparison with other sites, and these accelerate in the ~1990s (Palacios-Fest et al. 2005a). Absolute concentrations of TIC are relatively low as a result of siliciclastic dilution. TOC increases appear to be the result of both higher allochthonous plant matter inputs and high lacustrine productivity. TIC is mostly authigenic aragonite (as microscopic crystalline rosettes) generated by productivity pulses, except in the uppermost

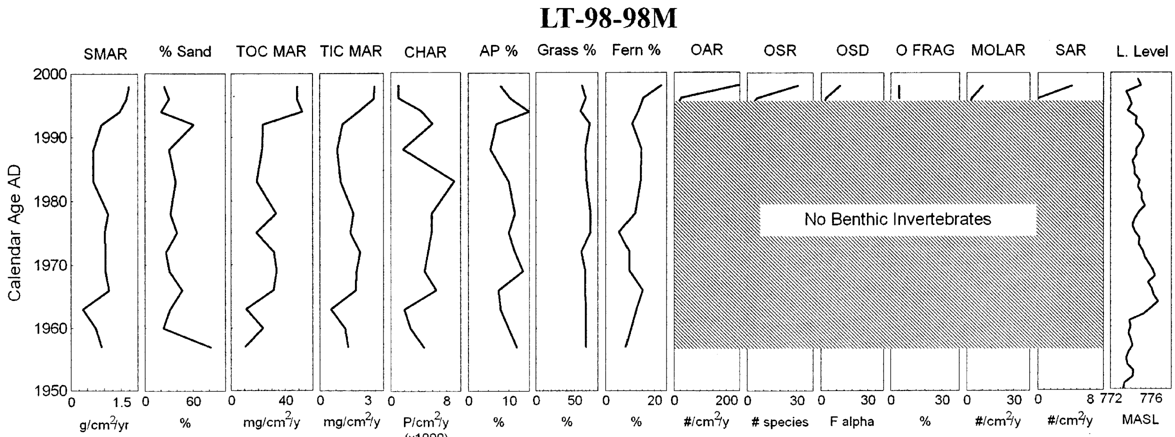

Figure 6. Composite chronology for key paleoenvironmental variables from core LT-98-98M (Nyamuseni River delta, northern Burundi, very highly disturbed watershed). Abbreviations as in Figure 1.

samples, where some shell material contributes to the total.

The core displays relatively constant charcoal concentrations and accumulation rates that gradually rise to a peak in the ~1980s, probably reflecting the timing of peak human-induced burning (Palacios-Fest et al. 2005a). This peak was followed by a sharp decline into the ~1990s. The pattern of increasing charcoal accumulation rates preceding increased sediment mass accumulation rates, as observed in this core, is also recorded in the other disturbed sites previously discussed. The palynological record shows gradually increasing fern spore abundances after the ~1970s, rising sharply in the ~1990s (Msaky et al. 2005). Arboreal and grass pollen concentrations do not vary systematically over this time interval.

For most of the past ~50 years, there are no benthic invertebrate fossils encountered on the Nyamuseni River delta record, demonstrating extremely high levels of ecological disturbance, which are almost certainly associated with the extraordinarily high rates of sediment inundation that invertebrates would experience in this area (Palacios-Fest et al. 2005b). Remotely operated vehicle (ROV) observations from northern Burundian deltas (Alin et al. 1999) show that these habitats are currently dysaerobic, with extremely unstable and water-rich sediment surfaces at the sediment water interface, as a result of high organic matter concentrations. Invertebrate fossils occur only in the late-1990s sediments, comprising a low diversity assemblage of disturbance-tolerant species. However, the high proportions of adult ostracodes and ostracode carapaces (anomalous for this water depth) suggest this assemblage may be transported.

Core LT-98-82M (3.5835° S, 29.3252° E). Karonge/Kirasa River, northern Burundi (very high disturbance watershed) (Figure 7)

Core LT-98-82M, collected in 96 m water depth, covers an interval of about 250–300 years, providing us with a longer-term environmental history from the currently highly disturbed northern Burundian portion of the lake than the LT-98-98M record. Although the coring site is offshore from the combined Karonge/Kirasa river delta, both the bathymetric profiling and some palynologic evidence (presence of *Acacia* pollen, uncommon in the local watershed but abundant in the Ruzizi River plain) suggest an input of at least some Ruzizi River sediment to this site (Cohen et al. 2005; Msaky et al. 2005). The Ruzizi River, whose delta lies ~30 km northwest of the coring site, drains a much larger watershed down the axis of the rift valley.

Much of core LT-98-82M is laminated, and lamination frequency increases upcore. The coring site lies within the currently oxygenated zone of the lake in this area. However, the ROV study mentioned above, off the Karonge River mouth, has shown that laminated sediments are accumulating in oxygenated waters where sediment accumulation rates are too high to allow bioturbation to efficiently disturb the sediment mass (A. Cohen

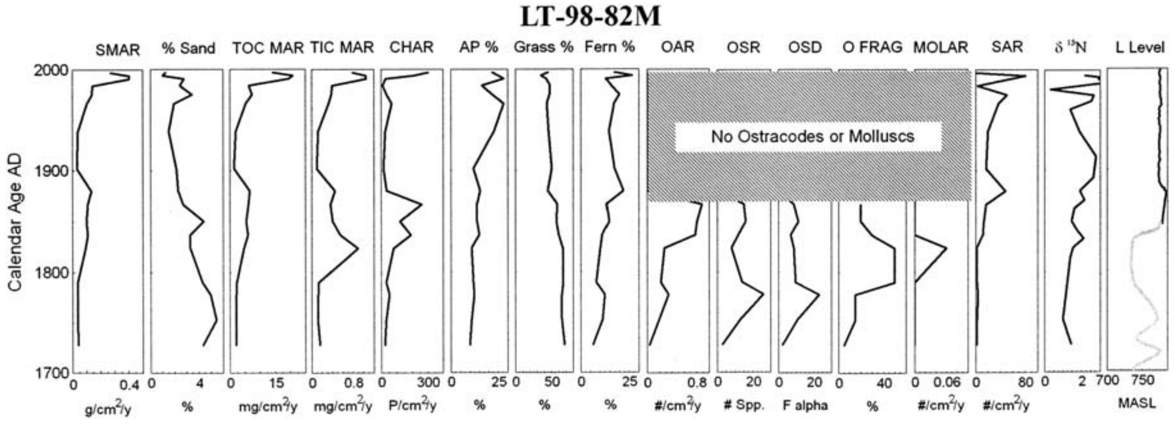

Figure 7. Composite chronology for key paleoenvironmental variables from core LT-98-82M (Karonge/Kirasa River delta, northern Burundi, very highly disturbed watershed). Abbreviations as in Figure 1.

pers. observ.) In fact, the ^{210}Pb profile from core LT-98-82M shows a remarkable record of sediment accumulation rates increasing 10-fold during the late-20th century (McKee et al. 2005), consistent with earlier work at the same area (Wells et al. 1999). Mass accumulation rates display an earlier episode of increased rates in about the mid- to late-19th century as well, which declined to much lower levels in about the early-20th century before rising again in the mid-20th century.

Sediment grain size generally decreases upcore, with reversals occurring at times of increasing sediment accumulation rates (Palacios-Fest et al. 2005a). TOC concentrations remain relatively constant through the core, whereas TIC is low and shows declining values. However, these are largely the result of background sediment dilution: when normalized for accumulation rates, both TOC and TIC input per unit time can be seen to have changed substantially over the core interval, probably the result of rising primary productivity and terrestrial plant debris input. As with the other terrigenous sediments and charcoal, peak accumulation rates occur in about the mid-19th century and again after ~1960, with a notable decline in about the early-20th century. Nitrogen isotope records show a trend toward more positive $\delta^{15}N$ values starting in about the early-19th century, with values consistently indicative of high input rates of soil nitrogen and/or sewage after that time (O'Reilly et al. 2005).

The commonly observed trend of decreasing grass pollen, increasing arboreal pollen, and increasing pteridophyte spores is evident in LT-98-82M, although here the change occurs in the early-19th century, much earlier than in other cores (Msaky et al. 2005). Starting in about the late-19th century we observe notable increases in low-elevation euphorbs, and after about 1930 a rise of Myrtaceae pollen, probably from the planting of many eucalyptus trees in Burundi starting at that time.

Prior to the ~1860s a low diversity assemblage of sedimentation-tolerant ostracodes occurs in core LT-98-82M (Palacios-Fest et al. 2005b). However, ostracodes, along with mollusk and fish fossils, are entirely absent from the core record for approximately the past 140 years. Taphonomic indications in the fossils at the base of the core suggest that even this assemblage was made up of reworked fossils and was not a life assemblage representative of conditions at the time of deposition. As with other moderately and highly disturbed sites, there is an upcore increase in sponge spicule accumulation rates, again contemporaneous with other rising indications of disturbance since about the early-19th century for this area of the Lake Tanganyika coastline.

Comparisons among coring sites and regions

The cores investigated in this study collectively provide evidence for significant differences in the watershed environmental history and lacustrine ecological response between the various Lake Tanganyikan watersheds investigated in our study. Some of these differences are associated with apparent climatic changes, some with local land use and land cover changes, and some with regional patterns of disturbance in the lake's catchment that override the detailed history of individual watersheds.

Differences related to climatic change

1. Sediment mass accumulation rates prior to the 18th century: Two locations, the Lubulungu and Mwamgongo deltas, provide us with pre-18th century records covering times of significant climatic change. Surprisingly, sediment accumulation rates at both appear to be lower during century-scale intervals when climate was more humid and higher when climate was more arid. However, it is important to note that even the highest accumulation rates observed during these apparently climatically driven increases in accumulation rates are 3–10 times lower than the rates encountered in disturbed watersheds during the 20th century. Sedimentation rate studies around Lake Tanganyika also yield variable results with respect to climate. Elsewhere we have found strong evidence for increasing sediment discharge associated with increased runoff at multidecadal time scales (Cohen et al. 2001). These differences in sediment accumulation rate response may be linked to differences in slope, original vegetation type, or bedrock lithology.
2. Charcoal accumulation: We record abundant evidence, in the form of higher charcoal accumulation rates, for increased fire activity during the

regionally arid, latter portion of the Little Ice Age (16th to early-19th century), consistent with other regional evidence for aridity at the same time. These patterns occur irrespective of a given watershed's current disturbance level, and there is considerable evidence for recovery from prior intervals of high fire frequency.

3. Lake level and water chemistry fluctuations: We observe abundant evidence for changes in lake level, manifest in both changing fossil assemblages and taphonomic indications of relative water depth. Lake level fluctuations are linked to hydrologic variability and P/E fluctuations within the Lake Tanganyika catchment. However, given the size of this catchment (spanning $\sim$1–10° S), lake level fluctuations may not be directly linked to local climate variability. In fact, we see evidence from contrasting lake level vs. local, terrestrial signals that climate changes have varied in different parts of the basin. The most likely source of this complication is the role of the upstream feeder Lake Kivu and its catchment, which has episodically overflowed into Lake Tanganyika depending on precipitation occurring well to the north of Lake Tanganyika. Lake Kivu is similarly important as a source of dissolved solids for Lake Tanganyika today, the system being unusual in that Lake Kivu is actually more saline and alkaline than the downstream Lake Tanganyika (Haberyan and Hecky 1987; Cohen et al. 1997). Counterintuitively, the closure of Lake Kivu therefore results in a solute deficit in Lake Tanganyika and much lower calcium carbonate availability, both for authigenic carbonates and the formation/preservation of shell-bearing invertebrates.

4. Primary productivity changes linked to water column stratification and climate: We see evidence in carbon isotope records from a number of our cores for a $\sim$20% decline in primary productivity of Lake Tanganyika since the early-20th century, a trend that accelerated in the late-20th century (O'Reilly et al. 2003). These stable isotope data are consistent with instrumental observations of rising temperatures, declining wind speeds and reduced fish catches over the same time period. We infer that rising epilimnetic temperatures in Lake Tanganyika, along with lower windiness during the 20th century, have resulted in more stable stratification of the water column, reducing the upwelling of deep-water nutrients and thereby reducing productivity of the lake.

Differences related to forested vs. deforested watersheds

1. Differences in sediment accumulation rates: Rates are much higher at present in the deforested watersheds. All deforested watersheds show sharp rises in sediment mass accumulation rates, which can be temporally linked to other indications of watershed disturbance, although, as discussed below, the timing of these mass accumulation rate changes varies between localities. In contrast, all undisturbed watersheds either show constant or, in some cases, declining sediment accumulation rates over the same intervals.

2. Differences in erosional and hydrological products: Core sediments from highly disturbed sites typically show evidence for profound compositional changes, such as increased concentrations of lateritic soil particles, lamination, and terrestrial plant debris relative to undisturbed sites. Sediments from disturbed watersheds show more positive $\delta^{15}N$ isotopic values, and these values increase in a manner consistent in timing with other indications of disturbance. No such trend is observed in the $\delta^{15}N$ record from the undisturbed LT-98–58M Nyasanga/Kahama site. Modern hydrological studies of disturbed vs. undisturbed watersheds indicates higher proportions of groundwater infiltration and evapotranspiration in forested watersheds, and conversely more rapid discharge, with increased proportions of overland flow, in deforested watersheds. This is manifested in more enriched $\delta^{18}O_{water}$ values in forested watersheds. The limited oxygen isotope data from fossils that grew within the zone of hydrologic influence of influent rivers suggests that such enrichment/depletion isotope signals can be transmitted to carbonate $\delta^{18}O$, resulting in a pattern of falling $\delta^{18}O$ during periods of deforestation.

3. Differences in faunal community structure related to sediment inundation: Our results show that high diversity ostracode assemblages are associated with low disturbance areas and that low diversity assemblages are associated with the highest levels of disturbance. At the extremes of disturbance, as in Northern Burundi, where relatively large watersheds discharge vast quantities of sediment onto broad depositional platforms, this can result in apparent extirpation of benthic, deltaic communities. There are clear associations of

particular taxa with high disturbance levels, and these species can be shown to become more common under increasingly disturbed (i.e., with more rapidly accumulating sediment) conditions. One of our cores, LT-98-18M, shows this transition well and its temporal links with watershed alterations. However, high levels of watershed disturbance may not translate into signs of community disturbance if the watersheds are very small or if the sub-lacustrine slopes are very steep. On the Mwamgongo delta, where the watershed is small and the sublacustrine slope relatively steep, short-term sediment accumulation may be limited by either total supply or the short-term nature of the storage. Here the ostracode diversity history differs little from the nearby paired/undisturbed delta of the Nyasanga and Kahama rivers. Although it is clear from the work of O'Reilly (2001), Alin et al. (2002) and others that the shallow lacustrine communities and ecosystems at Mwamgongo are qualitatively different from those of nearby areas inside of Gombe Stream National Park, it is less clear that these littoral impacts translate into major effects in deeper water downslope (at our coring sites). In this regard, it may be significant that sponge spicule accumulation rates are strongly correlated with disturbance levels for all sites. As explained by Palacios-Fest et al. (2005b), this seemingly counterintuitive result is probably best explained by a decline in top-down predation rates in highly disturbed deltas, where littoral, invertebrate-grazing fish populations are significantly diminished.

Differences related to regional patterns of deforestation-palynological profiles

The timing of transition to greatly elevated fern spore abundance, our most unambiguous evidence for disturbance, varies between regions of the lakeshore. The earliest evidence for this rise is in northern Burundi, where fern abundance rises significantly starting in about the late-18th century. In northernmost Tanzania, the rise begins in about the late-19th century. Moving farther south, the Nyasanga/Kahama River (undisturbed site) core records this shift in about the early-20th century, and the Kabesi River (central Tanzania) records the shift in about the mid-20th century. The Lubulungu River undisturbed site, our southernmost locality, does not show a significant rise in fern spores above background levels up to the present. It is noteworthy that this signal of disturbance is evident in the Nyasanga/Kahama record, despite the modern protected status of this watershed. This suggests both a regional advance in disturbance from north to south over the past ~250 years and a spatial averaging of readily transported components of the record, such as fern spores, that blankets local differences in the history of smaller watersheds. Low-elevation euphorbs, which are also common in disturbed areas, show a similar historic and geographic pattern to the ferns.

The most puzzling results of our palynological investigations are the trends towards increased arboreal pollen and decreased grass pollen over the last few centuries. The diachronous timing of this pattern is broadly similar to that of fern spore increases (i.e. earlier in the north). These findings are counterintuitive given that all other indications of landscape alteration point toward more erosion and presumably less forest cover, starting in about the late-18th to early-19th century in the north of the Lake Tanganyika catchment and sweeping south over time. As discussed by Msaky et al. (2005), a likely explanation of this finding comes from the observation that most subsistence farming systems adopted in the region after land is cleared involve the initial replacement of low-elevation grassy *Miombo* woodlands with well tended but unterraced hillslope farming of cassava and valley bottom production of bananas and oil palm. None of these replacement crops generate abundant pollen. Goats, which are a major part of the post-deforestation landscape, and are allowed to roam freely in most farm areas, probably consume most grasses before they flower, limiting grass pollen production. Thus, pollen rain in post-deforestation landscapes would be increasingly dominated by wind-blown arboreal pollen derived from remaining, forested, high mountain areas in the region. A second likely source of arboreal pollen in post-disturbance records is the eroded soil itself, which would provide a reservoir of pollen grains dominated by tree species while the living sources themselves are depleted.

One notable and major exception to the north to south trend in arboreal and grass pollen proportional changes comes from the southernmost area, the Lubulungu Delta, on the west side of the

Mahale Mountains. This undisturbed site (core LT-98-12M) records a gradual and long-term decline in grass pollen and increase in arboreal pollen starting in about the 18th century. This site is unique in that it is the only place where this transformation is not accompanied by rising fern spore abundance. This watershed today also experiences the highest precipitation of any studied region ($\sim$1600–1800 mm yr^{-1} vs. $\sim$1000–1200 mm yr^{-1} for all other areas at the lakeshore elevation). Given these observations, the most likely explanation of the long-term palynological trend at LT-98-12M is that it reflects the actual conversion of the landscape from a drier, woodland condition during the latter Little Ice Age to the evergreen-forested landscape that occurs in the western Mahale Mountains today.

Differences related to interactions of deforestation and climate effects – Sediment accumulation rates, charcoal, palynology and lake faunal response associated with the early-1960s event

One of the truly striking features of our combined records is the coincidence of changes in numerous variables indicating accelerated disturbance after about the early-1960s. The pattern is observed in all disturbed locality cores. With the exception of palynological and charcoal indicators at the Nyasanga/Kahama site, which arguably represent longer distance transport by flotation or wind, these signals are also absent in all undisturbed sites. Two hypotheses can be forwarded for this timing. First, it is possible that some regional change in land-use patterns occurred at that time, perhaps associated with the end of colonial rule, which dates approximately from this era. This explanation seems unlikely to us, since there are no historical records of such a change occurring, and since the land-use and tenure systems varied considerably between Tanzania and Burundi, despite the fact that the pattern is observed in cores from both countries.

A more likely explanation of the pattern involves a combination of climatic and anthropogenic causes. 1961 was a record wet year in East Africa (Nicholson 1999), with high water levels recorded in almost all lakes and gauging stations, as illustrated by the lake level curve in Figure 6. Although the sustained mid-20th century increase in sediment accumulation rates is ultimately a likely consequence of increased erosion rates on cleared farmland, it is uncertain how efficiently or quickly this sediment is delivered to Lake Tanganyika. Soil erosion rates were probably accelerating during the early- to mid-20th century in many heavily populated watersheds of the northern Lake Tanganyika catchment as a result of both rising human populations and the expansion of cassava cultivation (G. Maddox pers. comm. 2004). The latter development may be of particular importance since cassava is one of the few crops that can be effectively raised on the very steep slopes common to many Lake Tanganyika watersheds, and based on experimental studies in the region its planting is known to generate extraordinary acceleration in soil erosion (Bizimana and Duchafour 1991). Although it is a staple in the region today it was apparently not an important crop prior to the early 20th century. However, much of the sediment generated by local hillslope erosion goes into temporary alluvial storage in river valleys, and we do not see a gradual rise through the early 20th Century in sedimentation arriving at the lake but rather an abrupt change many years after cropping practices had begun to change. This suggests that a 'triggering mechanism' was required to stimulate sediment delivery to the lake. Extraordinary rainfall events are known to have such effects on alluvium, incising head cuts in soft alluvial sediments that propagate themselves upstream after the initial incisions are made. Greatly increased landslide activity occurred during the most recent strong ENSO wet season (1997/98) in the deforested watersheds around Lake Tanganyika, apparently the result of very rapid infiltration along exposed fault and gouge surfaces. This suggests that several mechanisms may link climate triggers to increased susceptibility of higher sediment discharge in deforested areas. Thus, a combination of anthropogenic and climate forcing is the most likely explanation for the coincidence of the early-1960s timing of accelerated sediment accumulation rates and the development of the unprecedented (for the past $\sim$300–400 years) rates of sedimentation observed along much of the northeastern Lake Tanganyika coastline today. This type of sediment storage may also help explain the lag of up to several decades between rising charcoal accumulation rates and terrigenous sediment accumulation rates that we observe in a number of our cores from disturbed sites.

Discussion

The results of this mulit-disciplinary study provide strong support for climate change, human activity, and the interactions between climate and land use, as driving mechanisms explaining the environmental history of the Lake Tanganyika catchment over the past millennium. Climatic controls are most strongly expressed in evidence for varying lake levels and extent of aridity, particularly for the arid latter part of the Little Ice Age and the transition to wetter climate conditions in the mid-19th century. Climate effects are manifested as near-synchronous events over the geographic scale of coverage of this study ($\sim$300 km north to south). However, lake-level fluctuations are decoupled from 'local' climate variability because of the strong influence that the northern portion of the Lake Tanganyika catchment, around Lake Kivu, can have on the Lake Tanganyika water budget. Our data imply that climate histories in the Kivu catchment may not be completely synchronous with those farther south, around the Lake Tanganyika coring sites.

Evidence for human-induced deforestation and its ecological consequences within Lake Tanganyika implies much earlier deforestation in the Burundian and northern Tanzanian coastal regions of the lake than along the central Tanzanian coast. This is consistent with what is known of the demographic history of human settlement in the study regions prior to the colonial period. Linguistic evidence points to a long history of well-defined cultural groups, and probably relatively high human population densities in what are now Burundi and northern Tanzania, probably stretching back at least several millennia (Schoenbrum 1998; Chrétien 2003). Archaeological data from many of these areas provides strong evidence that human-induced deforestation was widespread starting as early as $\sim$2500 years ago, primarily associated with demands for charcoal from iron production (e.g. Schmidt 1997).

Oral histories show that centralized rule under a long series of Burundian kings was established by the late-17th century (Lemarchand 1970; Chrétien 2003). More localized kingdoms were established in the Buha region of what is now northern Tanzania (the Kalinzi/Ujiji area) by the early- to mid-19th century (McHenry 1980; Wagner 1996 and pers. comm.) (Figure 8a). Records for the Mahale Mountains region are extremely limited but the low population densities of this area today, coupled with its general remoteness from lines of trade, suggest it was probably sparsely inhabited during the 18th and 19th centuries. The first organized caravans for slaves and ivory trade reached the Lake Tanganyika shoreline in the 1830s, probably exploiting older salt trading routes (Koponen 1988) (Figure 8b). The terminus for this trade at the lakeshore was either the Ujiji/Kalinzi area of northern Tanzania (just south of modern Kigoma) or slightly to the south, near the Malagarasi River mouth. The caravan trade was facilitated in the Kalinzi–Ujiji area by the agreements with the local mwami (king) (Wagner 1996) creating an important route for the rapid transmission of disease, especially cholera and smallpox epidemics, across Tanzania at this time. These epidemics led to a significant decline in human population in much of western Tanzania during the early- to mid-19th century (Koponen 1988). By the 1860–1890s, ivory trading, and therefore elephant depopulation, reached its peak in western Tanzania.

The combination of rampant disease, the effects of major reductions in elephant populations, slave raiding, and the widespread famines reported in western Tanzania from the 1860–1870s, all would have hastened the expansion of forest cover in less settled areas (Stanley 1878; Koponen 1988). Although slavery was legally outlawed in Zanzibar in the 1870s, the slave trade continued in the eastern Congo, and caravans continued to cross Lake Tanganyika to Ujiji until at least the late-1880s. In fact, slaves were acquired in great numbers by the Kalinzi mwami and his clans, to the extent that by the late 1880s, the majority of the inhabitants of Ujiji were slaves (Koponen 1988). Human population probably rose locally in the immediate vicinity of Ujiji and the Luiche River valley, as slaves were gathered from the eastern Congo to help in agricultural production necessary to support the western caravan routes (G. Maddox pers. comm. 2004). Stanley's (1878) accounts suggest a population in Ujiji proper at 3000 in 1878 and 36,000 in the Luiche River valley

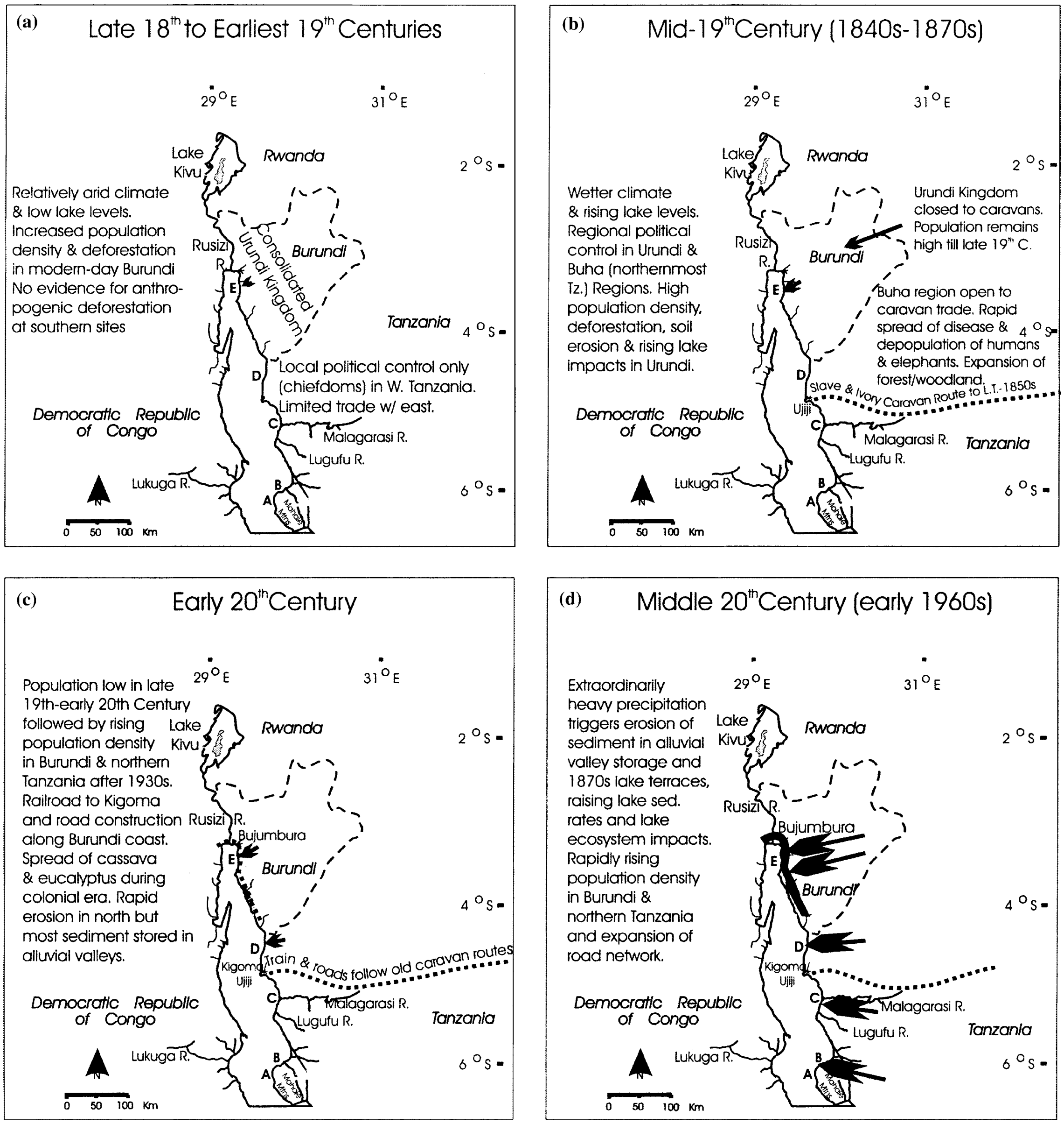

Figure 8. Summary maps of demographic and environmental history around northern Lake Tanganyika. Letters on maps indicate coring areas A: Lubulungu R. delta (LT-98-2M and 12M); B: Kabesi R. delta (LT-98-18M); C: Malagarasi R. delta (LT-97-14V); D: Nyasanga/Kahama and Mwamgongo R. deltas (LT-98-58M and 37M); E: Nyamuseni and Karonge/Kirasa R. deltas (LT-98-98M and 82M). Arrows indicate the approximate location and relative scale of enhanced sedimentation inputs to Lake Tanganyika and associated ecological impacts. Lines along the Burundi and northern Congo coastline in panels C and D indicate expanding road network.

hinterland (~15 people/km^2). Unfortunately we do not have any paleolimnological records from this area to determine the timing of deforestation in that watershed. However, Stanley reported that areas only a few tens of kilometers away from Ujiji were heavily forested at the same time. Control by the Buha mwamis extended north along the Tanzanian coast as far as the Nyasanga/Kahama area. It is significant for this study that Nyasanga was the frontier of Buha territory at this time (Burton 1860). Mwamgongo, just a few kilometers to the north, was under the control of Burundian princes (ganwas), who strongly discouraged contact with outsiders, especially the caravan traders.

Early European explorers in the region report numerous local wars, abandoned villages, and other evidence of depopulation during the mid-late 19th century (Bennett 1970; Koponen 1988), and by the 1880s, when the first Catholic missions were established along the Tanzanian coast of Lake Tanganyika, even Ujiji appears to have been largely depopulated (Koponen 1988). Overall, evidence points to a stagnating or locally declining human population throughout the central coastline regions of Tanzania through the late 19th century, culminating in devastating human and livestock population declines with the Rinderpest outbreak of the 1890s. The regional trend of population was not truly reversed until about the 1930s (Koponen 1996) (Figure 8c). More remote areas further south, such as our study area, the Kabesi River valley on the north coast of the Mahale Mountains, were probably never settled in large numbers during the 18th and 19th centuries. These areas experienced rising human populations even later in the 20th century.

In contrast, the Burundian watersheds feeding Lake Tanganyika were occupied by a population that, during the 18th to early-19th centuries, was coming under increasing control of the highland kings, culminating with the accession to power of Mwami Ntare in the 1850s (Lemarchand 1970; Gahama 1983). Areas along the Lake Tanganyika coast in Burundi were probably only indirectly controlled by the mwami, either through networks of local ganwa, or by non-ganwa chiefs allied with the mwami (Mworoha 1977). But the net result was a hierarchichal rule that could exert control, either directly or indirectly, over large areas, greatly reducing interaction with the coastal caravan traders. Although some Swahili caravan settlements existed in a few locations along the Burundi coast, these traders were effectively blocked from penetrating into the heavily settled hinterlands of Burundi, where the highest population densities in watersheds like the Karonge, Kirasa and Nyamuseni would have resided (Chrétien 2003). This, in turn, may have insulated these people during most of the 19th century from the depopulating effects of imported disease and slave raiders. Certainly, as mentioned above, caravan traders were strongly discouraged, or even attacked, when they tried to land along the 'Burundian' coast, anywhere north of Nyasanga up to the Rusizi River (Burton 1860). The earliest European missionaries who attempted to settle along the Burundi coast (at Rumonge) were killed in 1881 (Lemarchand 1970). As a result, there are no written accounts from European explorers or Arab traders of the Burundian coastline from the early to mid-19th century. However, when the Austrian explorer Oskar Bauman visited the Burundian coastal region in 1892, he already noted very dense human populations and extensive deforestation (Gahama 1983). The much earlier establishment of indirect control by the Burundian mwamis, and the exclusion of the caravan trade, with its many vectors of human depopulation, all suggest that high population density and deforestation were features of the Burundian and northernmost Tanzanian landscape long before these conditions existed along the west-central Tanzanian coast. This is consistent with the general timing of our records of watershed disturbance from both Mwamgongo and the northern Burundi watersheds.

At the very end of the 19th and during the early-20th centuries, regional outbreaks of human and cattle diseases (especially the infamous Rinderpest outbreak) affected much of central Africa. This resulted in massive depopulation in many formerly heavily populated areas such as Burundi, and hastened the decline in Tanzania. For example, it is estimated that Burundi did not attain the same population it had in the 1880s ($\sim$2 million) until 1950 (Chrétien 2003). It is noteworthy, therefore, that our single long sediment record from northern Burundi shows a major decline in deforestation and land disturbance indicators between the late19th through the mid-20th centuries.

Numerous records indicating an acceleration of watershed disturbance throughout the disturbed Burundian and Tanzanian study areas since the mid-20th century are also consistent with regional demographic trends. A lakeshore road running the length of the Burundian coastline was first constructed in the 1920s (Gahama 1983). This road facilitated human resettlement, development of large-scale agriculture along the coastal plain, and woodcutting throughout the coastal watersheds, all of which must have generated substantial new land disturbance. Furthermore, road construction itself is thought to generate enhanced sediment discharge in the Lake Tanganyika catchment (Donohue et al. 2003). By the 1930s population densities in the

Bujumbura area had reached about 45 people/km^2 (Gahama 1983). As discussed earlier, it may also be significant that cassava production does not appear to have been widespread in the region until the early-mid 20th century (McCurdy 2000; G. Maddox pers. comm. 2004). For example, in descriptions of Ujiji market trade in the mid 1870s, Stanley (1878) noted that cassava was an imported product from what is now the Congo (across Lake Tanganyika) and was not grown in what is now northern Tanzania or Burundi in significant quantities. Cassava is one of the few crops that can be successfully grown on very steep and nutrient-depleted soils in this region, and its successful introduction into the local economy may have accelerated soil erosion from steeply sloping areas, which had previously been unprofitable for farming. Its expansion as a food crop in Burundi was particularly promoted by the British and Belgian colonial authorities after the 1920s (M. Wagner pers. comm. 2004). However, the largest sediment accumulation rate increases in nearshore deltaic environments occurred in both Burundi and Tanzania after the 1950s Lemarchand 1970; Koponen 1996; Maddox 1996). By the early-1960s, when we observe the widespread spike in sediment accumulation rates, deforestation was probably widespread throughout much of the Burundian and northern Tanzanian coastline. Excess sediment that had accumulated in deforested alluvial valleys throughout the region would have been readily available for secondary erosion into Lake Tanganyika following the extraordinary floods of 1961 (Figure 8d).

In addition to documenting the timing of terrestrial changes in deforestation around Lake Tanganyika, our other goal in this project was to interpret the lake's ecological responses to these inferred disturbances. Our data suggest that there may be predictable linkages between landscape disturbance and lake ecological response that have important implications for how Lake Tanganyika and its catchment are managed.

First, the pattern of rapid local extinction and increase in the abundance of a small number of sedimentation-tolerant species we observe in the LT-98-18M record through the disturbance interval is consistent with earlier ecological models of Lake Tanganyika endemic species distribution based on modern observations (Cohen 2000; Michel et al. 2004). These models suggest that the 'populations' of many endemic invertebrates are actually organized as 'metapopulations', with extremely patchy and disjunct distributions of relatively small local populations. The long-term viability of these metapopulations may be dependent on regular recolonization of appropriate habitats by nearby founder populations. If excess sedimentation along major segments of the coastline becomes a barrier to recolonization to sediment-intolerant species, then population-level (and ultimate species-level) extinction can occur. This implies that lake conservation management strategies should strive to reduce sediment impacts along lake shore margins which are long enough to encompass multiple founder populations of the target species for conservation.

Second the northern Burundian coastline, where we observe the most severe impacts, has probably been particularly susceptible to sedimentation-generated disturbance because it experiences two aggravating factors. First, watersheds are relatively large, and thus capable of delivering large quantities of sediment to what are effectively point-source outlets (delta distributary discharge points), even if no disturbance were occurring. Second, underwater slopes along the Burundi coast are relatively gentle, encouraging short-term storage and accumulation. If the Rusizi River has been a long-term contributor to the sediment budget of the northeast part of the lake, it is predictable that this slope factor would become more aggravated as one moves further north in this region, whereas the watershed area factor would be more variable. If this hypothesis of enhanced vulnerability is correct, then particular attention should be paid to geomorphically similar parts of the lake basin which have not yet experienced such pervasive settlement, road construction and cultivation, particularly at the south end of the lake and on the major platform regions (South Malagarasi, in the Halembe area and the Ikola Platform). Mitigating problems associated with accelerated erosion in such areas will be a daunting challenge if they become highly disturbed in the future.

Conversely, the threats to lake systems are probably reduced in areas of steep slopes and small watersheds. Places like the Mwamgongo watershed are unlikely to generate the quantities of sediment required to impact large areas, and enhancement of sediment storage in the sublittoral zones may be relatively subdued or non-existent. Donohue et al. (2003) have argued that deforestation of 'small' watersheds around Lake Tanganyika may pose a much greater risk than large ones, in contradiction to what we suggest here and what one of us has argued elsewhere (Cohen et al. 1993b). Their study, based on a paired drainage comparison of the Kalambo River (2980 km^2) vs. the Lunzua River (1015 km^2) watersheds, indicated approximately 5-fold higher sediment yields in the smaller watershed, which they attribute largely to greater sediment retention capacities of larger watersheds. The 10-fold higher road density in the smaller watershed (measured as road meters/km^2 watershed area) makes a comparison of the two watershed's behaviors difficult to compare as a function of watershed size difficult. Furthermore, the size of both of these watersheds is actually quite large in comparison with the types of watersheds we are referring to as 'small' in this study (i.e. under 10 km^2). The latter type of watershed is extremely abundant along the major border fault escarpments of Lake Tanganyika, and it is these types of drainages that we would argue pose a lesser threat to lacustrine biodiversity when they become deforested. Clearly threats will exist in front of such watersheds to the littoral zones directly adjacent to the river discharge point when erosion rates accelerate, as shown by our Mwamgongo River data. However, these problems must be placed in context with the far more serious threats posed by disturbance in the more vulnerable large watersheds and gently sloping regions of the lake. An historical approach, such as we have taken here, demonstrates that it is precisely the large sediment retention capacity of larger, flatter watersheds that can make such areas vulnerable to massive sediment discharges when alluvium is remobilized by downcutting following extreme precipitation events.

Summary

Paleolimnological investigations of the Late Holocene history of Lake Tanganyika, Africa provide a record of the interactive impacts of human activities and climate change on the lake and its surrounding catchment. Our multidisciplinary studies of sediment accumulation rates, sedimentology, lacustrine paleoecology, palynology, organic and inorganic isotope geochemistry and hydrology demonstrate that strong historical differences exist between histories of currently disturbed and undisturbed watershed histories. Furthermore these differences can be interpreted in light of differences in the human demographic and environmental histories of Burundi and western Tanzania. In some areas, notably the northern watersheds of the lake, evidence of extensive deforestation greatly precedes the major population increases of the 20th century. However, several 20th century events probably played pivotal roles in accelerating the rate of soil erosion and causing erosional products to inundate many nearshore regions of the lake. These events include the large scale expansion of cassava cultivation (which can be grown on very steep and easily erodable slopes), starting in the early part of the 20th century, the expansion of lake-margin road construction in Burundi, and the extraordinary rainfall events of the early 1960s, which accelerated the delivery of previously trapped alluvium into the deltas of heavily impacted watersheds. Climatic events (arid-wet cycles) and lake level fluctuations prior to the 19th century also influenced sediment accumulation rates, palynology and lacustrine paleoecology However the magnitude of these effects was well below what is observed from the 20th century.

The impacts of these greatly increased sediment accumulation rates along the shorelines of deforested watersheds are evident from the lacustrine paleoecological records of our core sites. Declines in the diversity of rare species, or even wholesale elimination of significant portions of the lacustrine biota are apparent from the ostracode crustacean records of moderately to very highly impacted watersheds. We also observe evidence for top-down ecological impacts at heavily impacted deltas in the expansion of sponges whose abundances are normally controlled by grazing fish.

Our findings provide strong implications for future environmental management and conservation strategies at Lake Tanganyika and its catchment. We observe rapid (decadal time scale) local extinction of invertebrate species from heavily sedimented portions of the lake's littoral zone. This observation, coupled with earlier evidence that many species of fish and invertebrates in Lake Tanganyika have patchy distribution patterns, and are probably organized as loosely interacting metapopulations, suggests that conservation

strategies for the lake's extraordinary biota may require significant interconnectedness between unimpacted stretches of the coastline in order to be effective in forestalling endemic species extinction. Our comparative data of impacts at watersheds of varying size also suggests that large watersheds feeding onto relatively gently sloping lake floor areas are the zones of the lake at greatest risk from sedimentation impacts. Watershed management strategies whose primary goal is protection of Lake Tanganyika's lacustrine biodiversity should pay particular attention to areas such as the southern Zambian coastline or the south Malagarasi and Ikola platforms of the lake, which have these types of geomorphic characteristics, but whose watersheds are still relatively lightly populated.

Acknowledgments

We thank the Lake Tanganyika Biodiversity Project (LTBP) for major funding for this research, and especially the assistance of Drs Andy Menz, Graeme Patterson and Kelly West of LTBP for facilitating the work described here. Additional funding came from the US National Science Foundation (NSF Grant #s EAR 9510033, ATM 9619458 and ATM 0223920). We also thank Greg Maddox, John Smol and Bill Last, who all read and critiqued earlier drafts of this manuscript and Anthony Collins, for freely sharing his insight and knowledge of recent environmental history of the Lake Tanganyika coastline. This is contribution #172 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. Palaeogeogr. Palaeoclimatol. Palaeoecol. 199: 31–49.

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., Kimbadi S. and Ntakimazi G. 1999. Effects of landscape disturbance on animal communities in Lake Tanganyika. Conserv. Biol. 13: 1017–1033.

Alin S.R., O'Reilly C.M., Cohen A.S., Dettman D., Palacios-Fest M. 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.

Bennett N.R. (ed.) 1970. Stanley's Despatches to the New York Herald, 1871–1872, 1874–1877. Boston University Press, Boston 508 pp.

Birkett C., Murtugudde R. and Allan T. 1999. Indian Ocean climate event brings floods to East Africa's lakes and the Sudd Marsh. Geophys. Res. Lett. 26: 1031–1034.

Bizimana M. and Duchafour H. 1991. A drainage basin management study: The case of the Ntihangwa River Basin. In: Cohen A.S. (ed.), Report of the First International Conference on Conservation and Biodiversity of Lake Tanganyika. Biodiversity Support Program, Washington, DC, pp. 43–45.

Burton R.F. 1860. (1995 Dover reprint). The Lakes Regions of Central Africa. Harper Bros, NY, 572 pp.

Chrétien J.-P. 2003. The Great Lakes of Africa, Two Thousand Years of History. Zone Books, NY, 503 pp.

Clutton-Brock T.H. and Gillett J.B. 1979. A survey of forest composition in the Gombe National Park, Tanzania. Afr. J. Ecol. 17: 131–158.

Cohen A.S. (ed.) 1991. Report on the First International Conference on the Conservation and Biodiversity of Lake Tanganyika. Biodiversity Support Program, Washington, DC, 128 pp.

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. Advances in Ecological Research, Vol. 31. Academic Press, San Diego, CA, pp. 521–537.

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., 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. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: I. An introduction to the project. J. Paleolimnol. 34: 1–18.

Cohen A.S., Soreghan M.J. and Scholz C.A. 1993a. Estimating the age of formation of lakes: an example from Lake Tanganyika. Geology 21: 511–514.

Cohen A., Kaufman L. and Ogutu-Ohwayo R. 1996. Anthropogenic threats, impacts and conservation strategies in the African Great Lakes – a review. In: Johnson T. and Odada E. (eds), The Limnology, Climatology and Paleoclimatology of the East African Lakes. Gordon and Breach Publishers, Newark, N.J, pp. 575–624.

Cohen A.S., Lezzar K.E., Cole J.E., Dettman D.L., Eagle M., Michelo V., Zilifi D., Chororoka K., Plisnier P.D. and Ellis G. 2001. Paleolimnologic evidence for decadal to centurial scale climate and productivity linkages in Lake Tanganyika. EOS Trans. Suppl. 82: F759.

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, 354 pp.

Dettman D., Palacios-Fest M.R., Nkotagu H.H. and Cohen A.S. 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., Duck R.W. and Irvine K. 2003. Land use, sediment loads and dispersal pathways from two catchments at the southern end of Lake Tanganyika, Africa: implications for lake management. Environ. Geol. 44: 448–455.
Evert M.J. 1980. Le lac Tanganyika, sa faune, et la peche au Burundi. Thesis Université du Burundi, Bujumbura.
Gahama J. 1983. Le Burundi sous adminstration Belge. Éditions Karthala, Paris, 465 pp.
Haberyan K.A. and Hecky R.E. 1987. The late Pleistocene and Holocene stratigraphy and Paleolimnology of Lakes Kivu and Tanganyika. Palaeogeogr. Palaeoclimatol. Palaeoecol. 61: 169–197.
Jolly D. and Bonnefille R. 1992. Histoire et dynamique du marécage tropical de Ndurumu (Burundi), données polliniques. Revue Palaeobot. Palynol. 75: 133–151.
Koponen J. 1988. People and production in late precolonial Tanzania. Monogr. Finn. Soc. Ofr Devel. Studies 2, 434 pp.
Koponen J. 1996. Population, a dependent variable. In: Maddox G., Giblin J. and Kimambo I.N. (eds), Custodians of the Land, Ecology and Culture in the History of Tanzania. Ohio University Press, pp. 19–42.
Lemarchand R. 1970. Rwanda and Burundi. Praeger Publishers, New York, 562 pp.
Lowe-McConnell R.H., Crul R.C.M. and Roest F.C. (eds) 1992. Symposium on Resource Use and Conservation of the African Great Lakes, Bujumbura 1989. Soc. Int. Limnol. Mitt. v. 23.
Maddox G. 1996. Environment and population growth. In: Maddox G., Gilpin J.L. and Kimambo I.N. (eds), Custodians of the Land. Ohio University Press, pp. 43–65.
McCurdy S.A. 2000. Transforming associations: fertilities, therapy, and the Manyema Diaspora in urban Kigoma, Tanzania, c. 1850–1993. Ph.D. Dissertation, Columbia University.
McKee B., Cohen A.S., Dettman D.L., Palacios-Fest M.R., Alin S.R. and Ntungumburanye G. 2005. Paleolimnological investigations of anthropogenic change in Lake Tanganyika: II. Geochronologies and mass sedimentation rates based on ^{14}C and ^{210}Pb data. J. Paleolimnol. 34: 19–29.
McHenry D.E. 1980. Reorganization: an administrative history of Kigoma District. Tanzania Notes Records 84/85: 65–74.
Michel E., Todd J.A., Cleary D.F.R., Kingma I., Cohen A.S. and Genner M.J. 2004. Scales of endemism: challenges for conservation and incentives for evolutionary studies in a gastropod species flock from Lake Tanganyika. J. Conchol. Sp. Publ. 3: 155–172.
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.
Mworoha E. 1977. Peuples et rois de l'Afrique des lacs. Abidjan, Dakar.
Nicholson S.E. 1998. Historical fluctuations of Lake Victoria and other lakes in the northern rift valley of East Africa. In: Lehman J.T. (ed.), Environmental Change and Response in East African Lakes. Kluwer Academic Publishers, Dordrecht, pp. 7–36.
Nicholson S.E. 1999. Historical and modern fluctuations of Lakes Tanganyika and Rukwa and their relationship to rainfall variability. Climatic Change 41: 53–71.
Nkotagu H.H. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VIII. Hydrological evaluation of two contrasting watersheds of the Lake Tanganyika catchment. J. Paleolimnol. 34: 107–123.
O'Reilly C.M. 2001. The Effects of Land Use Change on Littoral Zone Dynamics of Lake Tanganyika, East Africa. Ph.D. dissertation University of Arizona, 144 pp.
O'Reilly C.M., Alin S.R., Plisnier P.D., Cohen A.S. and McKee B.A. 2003. Climate change decreases aquatic productivity of Lake Tanganyika, Africa. Nature 424: 766–768.
O'Reilly C.M., Dettman D.L. and Cohen A.S. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VI. Geochemical indicators. J. Paleolimnol. 34: 85–91.
Palacios-Fest M.R., Cohen A.S., Lezzar K.E., Nahimana L. and Tanner B.M. 2005a. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: III. Physical stratigraphy and charcoal analysis. J. Paleolimnol. 34: 31–49.
Palacios-Fest M.R., Alin S.R., Cohen A.S., Tanner B. and Heuser H. 2005b. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IV. Lacustrine paleoecology. J. Paleolimnol. 34: 51–71.
Schmidt P.R. 1997. Archaeological views on a history of landscape changes in East Africa. J. Afr. History 38: 393–421.
Schoenbrun L. 1998. A Green Place, A Good Place. Agrarian Change, Gender and Social Identity in the Great Lakes Region to the 15th Century. Heinemann Publishers, Portsmouth, NH, 302 pp.
Stanley H.M. 1878. Through the Dark Continent v. 2. Harper and Bros. Publishers, 566 pp.
Van Alstine J.M. and Cohen A.S. 2003. 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.
Verschuren D., Laird K.R. and Cumming B.F. 2000. Rainfall and drought in equatorial East Africa during the past 1100 years. Nature 403: 410–414.
Wagner M. 1996. Environment, community and history, "nature in the mind". In: Maddox G., Gilpin J.L. and Kimambo I.N. (eds), Custodians of the Land. Ohio University Press, pp. 175–199.
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.