Effects of land-use change on aquatic biodiversity: A view from the paleorecord at Lake Tanganyika, East Africa

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ABSTRACT

Population growth and watershed deforestation in northwestern Tanzania threaten the biodiversity of Lake Tanganyika through erosion and habitat degradation. We used cores collected offshore from Gombe Stream National Park and a deforested watershed to reconstruct how land-use changes in the Gombe Stream area since A.D. 1750 have affected lake biodiversity. Paleoenvironmental and paleoecological data reveal substantial changes in mass accumulation rates for sediment and organic matter, nitrogen stable isotope values, and benthic species composition offshore from the deforested watershed since 1880. Comparable changes were not observed offshore from the park.

Keywords: biodiversity, land use, paleoecology, stable isotopes, sedimentation rates, Lake Tanganyika.

INTRODUCTION

Numerous studies have demonstrated the effects of land-use change on erosion and sediment-loading patterns in lakes (e.g., Dearing et al., 1987; O'Hara et al., 1993; Cisternas et al., 2001). Increased sedimentation has detrimental impacts on biodiversity and ecological integrity in aquatic communities (e.g., Rogers, 1990; Detenbeck et al., 1999). In this study we consider the historical relationship between watershed land use and aquatic biodiversity through the use of paleorecords in a paired watershed approach.

Northwestern Tanzania harbors globally significant vertebrate and invertebrate biodiversity in Gombe Stream National Park and in Lake Tanganyika (Fig. 1) (Goodall, 1971; Coulter, 1994). Burgeoning human populations have diminished native forest cover in recent decades, and minimal shoreline area is protected in parks or reserves. Deforested hillslopes are susceptible to high erosion rates; sediment yields of 28–100 $t \cdot ha^{-1} \cdot yr^{-1}$ have been measured in experimental watersheds in Burundi (Bizimana and Duchafour, 1991). The resulting sediment influx to the lake affects both biodiversity (Cohen et al., 1993; Alin et al., 1999) and productivity (O'Reilly, 1999) in nearshore habitats in Lake Tanganyika. Effects of slope denudation are amplified by extreme precipitation events, triggering massive erosion at deforested sites (Drake et al., 1999).

Many watersheds in the densely populated northern Tanganyika basin are particularly vulnerable to erosion and sediment deposition in the lake as the steep, rift escarpment topography is deforested and converted to agriculture. Cores from each site reflect the influence of two small stream drainages (Fig. 1). All watershed study areas are comparable in area (<10 km^2), maximum elevation (1560–1720 m), slope (~15%; Nkotagu and Mbwambo, 2000), rainfall (~1600 mm/yr; Cohen et al., 1999), and bedrock geology (metasedimentary rocks). However, the Mwamgongo watershed currently has a human population density of ~800 people/km^2, whereas Gombe Stream National Park has <5 people/km^2 (Cohen et al., 1999). Vegetation in the park varies with elevation and slope from evergreen forests along lowland drainages to drier forests and woodlands on steep slopes at low to moderate elevation, and grasslands at the highest elevations (Bygott, 1992). In contrast, >90% of the hillside area above the valley floor at Mwamgongo has been deforested. Vegetation along the larger stream consists of agricultural species (oil palm, banana, and mango).

Reports of early explorers in East Africa indicate that population densities probably differed among the study areas in the mid-1800s. Burton (1961) and Stanley (1913) indicated that the study areas in present-day Gombe Stream National Park were inhabited by small fishing communities with limited pastoral development at the time of their respective journeys in 1858 and 1871, whereas areas north of the modern park were more extensively cultivated and populous. Because there is a broader river plain at the mouth of the larger stream at Mwamgongo (Ngonya), the population density in the Mwamgongo watershed was likely substantially higher even in the mid-1800s than in Gombe watersheds. In 1943, Gombe Stream became a game reserve to protect chimpanzees and their habitat, and local inhabitants were relocated to Mwamgongo village (Bygott, 1992; Cohen et al., 1999). In 1968, Gombe Stream achieved national park status. In the early 1970s, the Tanzanian government consolidated rural populations into Mwamgongo from surrounding areas, further increasing its population.

SEDIMENT DELIVERY TO OFFSHORE HABITATS

Mass accumulation rates (MARs) for bulk sediment in the Gombe Stream National Park

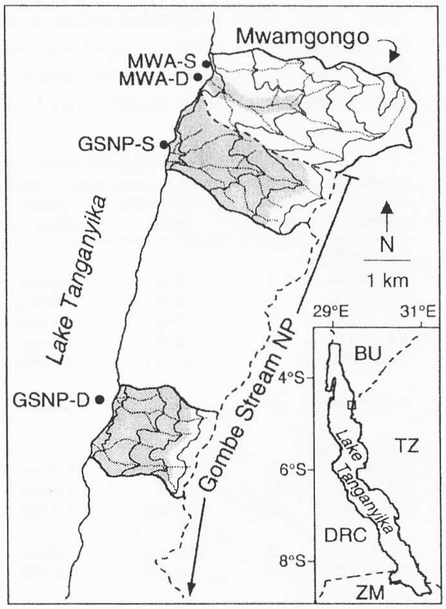

Figure 1. Location of coring sites (inset shows location of watersheds within Tanganyika catchment; countries: BU—Burundi, TZ—Tanzania, DRC—Democratic Republic of Congo, ZM—Zambia). Map details: fine dashed lines—stream drainages; fine solid lines—elevation, contour lines at 200 m intervals, 800 m contour closest to lake; thick dashed line—border of Gombe Stream National Park; thick solid lines—edges of drainage areas not formed by park boundary; shaded areas—approximate extent of woody vegetational cover in study watersheds.

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TABLE 1. DETAILS OF CORES

Core monikers (official names)	Water depth (m)	Core length (cm)	Depositional interval (yr)	Location		Watershed name	Catchment area (km^2)
				lat (S)	long (E)		
GSNP-D (LT98-58M)	76	42	250	4°41′18″	29°37′00″	Nyasanga-Kahama	3.77
GSNP-S (MIT-1)	15	19	100–250*	4°38′04″	29°37′57″	Mitumba	4.83
MWA-D (LT98-37M)	95	45	500	4°37′22″	29°37′40″	Mwamgongo	7.69
MWA-S (MWA-1)	10	16	450†	4°36′34″	29°38′34″	Mwamgongo	7.69

*Accumulation may be sporadic, with a possible hiatus of 100–200 yr at ~9–12 cm.
†A depositional hiatus of ~300 yr exists at ~9 cm.

deep-water core (core GSNP-D) were essentially constant from 1770 (base of core) to 1998; the average sediment MAR was 0.16 ± 0.02 $g \cdot cm^{-2} \cdot yr^{-1}$ (Tables 1 and 2; Figs. 2A and 2B). In contrast, MARs increased substantially offshore from Mwamgongo from 0.044 ± 0.006 $g \cdot cm^{-2} \cdot yr^{-1}$ between 1500 (base of core) and 1880 to 0.12 ± 0.03 $g \cdot cm^{-2} \cdot yr^{-1}$ between 1880 and 1998. A peak rate of 0.18 $g \cdot cm^{-2} \cdot yr^{-1}$ occurred between 1978 and 1990. Because no significant MAR increase has been observed offshore from the park, the increase in sediment MAR of ~300% offshore from Mwamgongo suggests that population density there was sufficient to register a sedimentary land-use signature as early as the late 1800s.

Suspended-sediment-load data for streams also reflect rates of watershed erosion and sediment yield. Total suspended-sediment loads in Ngonya Stream (Mwamgongo) were nearly two orders of magnitude greater than in Mitumba Stream (GSNP-S locality) (1997–1999 averages: 2583.7 vs. 34.2 $mg \cdot L^{-1}$; Nkotagu and Mbwambo, 2000).

ORGANIC MATTER AND $\delta^{15}N$ IN SEDIMENT CORES

Accumulation rates of sedimentary organic matter (SOM) in sediment cores can reflect changes in input from primary productivity stemming from either lake or watershed processes. SOM accumulation rates in core GSNP-D fluctuated very little (1770–1998 SOM average = 11.8 ± 1.4 $mg \cdot cm^{-2} \cdot yr^{-1}$) (Fig. 2C). In contrast, accumulation rates of SOM in Mwamgongo core MWA-D doubled after 1880, from an average of 4.2 ± 0.6 $mg \cdot cm^{-2} \cdot yr^{-1}$ (1500–1880) to 8.6 ± 0.3 $mg \cdot cm^{-2} \cdot yr^{-1}$ (1880–1955), and doubled again between 1955 and 1998 (15.8 ± 4.6 $mg \cdot cm^{-2} \cdot yr^{-1}$). We interpret the increases in accumulation rates of SOM offshore from Mwamgongo after 1880 to represent increased influx of terrestrial organic matter related to land-use change. We also note that the majority of particles in coarse-sediment fractions deposited from 1890 to 1998 consist of charcoal and terrestrial vegetation, whereas prior to 1890, clastic material dominated the coarse-sediment fractions. Furthermore, C:N ratios measured in nearshore river deltas indicate greater influence of terrestrial organic matter in the surface sediments at Mwamgongo (15.15 ± 0.63) compared to Gombe Stream National Park (Mitumba locality: 12.29 ± 0.69) (O'Reilly, 2001).

Soils and organic matter of the deforested Mwamgongo watershed are particularly vulnerable to erosion during high-rainfall events (Nkotagu and Mbwambo, 2000). After high-rainfall events, it is common to see terrestrial vegetation floating in the lake near Mwamgongo. Peak SOM concentrations in MWA-D between 1955 and 1985 probably represent an influx of terrestrial organic matter triggered by a period of anomalously high rainfall in East Africa in the early 1960s.

Changing nutrient sources are reflected in sediment-core nitrogen stable isotope ratios (reported as $\delta^{15}N$) (e.g., Talbot, 2001). Soil and waste sources of nitrogen are characterized by higher $\delta^{15}N$ values than found in many lacustrine primary producers; animal manure generally has $\delta^{15}N$ values in the range of 10‰–25‰, and most soils are between 2‰ and 5‰ (Kendall, 1998). Stream sediments from Mitumba and Mwamgongo have $\delta^{15}N$ values of 3.5‰ and 5.7‰, respectively (O'Reilly, 2001). In Lake Tanganyika, $\delta^{15}N$ values of −0.26‰ ± 0.53‰ have been measured for aquatic particulate matter collected during the dry season (May–August) when $\delta^{15}N$ values should be most enriched (O'Reilly, 2001), as relative abundance of cyanobacteria is an annual minimum (Hecky and Kling, 1981). On the basis of surface sediment samples from deltas offshore of disturbed and undisturbed watersheds around Lake Tanganyika, a reasonable benchmark for detecting anthropogenic watershed disturbance in surface sediments is $\delta^{15}N$ > 1.76‰ over the time scale discussed here (O'Reilly, 2001). In core GSNP-D, $\delta^{15}N$ values increased between 1845 and 1880 (Fig. 2D), after which they decreased slightly and hovered around a new mean (1760–1825 $\delta^{15}N$ average = 0.4‰ ± 0.2‰; 1845–1970 $\delta^{15}N$ average = 1.1‰ ± 0.3‰). Only a single value in GSNP-D (1845–1880 $\delta^{15}N$ = 1.89‰) surpassed the anthropogenic benchmark, which may be explained by influx of soil or waste matter from the watershed during the very wet 1850s to 1870s. The MWA-D $\delta^{15}N$ curve lacks the mid-1800s $\delta^{15}N$ enrichment, but a dramatic $\delta^{15}N$ enrichment began between 1935 and 1960, passing the anthropogenic threshold ca. 1960 and persisting through the remainder of the core (date of most recent isotope sample,

TABLE 2. RADIOCARBON DATES FROM GSNP AND MWA CORES

Sample number	Material dated*	Core depth (cm)	Fraction modern ^{14}C†	^{14}C age (yr)	2σ age ranges with relative probability >0.1 (A.D. calendar yr)
Core MWA-S					
AA-38063	S	2–3	1.0934	postbomb	1997 (N.A.§)
AA-38064	S	4–5	1.1254	postbomb	1992 (N.A.)
AA-41870	S	7–8	1.1729	postbomb	1987 (N.A.)
AA-41871	S	8–9	1.5133	postbomb	1971–2 (N.A.)
AA-38065	S	10–11	0.9689	254 ± 39	1616–1679 (0.478), 1516–1599 (0.290), 1755–1805 (0.188)
AA-38066	S	12–13	0.9590	336 ± 41	1466–1644 (1.000)
Core GSNP-S					
AA-41872	S	2–3	1.1889	postbomb	1985–6 (N.A.)
AA-41873	M	8–9	1.5255	postbomb	1970–1 (N.A.)
AA-41874	S	12–13	0.9782	177 ± 35	1722–1815 (0.542), 1654–1702 (0.197)#, 1914–1950 (0.174)
AA-43719	S	13–14	0.9660	278 ± 75	1442–1694 (0.792)#, 1726–1813 (0.159)
AA-41875	S	16–17	0.9749	204 ± 35	1726–1812 (0.566), 1640–1693 (0.293), 1919–1949 (0.138)
Core MWA-D					
AA-30560	S	3–4	1.1450	postbomb	1990–1 (N.A.)
AA-32720	M	30–31	0.9616	315 ± 55	1450–1663 (1.000)
AA-32724	M	43–44	0.9469	440 ± 60	1400–1530 (0.772), 1546–1634 (0.224)
Core GSNP-D					
AA-30561	M	2–3	1.0343	postbomb	early 1950s? (N.A.)
AA-32719	M	18–19	0.9647	290 ± 70#	1444–1682 (0.870), 1734–1806 (0.109)
AA-32728	M	37–38	0.9744	210 ± 60	1626–1891 (0.801), 1908–1951 (0.129)

*S = single leaf fragment, M = multiple leaf fragments.
†Where 1.0 = modern (i.e., 1950) atmospheric ^{14}C concentration.
§N.A. = not applicable.
#Dates conflict with ^{210}Pb data for the same stratigraphic level or are stratigraphically disordered and were not used.

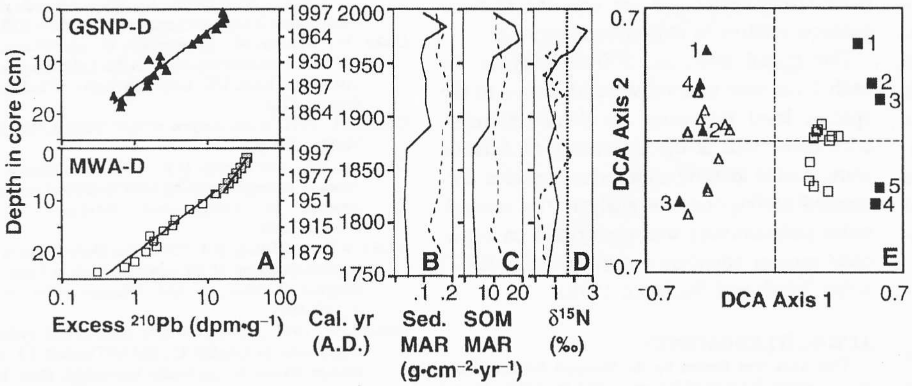

Figure 2. Geochronological, paleoenvironmental, and faunal data for deep-water cores (GSNP-D: triangles, dashed lines; MWA-D: squares, solid lines). A: ^{210}Pb data (interpreted ages in calendar years A.D.; MWA-D: open squares—1865–1965, filled squares—1965–1998). B: Bulk-sediment mass accumulation rates (MAR). C: Sedimentary organic-matter (SOM) MARs. D: δ^{15}N ratios (fine dashed line—anthropogenic threshold). E: Detrended correspondence analysis (DCA) plot (MWA-D: open symbols—1500–1930, filled symbols—1930–1998; numbers—core sample number, core top = 1).

ca. 1985). The coarse-sediment fraction in MWA-D showed a δ^{15}N enrichment from the 1500–1800 average of 1.1‰ ± 0.4‰ to 2.1‰ ± 0.8‰ during 1850–1998. The trend toward δ^{15}N enrichment appears to have been accelerated by watershed flooding and erosion during the early 1960s high-rainfall anomaly and suggests increased dominance of watershed nitrogen sources to the lake sediment in the twentieth century.

EFFECTS ON BIODIVERSITY

Ostracodes are abundant in sediment cores from Lake Tanganyika. Fossil ostracode assemblages appear to serve as conservative paleoindicators of benthic community change, thus a disturbance manifested in ostracode paleoassemblages likely represents a more substantial change in other taxonomic groups, such as fish and mollusks (cf. Alin et al., 1999). Extensively disturbed watersheds in Lake Tanganyika have been associated with decreased ostracode species richness in the surface sediments (Wells et al., 1999). However, watershed area is a critical factor in determining sediment supply to offshore ecosystems (cf. Cohen et al., 1993). Thus, in order to compare historical effects of land-use change on offshore communities, it is important to limit comparisons to watersheds of like size.

Although the watersheds used in this study were small (<10 km^2) and thus relatively insignificant as sediment sources, marked faunal transitions in ostracode assemblages were observed at Mwamgongo contemporaneously with indications of land-use change. Increased sedimentation at Mwamgongo did not diminish species richness of ostracode assemblages, although changes in species composition were observed in cores MWA-D and MWA-S. In deep water, contrasts between sites were most apparent in ordination plots (Fig. 2E). MWA-D assemblages form a cluster, representing deposition prior to 1930, and a more diffuse group of five samples deposited since 1930, which do not overlap with pre-1930 samples. The post-1930 ostracode assemblages in MWA-D show a trend toward more positive values on detrended correspondence analysis (DCA) axis 2, particularly in samples deposited since 1970 (samples 1–3 in Fig. 2E), indicating progressive change in species composition in more recent decades. Core GSNP-D ostracode assemblages did not manifest either of these patterns.

Shallow-water faunas are especially susceptible to anthropogenic disturbance, a result of their proximity to shoreline disturbance. Core GSNP-S represents episodic sediment deposition during the seventeenth to twentieth centuries, and core MWA-S represents snapshots of deposition during the sixteenth to seventeenth centuries (lower core) and the twentieth century (upper core) (Table 2; Fig. 3A). On the basis of grain-size data, it appears that ostracode assemblages in core GSNP-S represent varying water depths, whereas those in core MWA-S formed at roughly constant depth. Nonetheless, the ostracode fauna in MWA-S underwent a profound transition in its dominant species between earlier and later depositional intervals (Fig. 3B). No comparable shift in dominant species occurred in GSNP-S despite changes in water depth. We attribute the faunal transitions observed in both MWA-D and MWA-S ostracode assemblages to the influence of watershed disturbance in the twentieth century.

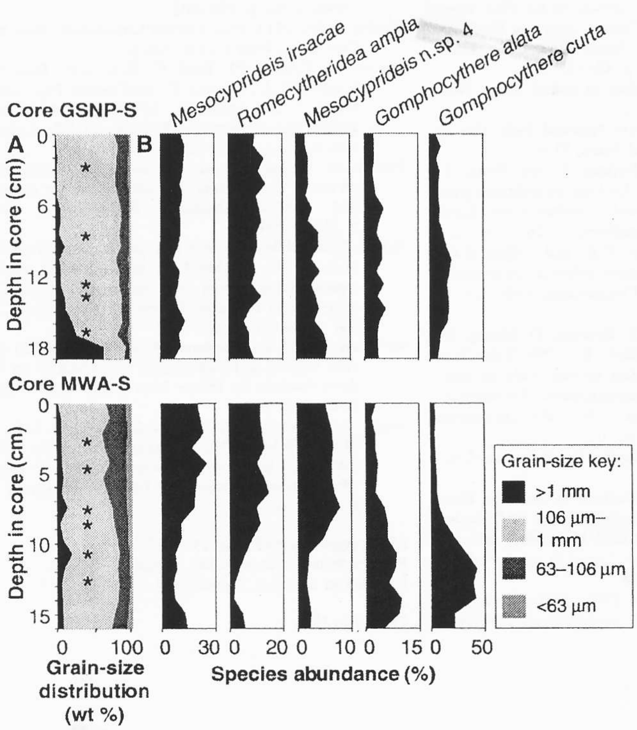

Figure 3. Sedimentology and paleoecology of shallow-water cores. A: Grain-size distributions (asterisks—radiocarbon samples). B: Profiles of relative species abundance for five of most abundant ostracode species at both sites.

CONCLUSION

Collectively, these paleorecords from the Gombe Stream National Park area illustrate the combined influence of land-use change and climate events on the ecology of Lake Tanganyika. Paleoenvironmental indicators support an interpretation of increased soil erosion in the deforested Mwamgongo watershed compared to Gombe Stream National Park. Despite the physical proximity of the two sites, it appears that the creation of Gombe Stream National Park has protected the offshore benthic fauna from undergoing the dramatic changes observed offshore from Mwamgongo. Population growth and land-use change render landscapes, and the lake habitat in turn, especially vulnerable to dramatic change when natural environmental events, such as the early 1960s high-rainfall years in East Africa, trigger them. The challenge to the future sustainability of the Lake Tanganyika ecosystem and its watersheds lies in our ability to predict and mitigate the coupled effects of direct alterations to the lake's catchment (e.g., deforestation), and indirect anthropogenic effects (e.g., global climate change).

APPENDIX. METHODS

Sediment cores were collected in 1998 in moderately deep (75–100 m) water with a Hedrick-Marrs Multicorer and in shallow (5–15 m) water offshore from Mwamgongo and Gombe Stream National Park with a handcoring apparatus (Table 1; Fig. 1). Cores GSNP-D and MWA-D were collected 450 and 300 m offshore, respectively, from relatively flat areas on the southern flanks of small canyons; sediment loads at both sites were largely suspension-carried muds.

The ^{210}Pb ($\tau_{1/2}$ = 22.3 yr) data were collected at 1 cm intervals in cores GSNP-D and MWA-D with the polonium method (Nittrouer et al., 1979; McKee et al., 1983) to depths where supported ^{210}Pb levels were reached. Linear sedimentation rates (LSRs) were determined according to an advection-diffusion model based on the slope and intercept of a linear regression of excess- ^{210}Pb data (Guinasso and Schink, 1975). Sediment MARs were calculated with water content and LSR data, assuming a dry matter specific gravity of 2.0.

The ^{14}C dates augmented ^{210}Pb chronologies for lower core sections (Table 2). All radiocarbon dates were on terrestrial plant material to circumvent problems with old carbon in Tanganyika's surface waters. Radiocarbon ages were measured at the Arizona Accelerator Mass Spectrometry Laboratory and calibrated with CALIB 4.3 (Stuiver et al., 1998a, 1998b). Midpoints of most probable 2σ age ranges were used in generating age models, except where noted. Postbomb dates were assigned by reference to atmospheric decay curves (Nydal and Lövseth, 1983; Levin and Kromer, 1997). Most postbomb dates were based on single leaf fragments, so decay curves allowed assignment of ages to within a few years of production. The Southern Hemisphere correction was not applied, because the study sites are equatorial (<5°S).

Sedimentary organic matter content was determined by loss on ignition (Bengtsson and Enell, 1986). The $\delta^{15}N$ ratios were measured on an Isochrom continuous-flow stable isotope mass spectrometer and are reported in delta notation relative to atmospheric nitrogen.

For faunal analyses, 500 individuals for each 1 cm core interval were identified to the species level following the literature; reference collections at the University of Arizona were used to identify undescribed species. Detrended correspondence analysis (by second-order polynomials) was performed on ostracode species abundance data with CANOCO 4 (ter Braak and Smilauer, 1998).

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