Climate warming reduces fish production and benthic habitat in Lake Tanganyika, one of the most biodiverse freshwater ecosystems

Andrew S. Cohen^{a,1}, Elizabeth L. Gergurich^{a,2}, Benjamin M. Kraemer^b, Michael M. McGlue^c, Peter B. McIntyre^b, James M. Russell^d, Jack D. Simmons^{a,3}, and Peter W. Swarzenski^{e,4}

^aDepartment of Geosciences, University of Arizona, Tucson, AZ 85721; ^bCenter for Limnology, University of Wisconsin, Madison, WI 53706; ^cDepartment of Earth and Environmental Sciences, University of Kentucky, Lexington, KY 40506; ^dDepartment of Earth, Environmental and Planetary Sciences, Brown University, Providence, RI 02912; and ^ePacific Coastal and Marine Science Center, US Geological Survey, Santa Cruz, CA 95060

Edited by Heike K. Lotze, Dalhousie University, Halifax, NS, Canada, and accepted by Editorial Board Member Alan Hastings June 17, 2016 (received for review February 26, 2016)

Warming climates are rapidly transforming lake ecosystems worldwide, but the breadth of changes in tropical lakes is poorly documented. Sustainable management of freshwater fisheries and biodiversity requires accounting for historical and ongoing stressors such as climate change and harvest intensity. This is problematic in tropical Africa, where records of ecosystem change are limited and local populations rely heavily on lakes for nutrition. Here, using a ~1,500-y paleoecological record, we show that declines in fishery species and endemic molluscs began well before commercial fishing in Lake Tanganyika, Africa's deepest and oldest lake. Paleoclimate and instrumental records demonstrate sustained warming in this lake during the last ~150 y, which affects biota by strengthening and shallowing stratification of the water column. Reductions in lake mixing have depressed algal production and shrunk the oxygenated benthic habitat by 38% in our study areas, yielding fish and mollusc declines. Late-20th century fish fossil abundances at two of three sites were lower than at any other time in the last millennium and fell in concert with reduced diatom abundance and warming water. A negative correlation between lake temperature and fish and mollusc fossils over the last ~500 y indicates that climate warming and intensifying stratification have almost certainly reduced potential fishery production, helping to explain ongoing declines in fish catches. Long-term declines of both benthic and pelagic species underscore the urgency of strategic efforts to sustain Lake Tanganyika's extraordinary biodiversity and ecosystem services.

climate change | Lake Tanganyika | freshwater biodiversity | fisheries | paleoecology

arming climates are rapidly transforming lake ecosystems worldwide (1), but the breadth of changes in tropical lakes is poorly documented. In the Great Lakes of tropical Africa, inconsistent monitoring of temperature and ecosystem dynamics has limited our understanding of how warming has affected their extraordinary biodiversity and critical fisheries (2, 3). Such changes in Lake Tanganyika, Africa's oldest and deepest (1,470 m) lake, are particularly problematic. This deep, stratified lake harbors spectacular freshwater biodiversity and endemism (2, 4, 5). It also yields up to 200,000 t of fish annually, comprising ~60% of regional animal protein consumed (3, 6). The productive surface waters are fertilized by upwelling of nutrient-rich deep water during the windy season (7), providing the biogeochemical basis for the fishery. However, this ecosystem has changed dramatically in recent decades; expanding deforestation (8), intensifying fishing efforts (9), rising water temperatures, and declining phytoplankton production (10–12) have all been concurrent with fishery declines. As a result, debate continues over the relative roles of fishing practices and climate change in Tanganyika's fishery declines (9–11).

Developing sustainable management strategies for this enormous fishery requires determining the impact of climate change on catch potential. Documentation of fishery yields and environmental conditions is sparse before the mid-20th century, making it difficult to infer the key drivers of ecosystem change. An alternative source of historical data on ecosystem dynamics can be derived from sediment cores from the lake bottom. Merging paleoclimatic and paleoecological perspectives has enabled estimation of fish population sizes and community dynamics before and after the onset of major fisheries elsewhere (13, 14), filling the information void before active monitoring.

In Lake Tanganyika, close coupling of physics, chemistry, and biology gives rise to a predictable cascade of warming effects: intensified stratification of the water column suppresses vertical mixing, leading to reduced nutrient delivery to the surface, which reduces algal production (10-12). Thus, rising temperatures could reduce fish populations by undercutting energy flow to the pelagic food web, by reducing their habitat as the low-oxygen zone rises, or by directly affecting fish physiology (15). With paleoecological data, this warming hypothesis can be tested by comparing fluctuations in fish fossil abundance to shifts in water

Significance

Understanding how climate change affects ecosystem productivity is critical for managing fisheries and sustaining biodiversity. African lakes are warming rapidly, potentially jeopardizing both their high endemic biodiversity and important fisheries. Using paleoecological records from Lake Tanganyika, we show that declines in commercially important fishes and endemic molluscs have accompanied lake warming. Ongoing declines in fishery species began well before the advent of commercial fishing in the mid-20th century. Warming has intensified the stratification of the water column, thereby trapping nutrients in deep water where they cannot fuel primary production and food webs. Simultaneously, warming has enlarged the low-oxygen zone, considerably narrowing the coastal habitat where most of Tanganyika's endemic species are found.

This article is a PNAS Direct Submission. H.K.L. is a guest editor invited by the Editorial Board.

CrossMark

Author contributions: A.S.C., J.M.R., and P.W.S. designed research; A.S.C., E.L.G., B.M.K., M.M.M., P.B.M., J.M.R., J.D.S., and P.W.S. performed research; A.S.C., B.M.K., M.M.M., P.B.M., J.M.R., and P.W.S. analyzed data; and A.S.C., B.M.K., M.M.M., P.B.M., J.M.R., and P.W.S. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. Email: cohen@email.arizona.edu.

²Present address: School of Geology and Geophysics, University of Oklahoma, Norman, OK 73019.

³Present address: Weston Solutions, Inc., Austin, TX 78746.

⁴Present address: International Atomic Energy Agency, Principality of Monaco, 98000, Monaco.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10. 1073/pnas.1603237113/-/DCSupplemental.



Fig. 1. Lake Tanganyika and coring locations. (Inset A) Commercial (purse seine) fishing boats on Lake Tanganyika at Mpulungu, Zambia; (B) Rift mountains flanking L. Tanganyika at Mahale Mountains National Park near core site LT98-07. Steep mountain slopes are indicative of underwater slopes. Base map source: US National Park Service.

temperature and algal production before intensive fishing. If the timing of fish declines instead matches the emergence of modern fisheries, then fishing practices rather than climate warming could be inferred to be an important driver of declining catches.

To test these predictions, we analyzed sediment cores from two nearshore sites (NP05-TB40 and LT98-07M) and one deep-water site (MC1/KH1) (Figs. 1–3, Tables S1–S6, and Fig. S1). In each case, we quantified geochemical proxies for temperature and algal production as well as the abundance of fossils from pelagic fishes and benthic invertebrates (ostracodes and molluscs). Benthic animals are of special concern because stronger stratification reduces oxygenated habitat in Lake Tanganyika (16, 17). In modern sediments, benthic invertebrates are generally absent from sediments deposited under anoxic conditions, although some ostracodes tolerate low oxygen (as low as 1 mg·L⁻¹) relative to molluscs (generally >4 mg·L⁻¹) (17–20). We quantified trends, correlations, break points in temporal patterns, and cross-factor correlations for temperature, algal production, and fossils to understand the respective roles of lake warming and fishing pressure in the recent history of the remarkable biota of Lake Tanganyika.

Results

Our TEX₈₆-inferred lake temperature data from core NP05-TB40 (Fig. 3*A* and Tables S7 and S8) together with published records from 200 km to the south (MC1/KH1; Fig. 2*A*) (12) show significant warming after the late 19th century [break points in ~1903 (\pm 31 y; MC-1) and ~1854 (\pm 50 y; NP05-TB40) (Table S9)]. Warming rates in the 20th century were unprecedented in the past ~1,500 y (Fig. 4, Tables S7 and S8, and Fig. S2). Similar temperature trends at both sites indicate lake-wide warming rather than localized changes in upwelling (21), although the impact of differences in oxycline depth on temperature between sites is also evident. Lake-level fluctuations over the past two millennia (22) (Fig. 3*B*) are uncorrelated with water temperature at the deeper core sites (MC1 and LT98-07M) but show a negative (*P* = 0.05) correlation at site NP05-TB40 before the onset of 20th century warming (Tables S10 and S11).

As an index of diatom primary production, biogenic silica (BiSi) (measured only at site MC1) shows a strong negative relationship with temperature; high diatom production is associated



Fig. 2. Paleoecological records from cores MC1/KH1 and LT98-07 from A.D. 1400 to 2000. (*A*) TEX₈₆ reconstructed lake temperatures (note inverted scale) (12), using a "cool-lake" calibration (29). (*B*) Percentage of sediment as BiSi, dominantly derived from diatom fossils (12). (C) Fish fossil flux (number of fossils per square centimeter of lake floor per year; 3-point running average). (*D*) LT98-07 fish fossil abundance (bones plus scales per gram dry weight of sediment), 3-point average, showing similar trends to the MC1/KH1 record. Green rectangles denote periods of high diatom and fish production. Pink rectangle denotes 20th century high temperatures, low diatom production, and low fish production.

(P < 0.001) with low water temperatures (Fig. 2B) (10). Some deviations from this correlation occur, presumably because of other factors like changes in wind intensity that affect vertical mixing. The correlation is somewhat stronger after the onset of the recent precipitous decline in BiSi (~1872 ± 27 y), as TEX₈₆ temperatures rose rapidly. The association was weaker when surface temperatures were cooler, which would have enabled seasonal mixing to boost primary production (21).

Fish fossil abundances decreased at all three sites during the 20th century (Figs. 2 C and D, and 3 C and D). At NP05-TB40,

fish fossils (total bones plus scales) are significantly negatively correlated with TEX₈₆ temperature and lake level for the entire period, whereas fish bones alone are reduced only after the shift toward recent rapid warming (Table S10). The lowest fish fossil abundances in this core are observed in the late 20th century. Changes in fish fossil flux in MC1 (primarily sardines Limnothrissa miodon and Stolothrissa tanganicae) show a marginally significant (P = 0.069) negative relationship with BiSi after the onset of warming but not before (Figs. 2C and 4A). Overall, the timing of changes in fish fossil flux (MC1) closely mirrors that of the BiSi record (MC1), being episodically high during cool periods of the early 17th and early 18th century, at intermediate levels through much of the 19th century, and low throughout the 20th century (break point, $\sim 1866 \pm 71$ y). The lowest temperatures at site MC1 (early 17th century) correspond with the highest fish fossil abundances in the entire record. Major swings in fish fossil flux, typical of boom/bust population cycles observed among pelagic sardines on 10^{1-2} -y timescales elsewhere (13), occurred well before to the start of commercial fishing in the mid-20th century. In the nearby LT98-07M core, fish fossils (mainly sardines plus their predators, Lates spp.) show a weak negative correlation with temperature, an earlier onset of declines (~1768 \pm 144 y), and especially sharp decreases since the late 19th century (Figs. 2D and 4C). Late-20th century fish fossil abundances are the lowest observed over the entire ~500-y record at LT98-07, and both decadal and running averages for the MC1 fossil fish flux and BiSi data are highly significantly correlated after the onset of recent warming (Table S11). Conversely, the highest fish fossil abundances occur about the mid-17th and early 18th century, when Lake Tanganyika temperatures were low and diatom production was high. Fish fossil abundances in NP05-TB40 were high but variable from the ~6th to 18th centuries, followed by long-term declines since ~ 1800 (Figs. 3 C and D and 4D and Fig. S2).

Two of our three cores were collected below the oxic zone, but the shallower (76-m) NP05-TB40 core allows us to assess



Fig. 3. Paleoecological records from core NP05-TB40 from A.D. 400 to 2000. (*A*) Lake temperature for NP05-TB40 (cool calibration; note inverted scale) (29). (*B*) Lake level history (8, 22). Preinstrumental (1870) measurements are $\pm 5m$ SD. (*C*) Fish scale abundance (3-point running average) number of scales per gram dry weight of sediment. (*D*) Fish bone abundance (3-point running average) number of bones per gram dry weight of sediment. (*E*) Mollusc fossil abundance (3-point running average, number of shell fragments per gram dry weight of sediment). (*F*) Ostracode fossil abundance (3-point running average, number of valves per gram dry weight of sediment). (*G*) Instrumental and fossil data since late-19th century lake level stabilization. All values normalized to 1 = maximum. Area K, proportion of lake floor oxygenated >4 mg O·L⁻¹ in the Kigoma area lake margin relative to 1946; Area M, same for north Mahale coast; BiSi, MC1 BiSi; Mol, NP05-TB40 fossil molluscs; Sar, annual Tanzanian sardine catch (www.fao.org/fishery/statistics/en); Temp-NP05-TB40 TEX temperature.



Fig. 4. Fossil abundances of fish, molluscs, and ostracodes relative to key paleoenvironmental variables, showing distinct 20th century trends and declining abundances in all fossils except ostracodes. Color and size of bubbles are proportional to the maximum value for each dataset, with warmer colors indicative of greater abundances. (*A*) Fish fossil flux for core MC1/KH1 for given lake levels and MC1 TEX temperatures (19th century ranges also shown). (*B*) Fish fossil flux for core MC1/KH1 for given MC1 WBiSi and MC1 TEX temperatures. (*C*) Fish fossil abundance for core LT98-07 for given MC1 %BiSi and MC1 TEX temperatures. (*D*) Fish fossil abundance for core NP05-40 for given lake levels and NP05-TB40 TEX temperatures. (*E*) Mollusc fossil abundance for core NP05-40 for given lake levels and NP05-40 TEX temperatures. (*F*) Ostracode fossil abundance for core NP05-40 for given lake levels and NP05-40 for given lake levels and NP05-40 TEX temperatures.

changes in the endemic benthic invertebrates in parallel with pelagic fish. Fossil concentrations of the dominant deep-water gastropods (*Tiphobia horei* and *Tomichia gulleimei*; Table S5) were consistently high between the ~6th and ~15th centuries, followed by a long-term decline (break point, ~1451 \pm 225 y), with extremely low numbers of shells encountered in the late 20th century (Figs. 3*E* and 4*E*). Mollusc abundances are strongly negatively correlated with lake temperature for both the entire period (*P* < 0.001) and under recent warming (*P* = 0.009), and are also positively related to lake level (entire dataset only, *P* = 0.018). Ostracode fossil abundances (Figs. 3*F* and 4*F*) are not correlated with temperature or lake level; 20th century concentrations are within the range observed before the ~18th century.

The large decline since about the 16th century in fossil mollusc abundances, which are negatively correlated with temperature (P = 0.0002), is consistent with shallowing depth distributions of deep-water snails as warming led to the shallowing of the oxycline (decreasing wind speeds could have also contributed to this, but we have no direct indicators of past wind speeds). The NP05-TB40 core site currently lies within the low oxygen zone of the lake floor (dissolved O₂ concentrations vary seasonally between 0.7 and 5.0 mg·L⁻¹), but historic water temperature measurements and TEX₈₆ data suggest that it transitioned from permanent oxygenation in the 19th century to the current state of intermittent low-oxygen conditions. During the same period, there was no trend in fossil ostracode abundance, presumably reflecting the adaptation of numerous species of ostracodes to low-oxygen waters. Although ostracodes cannot tolerate fully anoxic bottom waters, the core site appears to have been above the threshold concentrations of O_2 these animals require throughout the Late Holocene. There was no indication that major lake level fluctuations over the last ~400 y affected benthic invertebrates. The most extreme mollusc declines occurred under stable lake levels during the 20th century. These declines followed a ~10-m fall in lake level in the late 19th century (8); however, declining water levels would almost certainly have deepened profundal oxygenation, which would be expected to yield enhanced habitat for mollusc populations at the core site, contrary to what we observed.

The decline of deep-water snails for more than a century is concerning not only with regard to Tanganyika's remarkable endemic gastropods but also because numerous other animal groups would likely be affected by the same underlying environmental changes (17). The narrow, steep strip of littoral habitat at the lake margins (Fig. 1*B*) is home to most of Tanganyika's biodiversity (5). Combining historic dissolved oxygen (DO) trends with coastal bathymetry from both regions represented by our cores reveals enormous loss of oxic habitat. In 1946 [the earliest DO record (23)], the maximum depth (110 m) of the 4 mg·L⁻¹ oxygen threshold corresponded to habitable lake floor areas of 92.8 and 65.87 km² for the Mahale and Kigoma areas, respectively. As the threshold DO isobaths rose (90 m in 1956, 80 m in 1993, 70 m in 2002, and 62 m in 2012), habitable area shrank rapidly (Fig. 1*B*), culminating in a ~38% reduction in habitable lake floor since 1946 (Fig. 3*G*).

Discussion

Recognition of sharp declines in pelagic fish fossils as Lake Tanganyika warmed over the last ~150 y brings clarity to the causes of falling fishery yields. Declines in fish abundances began well before the explosive growth of commercial fisheries on the lake in the mid-20th century (ref. 3; United Nations Food and Agriculture Organization FishStat Database, www.fao.org/fishery/ statistics/en) (Fig. 3G) and are apparent across all study sites. The unprecedented lows in fish abundances during the 20th century, when temperature rose and primary production fell (Fig. 4), leave little doubt that climate warming has undercut fishery potential independent of fishing effort and practices. This is not to say that declines in sardine catches since the mid-20th century can be attributed solely to climate warming. The early phase of commercial fishing certainly overharvested some species, especially larger predators (www.fao.org/fishery/statistics/en). Nevertheless, the decline in fish fossil abundance before commercial fishing, and the striking correlations between fish. BiSi, and temperature since the early 20th century, suggest that pelagic fish production responds strongly to climate change on 10^{1-2} -y timescales. It is possible that rising fishing pressure has further decimated sardine stocks in recent decades, but this direct human pressure is operating against a backdrop of warming-induced shifts in ecosystem production that appears to limit pelagic fish biomass.

Paleoecological data also clearly show that the reduction in water column mixing in Lake Tanganyika has caused the oxygenated habitat to shrink, yielding mollusc declines. The broad negative correlation between lake temperature and mollusc and fish fossils suggests that climate warming and intensifying stratification have been important in rapidly altering both benthic and pelagic components of the Lake Tanganyika ecosystem. Furthermore, continued warming can be expected to exacerbate benthic habitat loss, potentially affecting dozens of profundal fishes and invertebrates as well as hundreds of littoral species (5).

The collapse of diatom production, pelagic fishes, and profundal molluscs over the last century coincides with the highest temperatures inferred for the past \sim 500 y (Fig. 4 and Fig. S2). There can be no doubt that climate change is playing a pivotal role in these trends, and that further warming and strengthening stratification lie ahead, barring a major increase in windiness. Moreover, our findings are consistent with a linkage between rising temperatures, increasing stratification, and declining primary production in low-latitude lakes (24) and oceans (25), emphasizing the need for ecosystem and fisheries managers to monitor these relationships carefully. To sustain Lake Tanganyika's extraordinary endemic biodiversity, the conservation community, cognizant governments, and international agencies must recognize these long-term trends in designing management plans. If fishery managers ignore ongoing reductions in the energy base of the pelagic food web, the susceptibility of this critical resource to overfishing will become even more acute.

Methods

Geochronology. The geochronology of the three core sites was established from downcore excess ²¹⁰Pb and ¹³⁷Cs profiles analyzed at the US Geological Survey (USGS) Santa Cruz radiochemistry laboratory, and corroborated by accelerator mass spectrometry ¹⁴C dates. ¹⁴C analyses were conducted at the University of Arizona Accelerator Mass Spectrometry Laboratory on terrestrial plant material found in the cores (Table S3). For further details, see Table S2.

- Shimoda Y, et al. (2011) Our current understanding of lake ecosystem response to climate change: What have we really learned from the north temperate deep lakes? J Great Lakes Res 37(1):173–193.
- 2. Salzburger W, Van Bocxlaer B, Cohen AS (2014) The ecology and evolution of the African Great Lakes and their faunas. *Annu Rev Ecol Evol Syst* 45:519–545.
- 3. Mölsä H, et al. (2002) Ecosystem monitoring in the development of sustainable fisheries in Lake Tanganyika. Aquat Ecosyst Health Manage 5(3):267–281.
- 4. Cohen AS, Soreghan M, Scholz C (1993) Estimating the age of ancient lake basins: An example from L. Tanganyika. *Geology* 21(6):511–514.
- Vadeboncoeur Y, McIntyre PB, Vander Zanden MJ (2011) Borders of biodiversity: Life at the edge of the world's large lakes. *Bioscience* 61(7):526–537.

Paleoecology. Wet sediment samples (~2 g) were collected every 1 cm from each core, disaggregated in deionized water, and sieved using a 125-µm stainless-steel sieve. Wet weights were determined for an aliquot from each sample, which was oven-dried and reweighed to determine water content and to calculate original dry weights for sieved samples. For MC1 where original water content data were available fossil flux rates (as numbers of fossils per square centimeter per year) were calculated based on sedimentation rates (Fig. S1). After sieving, residues were counted at 90× magnification for ostracodes (including taphonomic variables), fish bones and scales, and molluscs on an Olympus SZX stereomicroscope. Identifications of molluscs followed refs. 26 and 27; ostracode and fish identifications relied on reference collections in the University of Arizona Laboratory of Paleolimnology.

BiSi. BiSi methods and data were previously published in ref. 12.

Organic Geochemistry. Sediment samples were freeze-dried and homogenized with a mortar and pestle, and lipids were extracted using a Dionex 350 Accelerated Solvent Extractor using 9:1 dichloromethane (DCM)/methanol (MeOH). Lipid extracts were separated into nonpolar and polar fractions with an Al₂O₃ column using 9:1 hexane/DCM and 1:1 DCM/MeOH as eluents. The polar fraction was dried under N₂ gas, then redissolved in hexane/isopropanol (99:1), and filtered before analysis. The GDGTs were analyzed via HPLC/positive-ion atmospheric-pressure chemical ionization–MS at Brown University following the methods of ref. 28. Temperatures were estimated from the TEX₈₆ values using the calibration described in ref. 29.

Bathymetry and Oxygenation. Bathymetric mapping to a depth of >110 m was conducted at two sites: 34.1 km of shoreline flanking Kigoma Bay in northern Tanzania (adjacent to the NP05-40 core site), and 29.4 km of shoreline in central Tanzania just north of Mahale Mountains National Park (near the MC1 and LT98-07 core sites). In both areas, mapping was conducted using georeferenced echo sounding along sampling grids with 100-200 m between transects. Hypsographic curves were derived from areal integration using ArcGIS. Habitable (i.e., oxygenated) lake floor was estimated from DO profiles between 1946 and 2007, plus numerous new profiles from 2012 to 2013 (ref. 21 and this study); loss of oxygenated profundal habitat was calculated based on the depth at which DO dropped below 4 mg O·Lwhich we consider to be a threshold for molluscs and fish. For the 2012–2013 data, we used a linear regression through 110,611 observations (YSI optical probe) to identify the typical DO threshold depth, whereas earlier data are derived from refs. 17, 23, 30, and 31, and archival CTD Nyanza Project data (www.geo.arizona.edu/nyanza/pdf/Kinyanjui.pdf).

Statistical Methods. Pearson correlations and associated *P* values were calculated in R for all datasets, considering the entire time series for each core as well as separate time intervals before and after the TEX₈₆ temperature break points. Statistical break point analysis was performed in R (R Development Team) using the "segmented" package.

ACKNOWLEDGMENTS. We thank Ishmael Kimerei, Donatius Chitamwebwa, the Tanzania Fisheries Research Institute staff, Rashid Tamatamah, Kiram Lezzar, Simone Alin, and the students of the Nyanza Project for coring assistance; The Nature Conservancy and its Tuungane Project staff for logistical support; and Colin Apse and two anonymous reviewers for comments on an earlier draft of this paper. Research permits were kindly provided by the Tanzania Council for Science and Technology and the University of Dar es Salaam. Digital bathymetric model data in Fig. 1 are courtesy of tcarta.com. This project was funded by the National Science Foundation [Grants ATM 0223920 (to A.S.C.) and BIO 0353765 (to A.S.C.), The Nyanza Project and Grant DEB 1030242 (to P.B.M.)], the Lake Tanganyika Biodiversity Project (A.S.C.), the USGS Coastal and Marine Geology Program (P.W.S.), Society of Exploration Geophysicists Foundation Geoscientists Without Borders Program [Grant 201401005 (to M.M.M.)], a Packard Foundation Fellowship (P.B.M.), and the Nature Conservancy [Tuungane Project (P.B.M. and M.M.M.)].

- Mölsä H (2008) Management of fisheries on Lake Tanganyika. PhD dissertation (Kuopio University, Kuopio, Finland).
- 7. Plisnier P-D, et al. (1999) Limnological annual cycle inferred from physical-chemical fluctuations at three stations of Lake Tanganyika. *Hydrobiologia* 407:45–58.
- Cohen AS, et al. (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IX. Summary of paleorecords of environmental change and catchment deforestation at Lake Tanganyika and impacts on the Lake Tanganyika ecosystem. J Paleolimnol 34(1):125–145.
- 9. Sarvala J, et al. (2006) Fish catches from Lake Tanganyika mainly reflects changes in fishery practices, not climate. *Verh Int Ver Theor Angew Limnol* 29: 1182–1188.

- O'Reilly CM, Alin SR, Plisnier P-D, Cohen AS, McKee BA (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature 424(6950):766–768.
- Verburg P, Hecky RE, Kling H (2003) Ecological consequences of a century of warming in Lake Tanganyika. Science 301(5632):505–507.
- Tierney J, et al. (2009) Late-twentieth-century warming in Lake Tanganyika unprecedented since AD 500. Nat Geosci 3:422–425.
- Baumgartner TR, Soutar A, Ferreira-Bartrina V (1992) Reconstructions of the history of the Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. CCOFI Rep 33:24–40.
- Finney B, et al. (2010) Paleoecological studies on variability in marine fish populations: A long-term perspective on the impacts of climatic change on marine ecosystems. J Mar Syst 79(3-4):316–326.
- Rummer JL, et al. (2014) Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Glob Change Biol* 20(4): 1055–1066.
- Verburg P, Hecky RE (2009) The physics of warming of Lake Tanganyika by climate change. *Limnol Oceanogr* 54(6 part 2):2418–2430.
- van Bocxlaer B, Schultheiß R, Plisnier P-D, Albrecht C (2012) Does the decline of gastropods in deep water herald ecosystem change in Lakes Malawi and Tanganyika? *Freshw Biol* 57(8):1733–1744.
- Palacios-Fest MR, Alin SR, Cohen AS, Tanner B, Heuser H (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: IV. Lacustrine paleoecology. J Paleolimnol 34(1):51–71.
- Cohen AS, et al. (2007) Ecological consequences of early Late Pleistocene megadroughts in tropical Africa. Proc Natl Acad Sci USA 104(42):16422–16427.
- Blome MW, Cohen AS, Lopez M (2014) Modern distribution of ostracodes and other limnological indicators in southern Lake Malawi: Implications for paleoecological studies. *Hydrobiologia* 728(1):179–200.
- Kraemer BM, et al. (2015) Century-long warming trends in the upper water column of Lake Tanganyika. PLoS One 10(7):e0132490.
- Alin SR, Cohen AS (2003) Lake-level history of Lake Tanganyika, East Africa, for the past 2500 years based on ostracode-inferred water-depth reconstruction. Palaeogeogr Palaeoclimatol Palaeoecol 199(1-2):31–49.
- 23. Van Meel LIJ (1987) Contribution à la limnologie de quatre grands lacs du Zaïre oriental: Tanganyika, Kivu, Mobutu Sese Seko (ex Albert), Idi Amin Dada (ex Edouard). Les paramètres chimiques. Fascicule A: Le Lac Tanganyika (Institut Royal des Sciences Naturelles de Belgique, Brussels), Document de Travail 41.

- Michelutti N, Labaj A, Grooms C, Smol JP (2016) Equatorial mountain lakes show extended periods of thermal stratification with recent climate change. J Limnol 75(2): 403–408.
- Behrenfeld MJ, et al. (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444(7120):752–755.
- Brown DS (2004) Freshwater Snails of Africa and Their Medical Importance (Taylor and Francis, London), 2nd Ed.
- West KA, Michel E, Todd JA, Brown DS, Clabaugh J (2003) The Gastropods of Lake Tanganyika: Diagnostic Key and Taxonomic Classification with Notes on the Fauna (The International Association for Theoretical and Applied Limnology, Chapel Hill, NC), Vol 2, pp 1–132.
- Schouten S, Huguet C, Hopmans EC, Kienhuis MVM, Damsté JS (2007) Analytical methodology for TEX₈₆ paleothermometry by high-performance liquid chromatography/atmospheric pressure chemical ionization-mass spectrometry. *Anal Chem* 79(7): 2940–2944.
- Powers LA, et al. (2004) Crenarchaeotal membrane lipids in lake sediments: A new paleotemperature proxy for continental paleoclimate reconstruction? *Geology* 32(7): 613–616.
- Dubois JTh (1958) Evolution de la température de l'oxygène dissous et de la transparence dans la baie nord du Lac Tanganika. Hydrobiologia 10(1):215–240.
- Plisnier P-D (1997) Climate, Limnology and Fisheries Changes of Lake Tanganyika, FAO Technical Report (Food and Agriculture Organization, Rome), GCP/RAF/271/FIN-TD/72.
- 32. Van der Knaap M, Katonda KI, De Graaf GJ (2014) Lake Tanganyika fisheries frame survey analysis: Assessment of the options for management of the fisheries of Lake Tanganyika. Aquat Ecosyst Health Manage 17(1):4–13.
- Powers L, et al. (2010) Applicability and calibration of the TEX₈₆ paleothermometer in lakes. Org Geochem 41(4):404–413.
- Hopmans EC, et al. (2004) A novel proxy for terrestrial organic matter in sediments based on branched and isoprenoid tetraether lipids. *Earth Planet Sci Lett* 224(1-2): 107–116.
- Conaway CH, Swarzenski PW, Cohen AS (2012) Recent paleorecords document rising mercury contamination in Lake Tanganyika. *Appl Geochem* 27(1):352–359.
- McKee BA, et al. (2005) Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: II. Geochronologies and mass sedimentation rates based on ¹⁴C and ²¹⁰Pb data. J Paleolimnol 34(1):19–29.
- Odigie KO, Flegal AR, Cohen AS, Swarzenski PW, Flegal AR (2014) Using lead isotopes and trace element records from two contrasting Lake Tanganyika sediment cores to assess watershed - Lake exchange. *Appl Geochem* 51:184–190.

Supporting Information

Cohen et al. 10.1073/pnas.1603237113



Fig. S1. Age models and sample age assignments. For cores KH1/MC1, we used the age model previously published in ref. 12 for assignment of sample ages. (*A*) For core NP05-40, we combined the 210 Pb and basal 14 C age picks to generate a single polynomial regression for sample age assignments. (*B*) For LT98-07, a single polynomial combining both 210 Pb and 14 C data yielded a strong deviation from the nominal 210 Pb age model alone (Table S2). Therefore, we used a polynomial regression for age assignments of the samples that fell in the 210 Pb age range and linearly interpolated ages from the base of the 210 Pb interval through the 14 C date near the base of the core.



Fig. S2. Fossil abundances of fish, molluscs, and ostracodes in relation to key paleoenvironmental variables. Color and size of bubbles is proportional to the maximum value for each dataset. Colored polygons show range of variation for each century for the past 500 or 600 y. Note distinct cluster space and low values associated for all fish and mollusc abundances (but not ostracodes) for the 20th century clusters.

Table S1. Sediment core characteristics

Core name	Date collected	Latitude	Longitude	Water depth, m	Core length/core type	Adjacent human impacts near core site at time of collection
LT98-07	7 January 1998	6°9.058′	29°42.479′	151	53 cm/Hedrick Marrs Multicore	Minimal (south of and adjacent to Mahale National Park)
NP04-KH1/MC1	18 July 2004	6°33.147′	29°58.480′	303	KH1-534 cm/ Kullenberg Piston Core MC1-49 cm/Hedrick Marrs Multicore	Minimal at time of collection (North end of Mahale National Park near Lubulungu R. delta). Significantly increased since (ref. 32)
NP05-TB40-GC1	29 July 2005	4°52.563′	29°36.183′	76	43 cm/MUCK-Gravity Core	Significant (in Kigoma Bay, high human population density and fishing nearby)

Table S2. ²¹⁰Pb data

NAC DNAC

Core name	D, cm	MD, cm	CM, g⋅cm ⁻²	²²⁶ Ra, dpm·g ^{−1}	xs ²¹⁰ Pb, dpm·g ^{−1}	¹³⁷ Cs, dpm·g ^{−1}	LSR, cm∙y ⁻¹	MAR, mg·cm ⁻² ·y ⁻¹	AYI, year A.D., ±
NP05-TB40	1–2	1.5	1.41	4.1 ± 0.2	24.0 ± 1.2	0 ± 0.00	0.38	266.96	2002.9 ± 0.4
	2–3	2.5	2.76	4.2 ± 0.2	20.3 ± 1.2	0 ± 0.00	0.29	268.55	1997.8 ± 0.4
	3–4	3.5	3.99	4.3 ± 0.2	19.3 ± 1.2	0 ± 0.00	0.26	240.98	1992.7 ± 0.5
	4–5	4.5	4.99	3.5 ± 0.1	17.3 ± 0.9	0 ± 0.00	0.25	231.46	1988 ± 0.6
	5–6	5.5	6.13	3.6 ± 0.2	19.8 ± 1.1	0.1 ± 0.01	0.23	170.84	1982.4 ± 0.6
	6–7	6.5	7.18	3.6 ± 0.1	18.4 ± 1.0	0 ± 0.00	0.21	148.94	1975.6 ± 0.8
	7–8	7.5	8.13	3.2 ± 0.2	17.1 ± 1.0	0.1 ± 0.00	0.2	127.47	1968.3 ± 1
	8–9	8.5	9.22	3.4 ± 0.2	14.6 ± 0.8	0.1 ± 0.00	0.18	115.61	1959.8 ± 1.3
	9–10	9.5	10.16	4.0 ± 0.2	16.8 ± 0.9	0.2 ± 0.01	0.16	71.03	1948.3 ± 1.9
	10–11	10.5	11.28	3.4 ± 0.2	11.4 ± 0.8	0.2 ± 0.01	0.14	65.39	1932.9 ± 3.2
	11–12	11.5	12.31	3.4 ± 0.2	7.4 ± 0.7	0.1 ± 0.01	0.12	57.6	1914.9 ± 5.7
	12–13	12.5	13.34	4.2 ± 0.2	3.4 ± 0.8	0.1 ± 0.01	0.11	74.32	1898.6 ± 9.3
	13–14	13.5	14.27	3.7 ± 0.2	1.9 ± 0.8	0.1 ± 0.01	0.11	90.51	1886.4 ± 13.3
	14–15	14.5	15.28	3.8 ± 0.2	1.6 ± 0.7	0 ± 0.00	0.11	74.42	1874.4 ± 19.9
	15–16	15.5	16.18	3.1 ± 0.2	0.8 ± 0.9	0 ± 0.00	0.11	109.65	1863.3 ± 27.5
	16–17	16.5	17.05	3.6 ± 0.1	-0.1 ± 0.7	0 ± 0.00	_	_	_
	17–18	17.5	18.06	3.0 ± 0.2	0.8 ± 1.0	0 ± 0.00	_	_	_
	18–19	18.5	18.95	3.1 ± 0.1	-0.1 ± 0.7	0 ± 0.00	_	_	_
	19–20	19.5	19.97	2.8 ± 0.2	0.6 ± 1.0	0 ± 0.00	—	_	_
	20–21.25	20.625	20.8	2.7 ± 0.2	0.5 ± 0.7	0 ± 0.00	—	_	_
	21.25–22	21.625	21.47	3.0 ± 0.3	0.8 ± 1.1	0 ± 0.00	—	_	_
	22–23	22.5	22.42	3.5 ± 0.1	-0.2 ± 1.0	0 ± 0.00	—	—	_
	23–24	23.5	23.24	3.4 ± 0.2	-0.3 ± 0.7	0 ± 0.00	—	_	_
	24–25	24.5	24.05	3.8 ± 0.2	0.6 ± 0.8	0 ± 0.00	—	_	_
LT-98–07M	2–3	2.5	0.19	3.4 ± 0.2	124.8 ± 2.5	0.9 ± 0.01	0.32	24.84	1993.8 ± 0.3
	3–4	3.5	0.57	3.2 ± 0.1	58.0 ± 1.5	0.6 ± 0.03	0.22	40.18	1984.7 ± 0.3
	4–5	4.5	1.09	2.9 ± 0.1	42.5 ± 1.2	0.6 ± 0.02	0.18	41.26	1975.5 ± 0.4
	5–6	5.5	1.98	3.3 ± 0.1	12.4 ± 1.2	0.1 ± 0.01	0.19	114.82	1969.1 ± 0.5
	6–7	6.5	2.41	2.7 ± 0.1	18.1 ± 0.9	0 ± 0.02	0.19	69.12	1964.9 ± 0.5
	7–8	7.5	3.26	2.8 ± 0.1	15.9 ± 1.5	0 ± 0.01	0.19	66.34	1959.4 ± 0.7
	8–9	8.5	4.01	3.2 ± 0.1	26.1 ± 1.3	0.1 ± 0.00	0.16	30.75	1950.1 ± 1
	9–10	9.5	4.72	3.4 ± 0.1	16.4 ± 1.1	0 ± 0.00	0.15	32.44	1936.8 ± 1.5
	10–11	10.5	5.31	2.9 ± 0.1	5.2 ± 1.0	0.1 ± 0.00	0.15	73.82	1927 ± 1.9
	11–12	11.5	5.99	2.7 ± 0.2	4.5 ± 1.2	0.1 ± 0.00	0.15	70.57	1920.8 ± 2.4
	12–13	12.5	6.89	3.3 ± 0.2	5.2 ± 1.0	0 ± 0.00	0.14	48.04	1912.9 ± 3.2
	13–14	13.5	7.33	3.0 ± 0.1	4.3 ± 0.8	0 ± 0.00	0.14	42.14	1902.4 ± 4.6
	14–15	14.5	7.78	2.9 ± 0.1	4.4 ± 1.1	0 ± 0.00	0.12	26.75	1887.5 ± 8.2
	15–16	15.5	8.74	2.6 ± 0.1	3.5 ± 1.3	0 ± 0.00	0.11	16.68	1863.3 ± 20.6
	16–17	16.5	9.42	2.9 ± 0.1	2.3 ± 1.2	0 ± 0.00	_	_	_

The modern geochronology and mass sedimentation rate for select sediment cores (including NP04-KH1/MC1) collected in Lake Tanganyika are presented and discussed in refs. 12, 35–37. Cores NP05-TB40 and LT98-07 were processed and interpreted using identical analytical methods and modeling techniques. For all three cores, an age model was derived using multiple methods including a constant rate of supply (CRS) model that were corroborated by both ¹³⁷Cs and accelerator mass spectrometry ¹⁴C data. All sediment cores showed an exponential downcore decrease in unsupported (excess, xs) ²¹⁰Pb activity, readily interpretable as a mean linear sediment rate (0.05 cm·y⁻¹ in NP04-KH1/MC1, 0.13 cm·y⁻¹ in LT-98-07, and 0.1–0.38 cm·y⁻¹ in NP05-TB40. In cores LT98-07 and NP04-KH1/MC1, the excess ²¹⁰Pb activity exceeded 100 dpm·g⁻¹ in surface sediment and decreased to parent-supported values of ~3 dpm·g⁻¹ at depth. Excess ²¹⁰Pb activities in surface sediment from core NP05-TB40 did not exceed 24 dpm·g⁻¹. 2A NP-05-TB40; 2B LT-98-07. AYI, average year of interval; CM, cumulative mass; D, depth; LSR, linear sedimentation rate; MAR, mass accumulation rate; MD, midpoint depth.

Table S3. ¹⁴C age data

UA-AMS ID no.	Material/core and depth	$\delta^{13}C$	F (δ ¹³ C)	dF (δ ¹³ C)	¹⁴ C age B.P.	SD ¹⁴ C age	Cal age, year A.D.	SD cal age
AA103055	Plant fragment/LT98-07, 52–53cm	-24.7 -25.8	0.9471 0.856	0.0058	437 1249	49 75	1495 780	64 84
AA103809	Leaf/NP05-40, 38.5cm	-25.8	0.856	0.008	1249	75	780	

Cohen et al. www.pnas.org/cgi/content/short/1603237113

SANG SAL

CD	В	S	B+S	BG	SG	TG	0	OG	М	MG	Year A.D.
1	0	0	0	0	0	0	1	6.05	0	0	1994
2	9	0	9	1.08	0	1.08	11	1.32	0	0	1991
3	8	4	12	1.43	0.72	2.15	39	6.99	2	0.36	1986
4	35	3	38	5.67	0.49	6.16	71	11.50	0	0	1981
5	2	1	3	0.26	0.13	0.38	97	12.37	0	0	1975
6	6	5	11	1.07	0.89	1.97	89	15.93	0	0	1969
7	13	6	19	2.17	1.00	3.16	161	26.79	24	3.99	1962
8	62	3	65	8.73	0.42	9.15	57	8.03	0	0	1954
9	6	0	6	0.84	0	0.84	75	10.53	0	0	1945
10	10	5	15	1.46	0.73	2.18	69	10.04	0	0	1936
11	9	3	12	1.60	0.53	2.13	70	12.45	0	0	1925
12	3	10	13	0.58	1.92	2.50	60	11.52	0	0	1915
13	19	5	24	2.58	0.68	3.26	119	16.16	0	0	1903
14	16	3	19	2.30	0.43	2.73	0	0	0	0	1891
15	20	7	27	3.63	1.27	4.91	0	0	0	0	1877
16	11	12	23	1.91	2.08	3.99	0	0	0	0	1858
17	10	2	12	1.78	0.36	2.14	0	0	0	0	1848
18	61	15	76	9.37	2.30	11.67	0	0	0	0	1838
19	56	9	65	8.84	1.42	10.26	0	0	0	0	1828
20	5	1	6	0.64	0.13	0.77	0	0	0	0	1819
21	3	9	12	0.36	1.08	1.44	0	0	0	0	1809
22	13	28	41	1.51	3.25	4.76	0	0	0	0	1799
23	35	8	43	5.63	1.29	6.91	1	11.40	0	0	1789
24	30	3	33	5.63	0.56	6.20	3	26.29	0	0	1779
25	58	34	92	9.53	5.59	15.11	9	86.2	0	0	1769
26	27	10	37	3.99	1.48	5.47	0	0	0	0	1759
27	29	16	45	4.49	2.48	6.97	7	79.19	0	0	1749
28	32	31	63	4.71	4.56	9.27	3	35.93	0	0	1739
29	82	14	96	12.19	2.08	14.28	0	0	0	0	1729
30	54	8	62	7.17	1.06	8.23	0	0	0	0	1719
31	15	5	20	1.94	0.65	2.58	0	0	0	0	1709
32	15	15	30	2.68	2.68	5.36	0	0	0	0	1699
33	27	5	32	3.46	0.64	4.10	0	0	0	0	1689
34	13	15	28	1.84	2.12	3.95	0	0	0	0	1679
35	24	10	34	3.64	1.52	5.17	0	0	0	0	1669
36	43	16	59	5.53	2.06	7.58	2	0.26	0	0	1659
37	25	10	35	3.46	1.38	4.84	0	0	0	0	1649
39	108	6	114	17.68	0.98	18.66	0	0	0	0	1629
40	25	21	46	4.20	3.53	7.74	0	0	0	0	1619
41	15	7	22	2.22	1.04	3.26	0	0	0	0	1609
42	24	30	54	5.13	6.41	11.53	2	0.42	0	0	1600
43	11	2	13	2.07	0.38	2.44	0	0	1	0.19	1590
44	23	1	24	3.34	0.15	3.48	0	0	1	0.15	1580
45	20	8	28	2.56	1.02	3.58	0	0	0	0	1570
46	11	5	16	1.56	0.71	2.27	0	0	0	0	1560
4/	14	16	30	1.87	2.13	4.00	2	0.27	2	0.27	1550
48	64	6	70	8.15	0.76	8.92	0	0	11	1.40	1540
49	65	14	79	10.90	2.35	13.24	0	0	0	0	1530
50	17	14	31	2.05	1.69	3.73	1	0.12	2	0.24	1520
51	27	4	31	4.36	0.65	5.01	0	0	18	2.91	1510
52	22	18	40	2.73	2.24	4.97	0	0	0	0	1500
53	56	8	64	7.37	1.05	8.42	0	0	0	0	1490

Table header key: Age, assigned model ages based on Tables S2 and S3 (cal year A.D.); B, total fish bone count; B+S, total fish bones plus scales; BG, fish bones per gram dry weight of sediment; CD, core depth midpoint (in centimeters); M, total mollusc fossil count (all fragments counted); MG, mollusc fossils per gram dry weight; O, total ostracode count (valves); OG, ostracode valves per gram dry weight (note rare ostracodes in LT98-07 are fragmented and appear to have been transported downslope); OM, other identifiable molluscs present [A, Anceya; C, Chytra kirki; B, Bathanalia; M, Martelia; B, Burnupia caffra(?); Ca, Caelatura]; S, total fish scale count; SG, fish scales per gram dry weight of sediment; TG, total fish fossils per gram dry weight of sediment; TI%, percentage of identifiable molluscs that are *Tiphobia horei* (NP05TB40 only); TO%, percentage of identifiable molluscs that are *Tomichia gulleimei*. Sample at 38 cm lost during preparation. Fossil fish flux calculations (as numbers of fossils accumulating per square centimeter of lake floor per year) follows methods presented in ref. 18. Table S4 shows core LT98-07; Table S5 shows NP05-TB40; and Table S6 shows MC1/KH1. Note: There are no downcore trends in fish or mollusc fossil preservation in any of the cores that might suggest a taphonomic (i.e., recent preferential dissolution) explanation for quantitative trends observed in the data.

CD	В	S	BG	SG	0	OG	М	MG	TI%	TO%	ОМ	Year A.D.
1.5	12	22	12.61	23.1	379	398.38	32	33.64	16	83.3		2003
2.5	16	21	12.41	16.3	753	584.02	38	29.47	33.3	66.7		1998
3.5	39	35	19.86	17.8	1,420	723.12	90	45.32	20.0	40.0	A,C	1993
4.5	32	30	20.87	19.6	1,960	1,278.57	116	75.67	20.0	40.0	А	1988
5.5	42	44	22.62	23.7	1,394	750.66	90	47.93	7.1	78.6	В	1982
6.5	60	54	30.09	27.1	2,241	1,123.91	143	71.47	0.0	100.0		1976
7.5	67	53	27.89	22.1	2,663	1,108.40	160	66.60	60.0	33.3	В	1968
8.5	43	45	18.32	19.2	1,386	590.64	126	53.69	4.3	95.7		1960
9.5	49	46	30.60	28.7	1,168	729.43	87	54.33	14.3	85.7		1948
10.5	34	15	28.37	12.5	718	599.17	77	64.26	10.0	90.0		1933
11.5	23	27	16.53	19.4	720	517.33	81	58.20	33.3	66.7		1915
12.5	31	44	11.82	16.8	919	350.55	104	39.67	12.5	87.5		1899
13.5	61	62	25.60	26.0	1,122	470.91	177	74.29	92.9	7.1		1886
14.5	70	61	32.12	28.0	1,035	474.95	133	61.03	0.0	100.0		1874
15.5	75	58	36.63	28.3	1,913	934.21	161	78.62	25.0	75.0		1863
16.5	68	91	31.95	42.8	2,200	1,033.69	219	102.90	10.0	90.0		1809
17.5	72	46	42.84	27.4	1,326	788.94	132	78.54	0.0	100.0		1781
18.5	108	47	58.38	25.4	1,033	558.40	212	114.60	9.5	85.7	А	1752
19.5	70	45	53.26	34.2	842	640.63	209	159.02	17.4	78.3	В	1721
20.6	62	39	54.66	34.4	1,206	1,063.19	122	114.17	0.0	92.3	Ca	1688
21.6	38	33	46.58	40.5	1,018	1,247.88	68	83.36	0.0	100.0		1653
22.5	61	62	41.74	42.4	1,512	1,034.54	162	109.13	20.0	80.0		1616
23.5	73	86	38.35	45.2	1,185	622.52	168	88.26	26.3	68.4	Ca	1578
24.5	70	62	50.12	44.4	879	629.30	218	153.92	30.8	69.2		1538
25.5	61	69	41.69	47.2	1,132	773.74	223	157.21	27.3	72.7		1495
26.5	75	37	62.31	30.7	917	761.89	307	255.07	31.3	68.8		1452
27.5	59	51	48.08	41.6	546	444.90	244	198.82	30.0	70.0		1406
28.5	81	65	37.50	30.1	683	316.17	496	229.60	57.6	36.4	Μ	1358
29.5	71	69	53.39	51.9	717	539.19	272	198.15	15.0	85.0		1309
30.5	67	61	47.36	43.1	1,711	1,209.52	270	182.38	35.3	64.7		1258
31.5	95	70	43.73	32.2	542	249.50	305	140.40	38.9	55.6	Μ	1205
32.5	21	16	30.45	23.2	732	1,061.38	117	169.65	15.8	84.2		1151
33.5	63	64	51.38	52.2	1,198	977.03	203	159.03	14.3	85.7		1094
34.5	80	65	43.68	35.5	953	520.35	350	191.11	18.5	81.5		1036
35.5	88	51	66.65	38.6	2,169	1,642.66	285	206.37	30.0	70.0		976
36.5	91	54	76.41	45.3	612	513.89	245	205.73	39.1	47.8	М	914
37.5	123	42	76.35	26.1	536	332.70	323	204.52	64.7	35.3		850
38.5	82	52	71.30	45.2	908	723.84	238	203.17	52.4	47.6		785
39.5	55	58	38.13	40.2	1,290	894.26	286	198.26	61.9	38.1		717
40.5	60	56	42.23	39.4	688	484.23	399	280.83	57.1	39.3	А	648
41.5	55	52	51.57	48.8	984	922.71	191	179.10	52.9	35.3	M,B	577
42.5	47	46	38.64	37.8	303	249.13	338	277.91	85.2	14.8		505

Table S5. Fossil count data: NP05-TB40

PNAS PNAS

For details, please refer to the legend of Table S4.

Table 50.	rossii count data: MCI/KHI	
Core depth	Fish fossil flux, no.·cm ⁻² ·y ⁻¹	Year A.D.
0.25	0.07	1996
0.75	0.04	1986
1.25	0.04	1976
1.75	0.04	1966
2.25	0.00	1956
2.75	0.00	1946
3.25	0.05	1936
3.75	0.09	1926
4.25	0.05	1916
4.75	0.00	1906
5.25	0.38	1896
5.75	0.27	1886
6.25	0.21	1876
6.75	0.36	1866
7.25	0.17	1856
7.50	0.37	1851
8.00	0.25	1841
8.50	0.09	1831
9.00	0.00	1821
9.50	0.05	1811
10.00	0.17	1801
10.50	0.43	1791
11.00	0.04	1781
11.50	0.27	1771
12.00	0.22	1761
12.50	0.09	1751
13.00	0.71	1741
13.50	1.00	1731
14.00	0.11	1721
14.50	0.00	1711
15.00	0.07	1701
15.50	0.11	1691
16.00	0.00	1681
16.50	0.00	1671
17.00	0.17	1661
17.50	1.33	1651
18.00	0.49	1641
18.50	1.58	1631
19.00	0.18	1621
19.50	0.08	1611
20.00	0.15	1601
20.50	0.03	1591

Table S6. Fossil count data: MC1/KH1

For details, please refer to the legend of Table S4.

PNAS PNAS

Depth, cm	TEX ₈₆	Temperature, °C	Model age, cal year A.D.
1.5	0.7193191	26.2	2003
2.5	0.7131414	25.9	1998
3.5	0.7035016	25.4	1993
5.5	0.7020184	25.3	1982
7.5	0.6981632	25.1	1968
9.5	0.6894518	24.7	1948
10.5	0.6941301	24.9	1933
12.5	0.6920604	24.8	1899
14.5	0.6873199	24.6	1874
16.5	0.6790971	24.1	1809
18.5	0.6819401	24.3	1752
20.5	0.6840913	24.4	1688
22.5	0.6796431	24.2	1616
24.5	0.6730918	23.8	1538
26.5	0.6769116	24.0	1452
28.5	0.6801971	24.2	1358
30.5	0.6819589	24.3	1258
33.5	0.675911	24.0	1094
37.5	0.6866739	24.5	850
39.5	0.6740983	23.9	717
41.5	0.6798109	24.2	505

Table S7. TEX $_{86}$ data: Data for core NP05-TB40, with temperatures calculated from the global lakes calibration of ref. 33

This calibration yields excellent agreement between reconstructed and instrumentally determined modern temperatures, and a rate of warming in the last century (0.135 °C/decade) that is within error of instrumental and modeled temperatures 0.129 \pm 0.023 (21).

PNAS PNAS

Table S8.	TEX ₈₆ data: Data for core MC1-KH1, with	
temperatu	res calculated from the global lakes calibration of	f
Powers et	al. (33)	

Model age, cal year A.D.	TEX ₈₆	Temperature, °C
1996	0.752	27.844
1986	0.749	27.708
1976	0.733	26.873
1966	0.722	26.314
1956	0 720	26 206
1936	0.720	25.200
1026	0.710	25.725
1930	0.707	25.557
1926	0.705	25.474
1918	0.709	25.676
1898	0.698	25.100
1879	0.678	24.104
1865	0.679	24.144
1852	0.687	24.550
1838	0.698	25.107
1824	0.711	25.772
1809	0.700	25.226
1794	0.704	25,434
1779	0.696	25.028
1764	0.050	23.020
17.04	0.000	24.510
1748	0.694	24.881
1/33	0.700	25.222
1700	0.691	24.771
1683	0.672	23.767
1666	0.701	25.279
1649	0.672	23.779
1631	0.688	24.587
1614	0.688	24.581
1596	0.668	23.578
1577	0 702	25 325
1559	0.683	22.323
1555	0.005	24.520
1540	0.003	24.400
1521	0.697	25.047
1501	0.678	24.078
1481	0.680	24.214
1461	0.674	23.880
1441	0.676	23.967
1420	0.670	23.670
1400	0.700	25.183
1378	0.694	24.902
1357	0.700	25.219
1335	0.715	25,993
1319	0 707	25 553
1297	0.695	2/ 961
1237	0.000	24.301
1274	0.091	24.750
1252	0.710	25.996
1229	0.687	24.538
1205	0.698	25.109
1182	0.700	25.201
1158	0.694	24.918
1134	0.699	25.150
1110	0.704	25.387
1085	0.686	24.519
1060	0.679	24.122
1035	0.672	23,803
1009	0.680	24 177
003	0.000	24.1//
704		24.942
824	0.6/3	23.83/
931	0.676	23.970
905	0.675	23.945
878	0.680	24.206
851	0.681	24.220

PNAS PNAS

Table S8. Cor	٦t.
---------------	-----

Model age, cal year A.D.	TEX ₈₆	Temperature, °C
824	0.673	23.837
796	0.688	24.615
768	0.691	24.762
740	0.671	23.709
711	0.697	25.030
682	0.695	24.928
653	0.688	24.576
624	0.701	25.269
594	0.701	25.264
565	0.710	25.712
534	0.707	25.580
504	0.704	25.384

Reconstructed warming at this site exceeds the rate of instrumentally measured warming over the last century, likely due to the effects of a shallowing oxycline on the TEX₈₆ producers. This effect is less apparent at the shallower NP05-TB40 site. To explore potential changes in GDGT sources and their possible impact on the TEX₈₆ signal, we quantified the relative abundance of branched to isoprenoidal tetraethers (BIT) (34). BIT values were less than 0.3 in all samples and are uncorrelated to TEX₈₆ values.

Table S9. Break point analysis results for analyzed variables

Variable	Break point, cal year A.D.	95% CI (±)
NP05 (Kigoma)-TEX temperature, °C	1854	50.44
NP05-molluscs, g ⁻¹	1451	224.6
NP05-fish scales, g ⁻¹	1614	168.68
NP05-fish bones, g ⁻¹	1743	134.68
LT98-07-fish (bones + scales), g^{-1}	1768	143.52
MC1 (Kalya)-TEX temperature, °C	1903	31.06
MC1-BiSi	1872	27.08
MC1-fish fossil flux, no.·cm ⁻² ·y ⁻¹	1866	70.58

Break point calculations performed in R, using the "segmented" package.

Tab	le	S10.	Corre	lation	matri	ces (P	' va	lues)	for	core	NP05-4	0
-----	----	------	-------	--------	-------	--------	------	-------	-----	------	--------	---

PNAS PNAS

Variable	Lake level	NP05 fish scales, g^{-1}	NP05 fish bones, g^{-1}	NP05-mollusc fossils, g ⁻¹	NP05-ostracode valves, g ⁻¹
All data					
NP05-40 TEX ₈₆	0.425647536 (0.089)	-0.739406622 (0.0001)	-0.69723676 (0.0004)	-0.717773379 (0.0002)	-0.227091146 (0.322)
Lake level		-0.34537518 (0.066)	-0.463044933 (0.011)	-0.43455422 (0.018)	-0.140837543 (0.466)
NP05 scales, g ⁻¹			0.63387024 (< 0.00001)	0.603753726 (0.00002)	0.17391001 (0.271)
NP05 bones, g ⁻¹				0.699723 (< 0.0001)	0.109598205 (0.492)
NP05-molluscs					-0.092710154 (0.559)
Before TEX ₈₆ break	point				
NP05-40 TEX ₈₆	-0.256527936 (0.050)	-0.590435261 (0.094)	0.463804954 (0.209)	–0.131170937 (0.737)	-0.162866008 (0.676)
Lake level		-0.021700724 (0.939)	-0.18461004 (0.51)	-0.045158922 (0.873)	-0.381533844 (0.161)
NP05 scales, g ⁻¹			0.02621041 (0.927)	-0.002870965 (0.992)	0.180593293 (0.519)
NP05 bones, g ⁻¹				0.423737856 (0.116)	-0.090637948 (0.748)
NP05-molluscs					-0.218431839 (0.434)
Since TEX ₈₆ break p	oint				
TEX ₈₆	-0.419317445 (0.301)	-0.241843088 (0.449)	–0.703594418 (0.011)	-0.712301466 (0.009)	-0.104186517 (0.748)
Lake level		0.453087222 (0.104)	0.586726698 (0.027)	0.325791432 (0.256)	0.051469274 (0.863)
NP05 scales, g ⁻¹			0.620397724 (0.0006)	0.398679881 (0.039)	0.203741188 (0.308)
NP05 bones, g ⁻¹				0.757266734 (< 0.00001)	0.445658177 (0.02)
NP05-molluscs					0.587929328 (0.001)

Bold P values < 0.05. Shown are whole dataset, before TEX break point, and since TEX break point (1854).

Table S11. Correlation matrices (P values)

PNAS PNAS

Variable	MC1-TEX ₈₆	MC1-BiSi	MC1-fish fossil flux	LT-98-07 fish bones + scales
Whole dataset				
Lake level	0.102992553 (0.468)	-0.296201787 (0.033)	-0.034158582 (0.81)	-0.234932522 (0.0935)
MC1-TEX ₈₆		-0.362657167 (0.0004)	-0.164736782 (0.136)	-0.170319982 (0.113)
MC1-BiSi			0.071623235 (0.507)	0.0885958 (0.412)
			D.A. 0.17306 (0.276)	D.A. 0.32 (0.036)
			R.A. 0.174 (0.118)	R.A. 0.287 (0.008)
MC1-fish fossil flux				0.374053872 (0.0005)
After TEX break point	t			
Lake level	-0.070717394 (0.836)	-0.458591134 (0.156)	-0.191002533 (0.623)	-0.103476221 (0.762242)
MC1-TEX ₈₆		-0.388335405 (0.238)	0.264811575 (0.491)	-0.032544192 (0.924)
MC1-BiSi			0.630303332 (0.0688)	-0.435058112 (0.181)
			D.A. 0.972 (< 0.001)	D.A0.161 (0.51)
			R.A. 0.702 (0.003)	R.A0.0003 (0.999)
MC1-fish fossil flux				0.030200134 (0.93)
Before TEX break point	nt			
Lake level	-0.230045375 (0.139)	-0.116673264 (0.467)	0.089780085 (0.567)	-0.187370856 (0.241)
MC1-TEX ₈₆		0.166275287 (0.14)	-0.03442182 (0.763)	-0.080563863 (0.486)
MC1-BiSi			-0.052420197 (0.646)	-0.020266773 (0.861)
			D.A0.065 (0.738)	D.A0.019(0.922)
			R.A0.041 (0.731)	R.A. 0.044(0.711)
MC1-fish fossil flux				0.361346325 (0.001)

Mahale area core records (MC1 and LT98-07). Shown are whole dataset, since TEX break point (1903, \sim 50 y before the start of commercial pelagic fishing), and before TEX break point. MC1 BiSi data are compared with the nearby LT-98-07 fish bone record because there was insufficient mud available remaining in LT-98-07 samples after fossil preparations to perform BiSi analyses. D.A., decadal average smoothing calculations. All data gaps filled with nearest neighbor (as long as it is within 10 y of neighbor). All data used where at least one of the variables had raw data. R.A., Three-point running average smoothing calculations. Correlations with P < 0.05 are highlighted in bold.