

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

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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

Warming 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.

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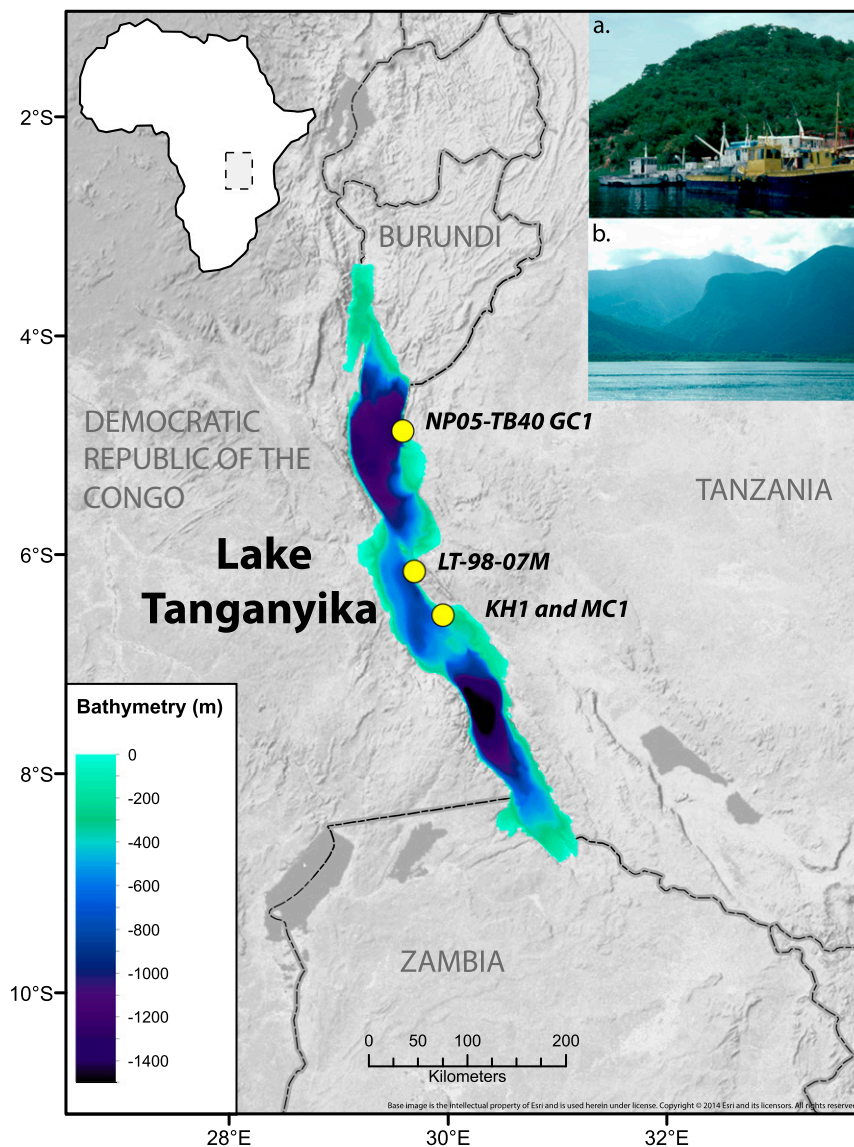


Fig. 1. Lake Tanganyika and coring locations. (Inset A) Commercial (purse seine) fishing boats on Lake Tanganyika at Mpulungu, Zambia; (B) Rift mountains flanking L. Tanganyika at Mahale Mountains National Park near core site LT98-07. Steep mountain slopes are indicative of underwater slopes. Base map 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 $1 \text{ mg}\cdot\text{L}^{-1}$) relative to molluscs (generally $>4 \text{ mg}\cdot\text{L}^{-1}$) (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 TEX_{86} -inferred lake temperature data from core NP05-TB40 (Fig. 3A and Tables S7 and S8) together with published records from 200 km to the south (MC1/KH1; Fig. 2A) (12) show significant warming after the late 19th century [break points in $\sim 1903 (\pm 31 \text{ y})$; MC-1) and $\sim 1854 (\pm 50 \text{ y})$; NP05-TB40) (Table S9)]. Warming rates in the 20th century were unprecedented in the past $\sim 1,500 \text{ y}$ (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. 3B) 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

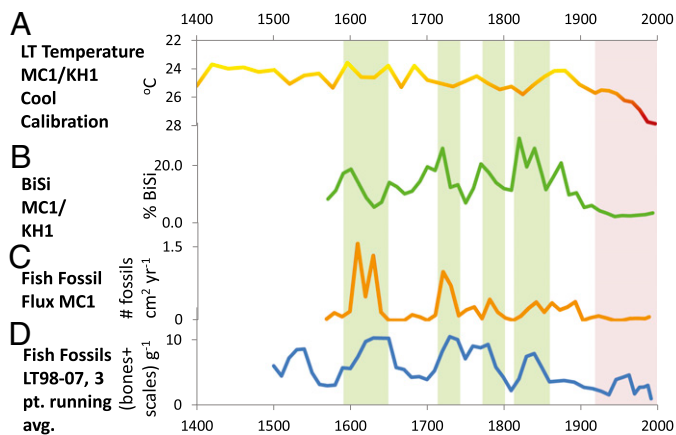


Fig. 2. Paleoecological records from cores MC1/KH1 and LT98-07 from A.D. 1400 to 2000. (A) TEX_{86} reconstructed lake temperatures (note inverted scale) (12), using a “cool-lake” calibration (29). (B) Percentage of sediment as BiSi, dominantly derived from diatom fossils (12). (C) Fish fossil flux (number 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 ($\sim 1872 \pm 27$ y), as TEX_{86} 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. 2C and D, and 3C and D). At NP05-TB40,

fish fossils (total bones plus scales) are significantly negatively correlated with TEX_{86} 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 tanganyicae*) 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 ($\sim 1768 \pm 144$ 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 ~ 6 th to 18th centuries, followed by long-term declines since ~ 1800 (Figs. 3C 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

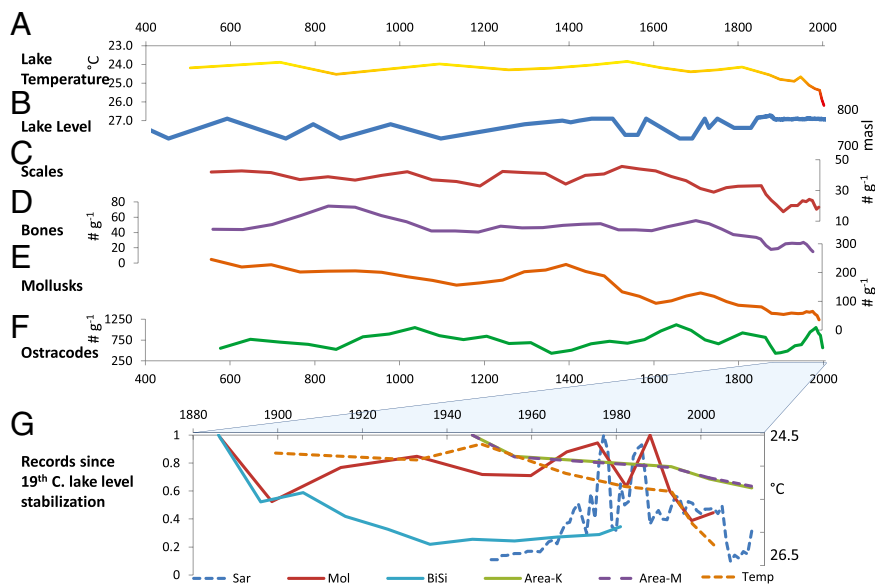


Fig. 3. Paleoecological records from core NP05-TB40 from A.D. 400 to 2000. (A) Lake temperature for NP05-TB40 (cool calibration; note inverted scale) (29). (B) Lake level history (8, 22). Preinstrumental (1870) measurements are ± 5 m SD. (C) Fish scale abundance (3-point running average) number of scales 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 $O_2 L^{-1}$ in the Kigoma area lake margin relative to 1946; Area M, same for north Mahale coast; BiSi, MC1 BiSi; Mol, NP05-TB40 fossil mollusks; Sar, annual Tanzanian sardine catch (www.fao.org/fishery/statistics/en); Temp-NP05-TB40 TEX temperature.

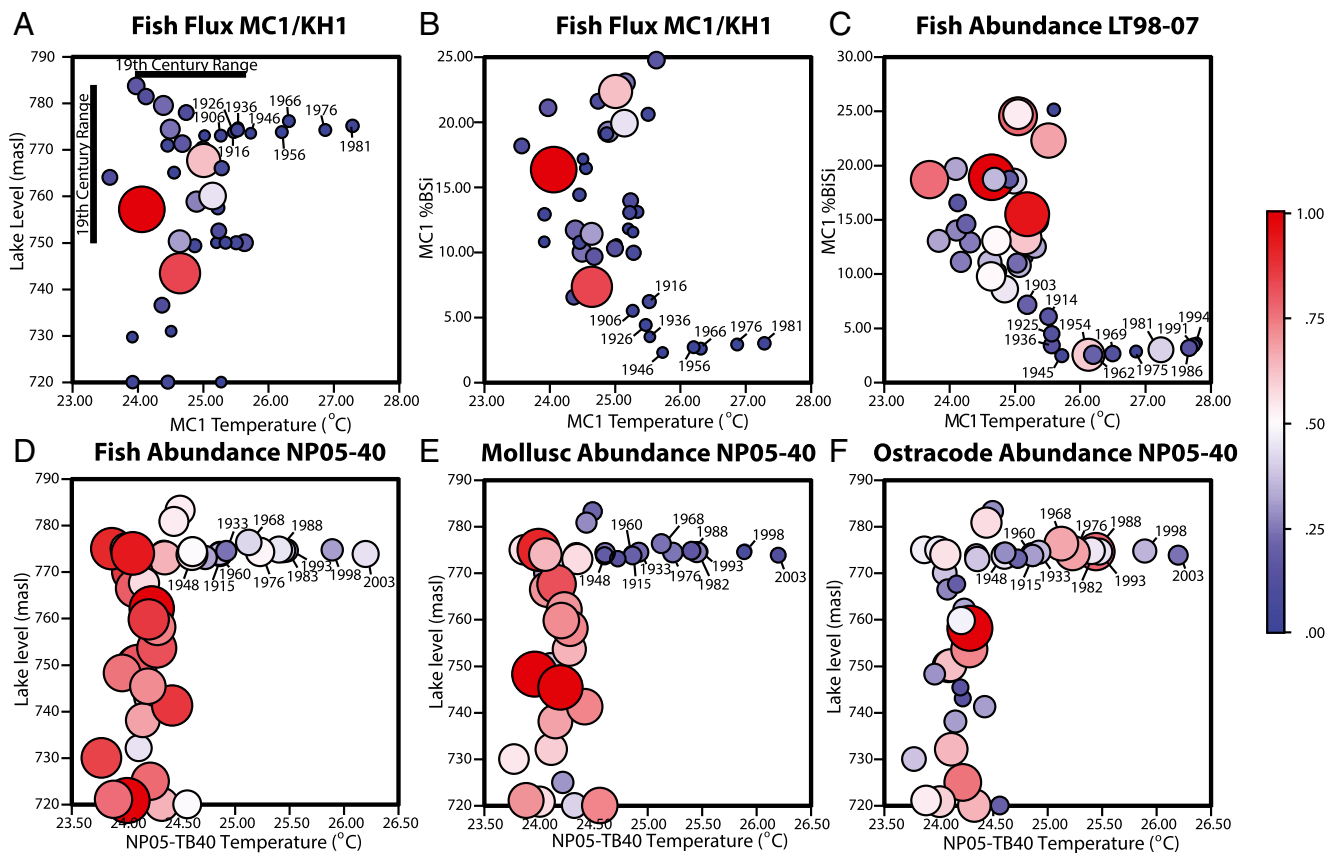


Fig. 4. Fossil abundances of fish, molluscs, and ostracodes relative to key paleoenvironmental variables, showing distinct 20th century trends and declining abundances in all fossils except ostracodes. Color and size of bubbles are proportional to the maximum value for each dataset, with warmer colors 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 %BiSi 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 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 gulleimeii*; Table S5) were consistently high between the ~6th and ~15th centuries, followed by a long-term decline (break point, $\sim 1451 \pm 225$ y), with extremely low numbers of shells encountered in the late 20th century (Figs. 3E and 4E). 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. 3F and 4F) 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 O_2 concentrations vary seasonally between 0.7 and 5.0 $mg \cdot L^{-1}$), but historic water temperature measurements and TEX_{86} 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. 1B) 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 $mg \cdot L^{-1}$ oxygen threshold corresponded to habitable lake floor areas of 92.8 and 65.87 km^2 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. 1B), culminating in a ~38% reduction in habitable lake floor since 1946 (Fig. 3G).

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 ~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 ^{210}Pb and ^{137}Cs profiles analyzed at the US Geological Survey (USGS) Santa Cruz radiochemistry laboratory, and corroborated by accelerator mass spectrometry ^{14}C dates. ^{14}C 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.

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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 \times 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 Al_2O_3 column using 9:1 hexane/DCM and 1:1 DCM/MeOH as eluents. The polar fraction was dried under N_2 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 TEX_{86} 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 $4 \text{ mg O}_2 \text{ L}^{-1}$, which 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 TEX_{86} temperature break points. Statistical break point analysis was performed in R (R Development Team) using the “segmented” package.

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