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Table S1  
References and Notes

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## Ecological Consequences of a Century of Warming in Lake Tanganyika

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Deep tropical lakes are excellent climate monitors because annual mixing is shallow and flushing rates are low, allowing heat to accumulate during climatic warming. We describe effects of warming on Lake Tanganyika: A sharpened density gradient has slowed vertical mixing and reduced primary production. Increased warming rates during the coming century may continue to slow mixing and further reduce productivity in Lake Tanganyika and other deep tropical lakes.

Evidence for global climate warming is accumulating, and most of the data that are relevant to inland waters are coming from long-term monitoring records on temperate lakes and glacial and high-latitude systems (1, 2). Tropical ecosystems, including lakes, are less frequently analyzed quantitatively. Consequently, recorded impacts of climatic change on tropical terrestrial and inland water ecosystems are rare. The stratified water column and the large volume and low flushing rates of deep tropical lakes allows them to store heat and furnish a record of long-term trends. Lake Tanganyika records a century-long warming trend, and the impacts on its pelagic ecosystem are evident.

Lake Tanganyika is a large Rift Valley lake (670 km by 50 km) (Fig. 1) in East Africa, just south of the equator (3° to 9°S), with deep basins in the north (maximum depth 1310 m) and the south (maximum depth 1470 m), separated by a sill of 600 m. A few surveys in the past century have published profiles of its nutrients and temperature (3–7). Temperatures in the north basin have increased since 1913 by 0.2°C near the bottom and by 0.9°C at 100 m (8) (Fig. 2A).

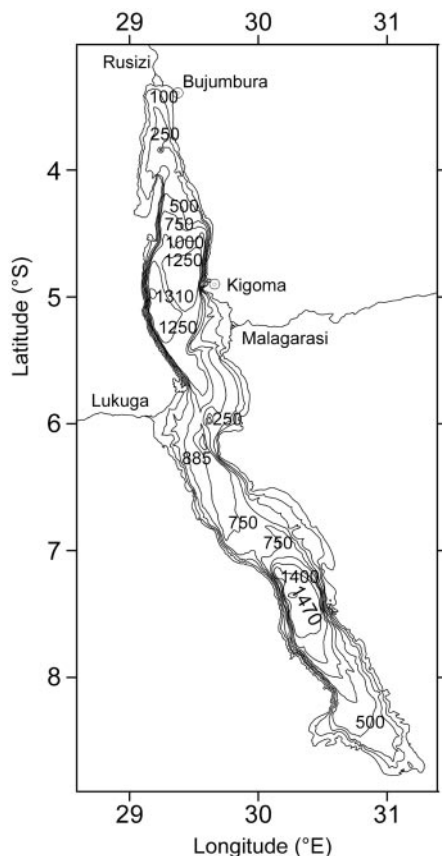
Fifty percent of the heat gained by the lake between 1913 and 2000 is in the upper 330 m (8), increasing the vertical temperature gradient (Fig. 2B). Density decreases with increasing temperature and increases with salinity. The temperature gradient largely determines the density gradient at Lake Tanganyika because salinity varies only from 0.57 to 0.63 per mil from the surface to the bottom (9). Although absolute temperature differences are small in this tropical lake [annual mean air temperature was 1.6°C above bottom potential (corrected for pressure) temperature in 2000], density differences per degree Celsius are pronounced at these high water temperatures (10). Between 1913 and 2000, density gradients (8) roughly tripled between 110- and 200-m depth and between 200- and 800-m depth (Fig. 2C). The amount of work required to mix water layers is proportional to the difference in density (10). The density gradient in Lake Tanganyika combined with the extreme depth of the lake impedes vertical mixing.

Global air temperatures correlated well with air temperature at the north end of the lake based on annual means from between 1964 and 1991 ( $r^2 = 0.75$ ,  $P < 0.0001$ ) (11, 12). Air temperature at the north end of the lake increased by 0.81°C over only these 27 years ( $r^2 = 0.56$ ,  $P < 0.0001$ ), much above the global average (+0.42°C). The lake effect on the surrounding climate should be largest at the north end of Lake

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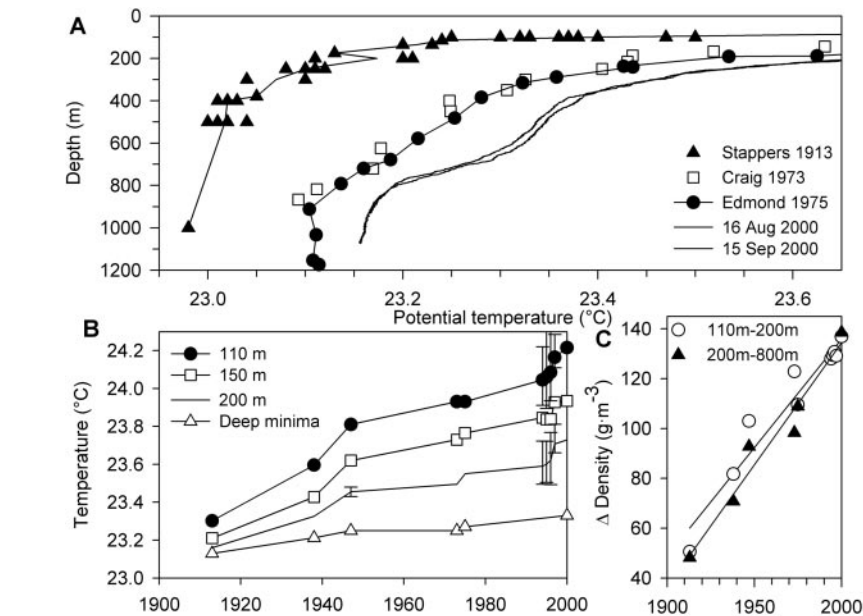
REPORTS



**Fig. 1.** Map of Lake Tanganyika with isobaths (depth shown in 250-m intervals).

Tanganyika because of the prevailing southeast trade winds (10). At the north end, air temperature in the warm seasons (November to April) increased more ( $r^2 = 0.58$ ,  $P < 0.0001$ ), and more consistently, than in the cool seasons ( $r^2 = 0.17$ ,  $P < 0.05$ ) since 1964. Lake surface water at the north end was, on average, 2°C warmer than the mean daily air temperature over the lake (at 2.6-m height) during the warm season, whereas lake surface and air temperatures were similar toward the end of the cool season. Upwelling of deep cool water by wind forcing at the south end of the lake during the cool season produces surface temperatures only slightly higher than those earlier in the century, whereas surface water temperature increased more during the warm season.

The increased density gradient in the water column retards vertical mixing, affecting the mixed-layer depth, the depth of penetration of oxygen, and upward mixing of nutrients. Lake Tanganyika is meromictic, with concentrations of nutrients (P and Si) that increase substantially with depth (7). The nutrient levels are low in the epilimnion, and primary production in the upper mixed layer depends on the recycling of nutrients by vertical mixing (13). Evidence for a reduced depth of oxygen penetration was first recog-



**Fig. 2.** (A) Depth profiles in the north basin of Lake Tanganyika of potential temperature for 1913 (3), 1973 (6), 1975 (7), 16 August 2000, and 15 September 2000 (8). The profile of 1913 includes data from the south basin (8). Surface temperatures are 26° to 27°C and are not shown. The legend shows authors with year of data collection. (B) Development of the temperature gradient through the 20th century. In situ temperatures at 110, 150, and 200 m, and minimum temperatures. Minimum in situ temperatures were at about 900-m depth between 1973 and 2000 but shallower between 1913 and 1947 when the water column was more homogeneous. Below the minima, the in situ temperature increases as a result of pressure effects (SOM text). Data for 1938 (4) and 1947 (5) were read from graphs. Vertical bars indicate the annual range of daily mean temperatures at 110 and 200 m for 1994 to 1996 (8). Ranges are also given for temperature at 200 m (32 profiles, lakewide) in December 1946 to August 1947 (5) and for 110 and 200 m in April to September 1997 (8). (C) Density gradients tripled across depth ranges 110 to 200 ( $r^2 = 0.94$ ,  $P < 0.0001$ ) and 200 to 800 m ( $r^2 = 0.95$ ,  $P < 0.0001$ ).

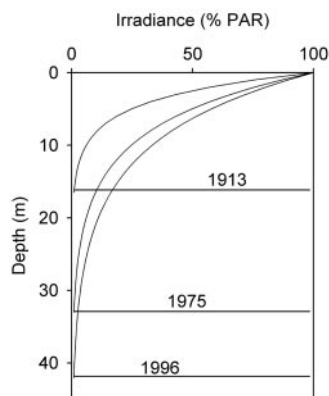
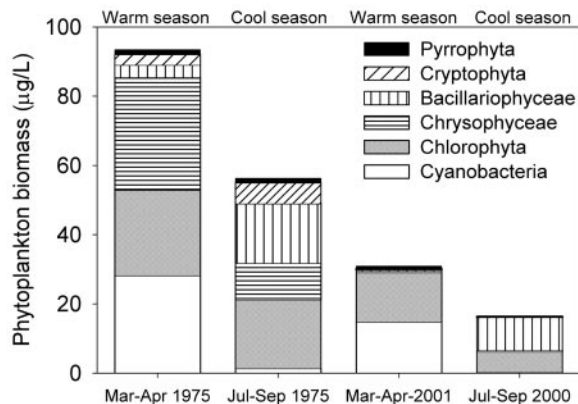
nized in 1950 (14) from the depth distribution of a gastropod (*Tiphobia horei*). In 1895, this snail was found down to 300-m depth but not above 76 m, despite extensive sampling [supporting online material (SOM) text, fig. S1]. In 1938 and 1947, it was found only above 100-m depth and up to the surface. Apparently, oxygen was present to 300-m depth a century ago, but it was not found below 182 m in April and August of 1997 (8). There are, however, few data on oxygen concentrations in the literature. Evidence for shallower anoxia is provided by the distribution of sulfur. In the mixed layer,  $SO_4$  has decreased from  $>4$  to  $<1$  mg/liter since 1938 (4, 15, 16). There is no evidence of lower riverine input of  $SO_4$ , and almost all of it (98%) is lost by  $SO_4$  reduction at the oxic-anoxic boundary. This agrees with the occurrence of  $H_2S$  at shallower depths. The shallowest depth of detectable  $H_2S$  in the north basin changed from 300 m in 1938 to 176 m in 1975 (4, 7, 15), and  $H_2S$  is now present at 120-m depth.

Few historic data on nutrient concentrations are available for comparison with the modern distributions. There is some evidence for lower concentrations of soluble reactive phosphorus (SRP) in the mixed layer. SRP was below detection limits (0.01  $\mu\text{mol}$ ) down

to 60 m in March to April 1998 in the north basin (17) and higher in April 1947 (18), February 1973 (6), and April 1975 (7) (mean  $\pm$  SD,  $0.29 \pm 0.25 \mu\text{mol}$ ;  $n = 13$ ). The distribution of dissolved silica presents a completely different aspect. Silica concentration below 100 m in the north basin was similar in 1938 (4), 1947 (18), 1973 (6), 1975 (7, 8), 2000, and 2001 (8), but in the upper 50 m it has tripled since 1975 (19). Sparse published data show no evidence of a change in silica loading by rivers (4, 6, 20, 21). The increase in silica in the mixed layer is a result of decreased diatom production, driven by a lower availability of nutrients such as phosphorus. Nutrient limitation lowers diatom sedimentation rates, and silica accumulates in the mixed layer.

Phytoplankton biomass in March to April 2001 and July to September 2000 (8) was much lower than in 1975 (22) during the same seasons, in both seasons by about 70% (Fig. 3) ( $P < 0.05$ ). Its composition also changed; cryptophytes and the chrysophytes (totaling 34% of the biomass in 1975) were nearly absent in the north basin in 2000 to 2001 (3%). Chrysophyceae were still present in the south basin (7% of the biomass in September 2000), where mixing is more intense because of upwelling and where

**Fig. 3.** Phytoplankton wet biomass and composition in the north basin, 6 to 10 km offshore from Kigoma, in 1975 (22) and in 2000 to 2001. Diatom (Bacillariophyceae) biomass is lowest in the stratified warm season.



**Fig. 4.** Underwater light [photosynthetically active radiation (PAR)] transmission and photic zone depth from 1913 to 1996. Horizontal bars indicate the depths at which light levels are 1% of light at 0-m depth. Vertical attenuation of light in 1913 was estimated from Secchi transparency.

epilimnetic nutrient concentrations are higher. Diatoms still constitute much of the north basin biomass in the mixing season. Their absolute biomass, however, decreased by 44% in the mixing season and by 88% in the stratified season between 1975 and 2000 to 2001 (Fig. 3).

Transparency over the past century showed a dramatic change in the pelagic ecosystem of Lake Tanganyika. Offshore Secchi depth, a measure of transparency, increased from a mean of 6.1 m to 15.5 m between 1913 and 1946 to 1947 (8). There was no change in mean transparency between 1947 and 1975 (8) (fig. S4), when global air temperature was stable (12). In the surveys of 1946 to 1947 and 1975, Secchi disk measurements were evenly distributed over the southern 550 km of the lake, but in the survey of 1913 there was a strong bias toward the south end (fig. S2). Data from 1913 were collected in January to February, when waters are clearest at the south end (about 20 m Secchi depth in 1960 to 1962; fig. S3) and clearer than at the north end of the lake (23, 24). If seasonality in transparency in 1913 was similar to that around 1960, then 6.1 m may be near the maximum transparency of the time.

Underwater light attenuation ( $K_d$ ), only available for 1975 and 1995 to 1996, has also declined (8). The euphotic zone ( $Z_{eu}$ ), defined as the depth at which light levels are 1% of light at the surface, was a mean of 33 m in 1975. In 1995 to 1996,  $Z_{eu}$  was deeper, measuring 42 m (Fig. 4). The amount of light reaching 20 m had doubled since 1975. With  $K_d = 1.7/\text{Secchi depth}$  (25) and a Secchi depth of 6.1 m in 1913, attenuation would be estimated as  $K_d = 0.28 \text{ m}^{-1}$ , and  $Z_{eu}$  was 16.5 m in 1913 (Fig. 4; SOM text). This is probably a conservative estimate if the lake-wide mean Secchi depth was <6.1 m in 1913.

Climate warming, through increased water density gradients, has apparently slowed vertical mixing and reduced primary production in Lake Tanganyika. Reduced mixing rates have also been reported for Lake Malawi, a similar deep Rift Valley lake in East Africa. Deep-water renewal rates in Lake Malawi as estimated with a CFC-12 gas tracer in 1997 were one-third to one-half of those in 1976 (26). In Lake Malawi, however, there is no evidence for the biological impacts observed on Lake Tanganyika because the historical data record is poorer.

While Lake Tanganyika has warmed in the past century, an increase in the temperature gradient in the water column reduced exchange rates between shallow and deep water. This reduced internal nutrient loading and primary production and allowed expansion of the anoxic water mass.

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