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Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa

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Although the effects of climate warming on the chemical and physical properties of lakes have been documented[1], biotic and ecosystem-scale responses to climate change have been only estimated or predicted by manipulations and models[1]. Here we present evidence that climate warming is diminishing productivity in Lake Tanganyika, East Africa. This lake has historically supported a highly productive pelagic fishery that currently provides 25–40% of the animal protein supply for the populations of the surrounding countries[2]. In parallel with regional warming patterns since the beginning of the twentieth century, a rise in surface-water temperature has increased the stability of the water column. A regional decrease in wind velocity has contributed to reduced mixing, decreasing deep-water nutrient upwelling and entrainment into surface waters. Carbon isotope records in sediment cores suggest that primary productivity may have decreased by about 20%, implying a roughly 30% decrease in fish yields. Our study provides evidence that the impact of regional effects of global climate change on aquatic ecosystem functions and services can be larger than that of local anthropogenic activity or overfishing.

Lake Tanganyika is a large (mean width, 50 km; mean length 650 km), deep (mean depth, 570 m; maximum depth, 1,470 m) north–south trending rift valley lake that is an important source of both nutrition and revenue to the bordering countries of Burundi, Tanzania, Zambia, and the Democratic Republic of Congo. The lake has historically supported one of the world's most productive pelagic fisheries[3], and the annual harvest in recent years has been estimated to be between 165,000 and 200,000 metric tons (54–66 kg ha^{-1}), with an equivalent value of tens of millions of US dollars[2]. The lake is oligotrophic and permanently thermally stratified with an anoxic hypolimnion. During the cool windy season (May to September), strong southerly winds tilt the thermocline, causing upwelling of deeper nutrient-rich waters at the south end of the lake and initiating seiche activity[4,5]. Cooling during this season also contributes to a weaker thermocline, and entrainment of deep nutrient-rich waters from the hypolimnion occurs in this time period[4]. Overall, these mixing events provide the dominant source of some limiting nutrients (P, Si) to the surface waters and are important in maintaining the pelagic food web[4–6].

Local records of air temperature from the Lake Tanganyika region show warming that is consistent with global patterns. Historical records show a rise of 0.5–0.7 °C in average annual air temperatures (Fig. 1a), consistent with the global increase of 0.6 ± 0.2 °C (ref. 7). The trend towards higher temperatures began primarily in the late 1970s and coincides with the timing of regional precipitation and temperature changes documented in several climate studies[8,9]. On a regional scale, East Africa showed warm temperature anomalies from 1910 to 1930, from 1940 to 1960, and since the late 1970s (ref. 9).

The effects of climatic warming can be seen in water temperature data from Lake Tanganyika[10–16]. Upper water-column temperatures (150-m depth) show a significant warming trend of 0.1 ± 0.01 °C per decade since 1913 ($r^2 = 0.76$, $F = 164$, $P < 0.0001$, $n = 53$, linear regression; Fig. 2a). Deep-water temperatures (600-m depth), which do not show seasonal variation and are generally homothermal between 400 m and 1,000 m, increased from 23.10 °C in 1938 to 23.41 °C in 2003 ($r^2 = 0.90$, $F = 74.3$, $P < 0.0001$, $n = 10$; refs 10–16 and Fig. 2b). This increase of 0.31 °C in deep-water temperature is comparable to that found in other African Great Lakes: Lake Victoria has warmed 0.3 °C between the 1960s and 1991 (ref. 17), the deep waters of Lake Malawi have warmed 0.29 °C since 1953 (refs 18, 19), and Lake Albert has warmed 0.5 °C since 1963 (ref. 20).

Along with increased temperatures, wind velocities in the Lake Tanganyika watershed have declined by 30% since the late 1970s (Fig. 1b). Records show that monthly averages of wind velocity during the cool windy season in the north remained constant at 2.2 ± 0.4 m s^{-1} until 1985, after which they decreased significantly to 1.6 ± 0.3 m s^{-1} (z-test, $Z = 7.54$, $P < 0.0001$, $n = 127$). In the

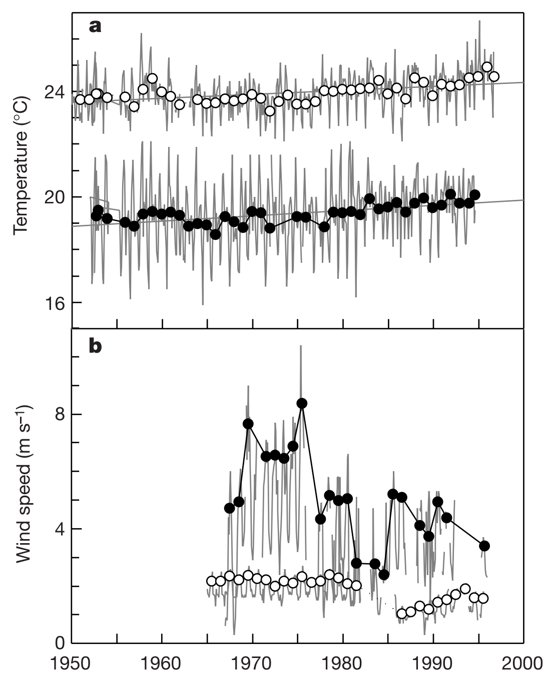

Figure 1 Historical meteorological records for the north (open circles) and south (filled circles) of Lake Tanganyika. **a**, Air temperatures. Monthly averages are shown in grey and are superimposed by annual means; regression (broken) lines are based on the full dataset. **b**, Wind speed. Monthly averages are shown in grey and are superimposed by windy season (May to September) means.

south, monthly averages for the cool windy season decreased significantly from $5.8 \pm 1.6\,\mathrm{m\,s^{-1}}$ to $4.0 \pm 1.3\,\mathrm{m\,s^{-1}}$ after 1977 (z-test, $Z = 7.38$, $P < 0.0001$, $n = 99$). Wind gusts were of short duration (hours) and were as high as $7.3\,\mathrm{m\,s^{-1}}$, and velocities were dominated by the southern vector (data from May to September in 1993–1995 (ref. 21): $\mathrm{E} = 1.3 \pm 0.3$, $\mathrm{W} = 0.32 \pm 0.03$, $\mathrm{N} = 0.7 \pm 0.2$, $\mathrm{S} = 2.08 \pm 0.04\,\mathrm{m\,s^{-1}}$).

The combined effect of increasing temperatures and decreasing wind speeds is to increase the stability of the lake and to reduce the mixing depth. We calculated that the stability of the water column during the non-windy season (defined as the work required to mix the water column to uniform density[22]) increased by 97% from $84.4\,\mathrm{kJ\,m^{-2}}$ in 1913 to $166.3\,\mathrm{kJ\,m^{-2}}$ in 2003. Empirical evidence for reduced mixing is given by the depth of the oxygenated zone, which showed a significant shallowing trend of $1.3 \pm 0.2\,\mathrm{m\,yr^{-1}}$ since 1939 to a current depth of around 80 m ($r^2 = 0.44$, $F = 27.1$, $P < 0.0001$, $n = 37$ linear regression; refs 11–16, 23, and Fig. 2c). If the 1938 measurements[11] are discarded because their determination involved visual colorimetric assessment (and is thus highly subject to bias), the trend is statistically stronger with a shallowing of $1.6 \pm 0.2\,\mathrm{m\,yr^{-1}}$ ($r^2 = 0.67$, $F = 63.9$, $P < 0.0001$, $n = 34$). Together, these data suggest that increased thermal stability, coupled with a decline in wind velocity, has reduced mixing depth in the lake. This reduced mixing can be expected to diminish deep-water nutrient inputs to the surface waters, subsequently causing a decline in primary productivity rates.

A lake-wide decrease in productivity is consistent with trends seen in four sediment cores taken along 225 km of the eastern shoreline from watersheds with a range of land-use patterns (see Supplementary Information). Atomic C/N ratios of bulk organic matter were low throughout all cores (grand mean 13.4 ± 0.3), indicating that organic matter was predominantly derived from autochthonous sources[24]. Diagenetic alteration of organic material in these cores appeared to be negligible (see Supplementary Information). Carbon stable isotope records showed a trend towards more negative values beginning in the mid-1900s (Fig. 3). Carbon isotopes in sedimentary organic matter are widely regarded as indicators of phytoplankton productivity[24–26], and the sedimentary record of other lakes has been shown to record both isotope enrichment with increasing productivity and isotope depletion with decreasing productivity[27]. Other possible explanations for a shift towards more negative carbon isotopes in Lake Tanganyika, such as the decrease in atmospheric isotope ratio δ^{13}C from fossil fuel combustion (the Suess effect), an increase in terrestrial organic matter, or a change in phytoplankton composition, can be discounted, and the shift occurs independently of the rates of sediment mass accumulation (see Supplementary Information).

There is evidence for rapid uptake of introduced deep-water nitrate after an upwelling event[6], but phytoplankton do not seem to take up significant amounts of deep-water dissolved inorganic carbon (DIC), which has a δ^{13}C value that is 1.5‰ more negative than that of surface DIC[15]. Phytoplankton δ^{13}C values after an upwelling event were not significantly different from those before upwelling (t-test, $F = 0.25$, $P < 0.63$). Uptake of deep-water DIC may be limited because upwelling of nitrate (maximum concentration at a depth of 70–90 m)[16] is not necessarily accompanied by significant upwelling of DIC (maximum concentration below a depth of 100 m)[16]. Generally, percentage carbon values in the sediment cores remain low (grand mean, $2.9 \pm 0.1\%$; see Supplementary Information), but three cores do indicate a decrease in carbon mass accumulation rates during the mid-1900s. Thus, paleolimnological indicators are consistent with a lake-wide decline in primary productivity over the past 80 years.

The timing of this shift towards more negative carbon isotope ratios coincides with changes in climatic temperature records, with the initial timing potentially obscured by human land use in the developed watersheds. The declining isotope trend began in the early 1900s immediately after the initial period of regional warming. The post-1950s trend followed the warm period of 1940, with an overall average decline slightly greater than 1.0‰ δ^{13}C. Assuming that the observed isotopic shift is wholly due to productivity changes, this would imply a roughly 20% drop in primary productivity rates[25]. Previously established relationships for large, highly productive aquatic systems suggest that a 20% decrease in

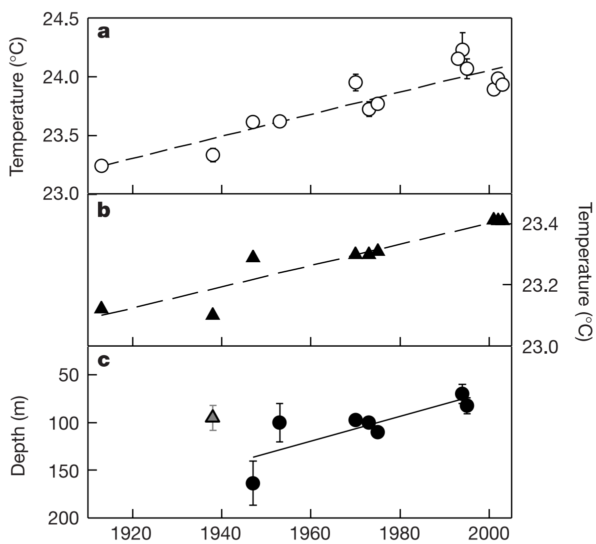

Figure 2 Historical and recent limnological measurements from the middle basin of Lake Tanganyika. **a**, Temperatures at 150 m in the non-windy warm season with linear regression line. Error bars represent the s.d., which provides an indication of intra-seasonal variability. Upper water temperature data for 150 m are from 1912 ($n = 1$)[10], 1938 ($n = 3$)[11], 1946 ($n = 18$)[12,13], 1953 ($n = 3$)[13], 1970 ($n = 2$)[14], 1973 ($n = 11$)[15], 1975 ($n = 1$)[16], 1993 ($n = 2$), 1994 ($n = 3$), 1995 ($n = 3$), 2001 ($n = 1$, from the windy season), 2002 ($n = 3$, from the windy season) and 2003 ($n = 1$). **b**, Deep-water temperatures with linear regression line. Data shown are for 600 m and represent the relatively homothermal waters (± 0.02 °C) between 400 and 800 m (refs 10–16). **c**, Oxycline depth in the non-windy warm season. Oxycline data are from 1938 ($n = 3$)[11], 1946 ($n = 17$)[12,13], 1953 ($n = 3$)[23], 1970 ($n = 2$)[14], 1973 ($n = 1$)[15], 1975 ($n = 1$)[16] and 1995 ($n = 10$). Grey triangle indicates the colorimetric visual measurements made in 1939 (ref. 11), which may be inaccurate because of methodology. The regression line does not include these data. Error bars represent the s.d.

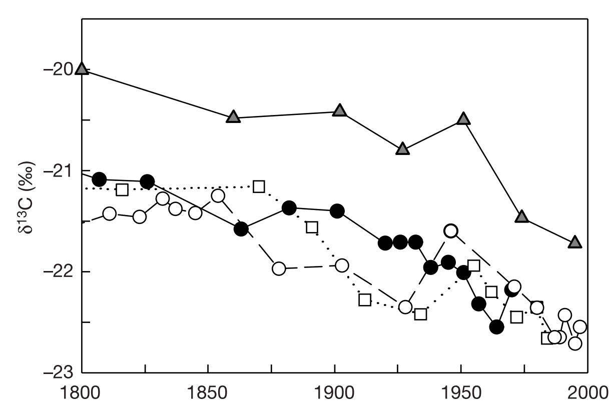

Figure 3 Carbon isotope records in sediment cores. δ^{13}C values indicate a post- 1950s trend towards more negative values in all cores. Filled symbols represent cores from relatively undisturbed watersheds (filled circles, LT-98-58M; grey triangles, LT-97-56V), and open symbols represent cores from developed watersheds (squares, LT-98-37M; circles, LT-98-82M).

primary productivity would reduce fisheries yields by about 30% (ref. 3).

Finally, this inferred decrease in primary productivity helps to explain recent declines in the pelagic fishery that had been attributed to unknown environmental factors rather than to overfishing[2,28–30]. The fishery is dominated by two clupeid species (*Stolothrissa tanganicae* and *Limnothrissa miodon*) and a piscivore (*Lates stappersi*). The clupeid fishery is primarily supported by a cohort recruited during the cool windy season[29], and this seasonal pattern has been attributed to increased nutrient availability associated with upwelling[4]. Various studies have attributed the large (30–50%) decline in clupeid catch since the late 1970s partially to environmental factors because the lake had sustained high yields under similar fishing pressure for the previous 15–20 years (refs 2, 28–30). This decline was coincident with the disappearance of previously strong seasonal patterns in catch[28,30], suggesting a decoupling from ecosystem processes driven by the weakening of hydrodynamic patterns. The contribution (by weight) of the predator *Lates* species to the fish catch also declined from 20–60% beginning in 1955 to 2% after 1977 (ref. 30). These changes in the pelagic fishery are consistent with a lake-wide shift in ecosystem function.

The combined historical and paleolimnological data provide evidence that climate change has contributed to diminished productivity in Lake Tanganyika over the past 80 years. Within the next 80 years, air temperature increases of 1.3–1.7 °C are predicted for the Great Lakes region of East Africa[9], which may further increase thermal stability and reduce productivity in these large lakes, provided that wind velocities remain low. The human implications of such subtle, but progressive, environmental changes are potentially dire in this densely populated region of the world, where large lakes are essential natural resources for regional economies. □

Methods

Data

Meteorological data from the north were for Bujumbura (3° 32′ S, 29° 32′ E, 772 m), obtained from the Institut Géographique du Burundi, and data from the south were for Mbala (8° 85′ S, 31° 33′ E, 1,632 m), obtained from the Department of Meteorology, Zambia.

Historical water temperature data were taken from the pelagic zone (>5 km offshore) of the middle basin of the lake near Kigoma, Tanzania, which has the most extensive historical record. Unless otherwise stated, all temperature and oxygen measurements were taken during the non-windy, warm season (October to April), when the lake is more stable. Early temperature measurements in 1913 and 1938 were determined using bottle samples rather than reversing thermometers, and we corrected these deep-water temperatures for adiabatic expansion. Stability of the water column was calculated with temperature profiles from the non-windy season to 700 m (ref. 22). Because salinity in Lake Tanganyika is low and we do not have historic salinity profiles, we assumed that salinity was negligible, which makes the stability values conservative estimates. The depth of the oxycline was conservatively defined as the last depth at which more than 0.5 mg l^{-1} O_2 was measured.

Analysis of sediment cores

Cores LT-98-58M, LT-98-37M and LT-98-82M were dated using ^{210}Pb (see Supplementary Information). For these cores we analysed bulk organic matter for carbon isotopes roughly every 3 cm, with the exception of the top 3–6 cm, for which there was not enough material remaining after earlier work on some of these cores. Core LT-97-56V was dated using ^{14}C (see Supplementary Information) and only the fine sediment fraction (<63 μm) from core intervals 0–1, 4–5, 8–9, 12–13, 16–17, 22–23 and 30–31 cm was analysed for $\delta^{13}C$, as the fine sediment fraction should be influenced more directly by changes in autochthonous organic matter than should coarser sediment fractions[31]. The $\delta^{13}C$ data from this core are potentially inconclusive, although they are consistent with data from the other cores.

All $\delta^{13}C$ samples were acidified with 10% HCl for at least 24 h and rinsed three times by decanting after centrifugation. Bulk sedimentary organic matter was analysed at the University of Waterloo Environmental Isotope Lab on an Isochrom continuous flow stable isotope mass spectrometer (Micromass) coupled to an elemental analyser CHNS-O EA1108 (Carla Erba) with a standard error of 0.05‰ for $\delta^{13}C$, 0.15‰ for $\delta^{15}N$, 0.02% for %C, and 0.3% for %N. The isotope ratios are expressed in delta notation ($\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard}] - 1$) with respect to deviation from a standard reference material (Pee Dee Belemnite).

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