Deoxygenation of the Deep Water of Lake Victoria, East Africa

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Deoxygenation of the deep water of Lake Victoria, East Africa

Abstract—The annual cycle of the vertical distri-
bution of oxygen concentrations at a deep water sta-
tion on Lake Victoria in 1990–1991 was compared
with data collected in 1960–1961. Oxygen concen-
trations in the mixed layer are higher now, with near-
ly continuous oxygen supersaturation in surface wa-
ters. Oxygen concentrations in hypolimnetic waters
are lower now for a longer period, with values <1
mg liter^{-1} occurring in water as shallow as 40 m
compared with a shallowest occurrence of >50 m in
1961. The changes in oxygenation are consistent with
measurements of higher algal biomass and produc-
tivity. The causes for the eutrophication of Lake Vic-
toria are as yet undetermined, although higher nu-
trient loading, altered climate, and food-web changes
are all potentially involved. The persistent and areal-
ly extensive deoxygenation of the hypolimnion must
negatively affect the formerly productive and spe-
cies-rich demersal fish community.

Lake Victoria is the world's second largest
lake (68,800 km^2). It lies across the equator in
eastern Africa and is bounded by Tanzania,
Uganda, and Kenya. Victoria's fish commu-
nity has become greatly simplified since the
introduction of the Nile perch (*Lates niloticus*)
in the late 1950s (Ogutu-Ohwayo 1990; Barel
et al. 1985). The establishment and success of
the Nile perch population in Lake Victoria re-
sulted in a stimulation to the lake's fishery,
with yields increasing fivefold throughout the
1980s. The success of the Nile perch fishery
has been accompanied by a dramatic decline
in many native fish. Victoria formerly had one
of the most species-rich freshwater fish com-
munities in the world, with over 300 species
(Greenwood 1974; Witte et al. 1992), nearly
all endemics, known collectively as haplo-
chromine cichlids. Up to half the endemics can
no longer be found and may be extinct (Witte
et al. 1992). An additional 39 species of native
nonhaplochromine fish have been similarly
impacted. Predation by Nile perch as well as
overfishing have certainly contributed to what
may be the highest rate of vertebrate species
extinction in modern time, but other changes
in the Victoria ecosystem may be contributing.

Evidence of increasing algal abundance
(Ochumba and Kibaara 1989; Hecky and Bu-
genyi 1992; Mugidde 1993) and fish kills raises
the possibility of declining oxygen concentra-
tions in the deeper water of the lake. Increasing
and widespread deep-water anoxia would put
at risk the remnants of benthic haplochromine
species throughout the lake (Kaufman 1992).

Deoxygenation would make large areas of the lake bottom at least seasonally unavailable for all fish. This report documents increasing deoxygenation in Lake Victoria since the 1950s and 1960s.

Talling (1966) followed the annual cycle of thermal and oxygen stratification at a deep (60 m) offshore station in Uganda in 1960–1961 and compared his results with the earlier studies of Fish (1959) in 1952–1953, his own in 1956 (Talling 1957), and those of Newell (1960) in 1957–1958. Talling concluded that the 1960–1961 results were very similar to the earlier studies. The distribution of oxygen over depth in the lake was strongly affected by the annual cycle of thermal stratification. Oxygen gradients with depth were weak or nonexistent when the water column was almost isothermal during the mixing season of July and August. With the establishment of thermal structure in September, vertical gradients of temperature and oxygen were found throughout the water column, but by January there was a single, major discontinuity between 30- and 60-m depth. This discontinuity as well as the earlier gradients could be displaced vertically by wind stress on the lake's surface and the resulting internal waves (Fish 1959; Newell 1960). Fish, Newell, and Talling recorded low oxygen conditions (<0.7 mg liter^{-1}) only below 55 m and complete deoxygenation (<0.1 mg liter^{-1}) very infrequently (only just off the bottom at 60 m in February 1961). Surface waters in 1960–1961 were always near saturation with atmospheric oxygen (94–100%) except during mixing, e.g. 90% in July 1961. Kitaka (1971) found conditions consistent with this description as late as February–March 1969.

In 1990 and 1991, we revisited Talling's (1966) offshore station at about monthly intervals in order to compare modern oxygen conditions with the data from 1960–1961. We also compared contemporaneous oxygen vs. depth and temperature observations from Uganda and Kenya to examine how widespread low-oxygen conditions were at two times of the year. Oxygen measurements in 1990–1991 were made with a Hydrolab SVR-II profiling system calibrated against oxygen concentrations in surface waters determined by Winkler titration. Mean oxygen concentration of the mixed layer (0–20 m) and hypolimnion (40–60 m) at Bugaia was calculated on a volume-corrected basis. Oxygen saturation of surface water and depth of 1 mg liter^{-1} oxygen concentration were determined from the oxygen and temperature profiles and oxygen saturation algorithm of Benson and Krause (1980).

By 1990–1991, oxygen conditions at a deep, offshore station near Talling's station were substantially altered from conditions of 1960–1961 (Table 1). Oxygen concentrations in the upper 20 m were consistently higher than for similar time periods in 1960–1961 and consistently lower between 40- and 60-m depth from October through March. The higher concentrations in the upper water column were especially evident in surface waters which were now above saturation with respect to the atmosphere in 1990–1991. Low-oxygen conditions (<1 mg liter^{-1}) occurred at shallower depths than formerly, especially October–March. However, the months of minimal deep-water oxygen concentrations in 1961, April and May, were better oxygenated in 1991. This better oxygenation in April–May 1991 likely was the result of the earlier onset of thermal destratification compared to 1961 (Hecky 1993). The modern conditions extended at least from Ugandan waters to the eastern side of the lake in Kenya (~ 200 km between these stations), where deep-water oxygen profiles were also taken on a regular basis (Fig. 1). Although the shapes of the profiles often differed (e.g. Fig. 1B) because of sloping isopycnal surfaces due to internal waves (Fish 1959; Newell 1960), the stations had quite similar oxygen concentrations at similar temperatures (Fig. 2). Consequently, the oxygen conditions described in Uganda and Kenya were widespread. In both November and March, anoxia was associated with water temperatures of 24.2°C or less. The area of lake bottom exposed at least periodically to anoxic water would depend on wind conditions which can displace isopycnal surfaces from the horizontal, but at 55-m depth or greater, anoxic conditions (<1.0 mg liter^{-1}) persisted from October to March over a depth zone covering $\sim 35\%$ of the lake's total bottom area. This area would be a minimum estimate of the bottom area affected by anoxic conditions as water displacement by internal waves would spread anoxic water over an even larger area.

The change in the oxygenation of Lake Victoria is consistent with and contributes to the

Table 1. Oxygen conditions in Lake Victoria during 1960–1961 (Talling 1966) and 1990–1991. Oxygen concentrations were measured at 10-m depth intervals.

|	Mean oxygen concn (mg liter^{-1})				% saturation		1 mg liter^{-1} depth (m)	
	1960	1990	1960	1990				
	0–20 m	0–20 m	40–60 m	40–60 m	1960	1990	1960	1990
Sep	7.10	8.90	3.48	3.25	96	138	>60	>60
Oct	7.08	9.52	3.99	1.46	98	146	>60	52
Nov	6.94	6.17	3.48	0.52	97	109	>60	40
Dec	6.73	7.57	2.91	0.87	96	110	>60	45
Jan	6.71	7.60	4.34	2.20	91	112	60	54
Mar	6.81	7.46	6.29	2.21	94	110	>60	53
Apr	5.15	6.25	1.79	3.76	94	122	51	>60
May	6.64	9.63	2.75	6.74	91	143	53	>60
Jul	6.59	8.43	6.34	7.72	90	115	>60	>60
Aug	7.23	6.72	5.66	4.16	97	107	>60	>60
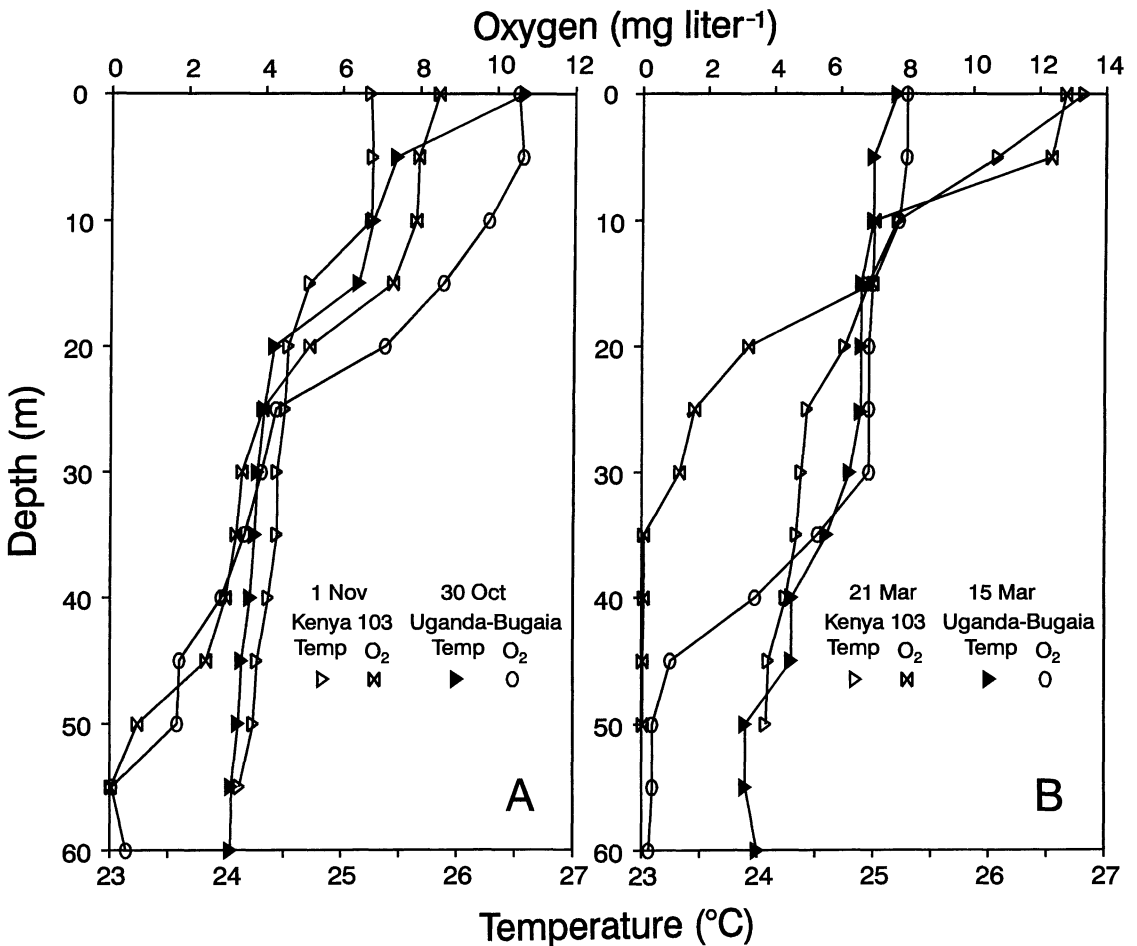
Fig. 1. Comparison of temperature and oxygen concentration profiles at two stations on Lake Victoria. The Bugaia station in Uganda was the site of the 1960–1961 and 1990–1991 time series in Table 1. Station 103 is in Kenya and >200 km from Bugaia.

evidence of higher phytoplankton biomass and photosynthesis reported by others (Ochumba and Kibaara 1989; Hecky and Bugenyi 1992; Mugidde 1993). High rates of photosynthesis in surface waters create supersaturated oxygenated conditions, as has been reported for other African lakes (Melack and Kilham 1974), while the sedimentation and decomposition of the organic matter thus produced consumes oxygen in those depths isolated from the atmosphere by temperature-dependent density stratification.

Deoxygenation has likely contributed to the observed decline of haplochromine stocks in Lake Victoria. Anoxia forces the demersal populations (Witte et al. 1992; Kudhongania and Cordone 1974) to shallower water where they are exposed to Nile perch predation. Nile perch require high concentrations of oxygen (Fish 1956), while some haplochromines can tolerate oxygen as low as 2–3 mg liter^{-1} for extended periods (Oijen et al. 1981). Such a difference in oxygen tolerance creates a potential deep-water refugium for at least some haplochromines, but complete deoxygenation of the lower water column causes the benthic distribution of the haplochromines to contract. More importantly perhaps, the formation and persistence of a low-oxygen water mass creates the potential for rapid change in oxygen concentrations near the bottom. If the anoxic boundary is displaced vertically by a distance of 10 m (Fig. 1B), it travels tens of kilometers across the bottom of the lake because of its low bottom slope (Newell 1960). Even nearshore surface waters are rapidly deoxygenated during upwelling events along steep-sided shorelines (e.g. Kenyan waters in the northeastern sector of the lake have had increasing frequency of fish kills, Ochumba and Kibaara 1989).

The decline in haplochromine species during the 1980s has been best documented in nearshore, shallow environments (Witte et al. 1992). However, the deep-water haplochromines stocks also declined by 90% between 1968 (Kudhongania and Cordone 1974) and 1984 (Witte et al. 1992), and by 1986, haplochromines could no longer be caught in trawls at 40–50-m depth where they formerly had been numerous (Witte et al. 1992). Deoxygenation of the extensive (Kudhongania and Cordone 1974), deeper, offshore waters has fore-
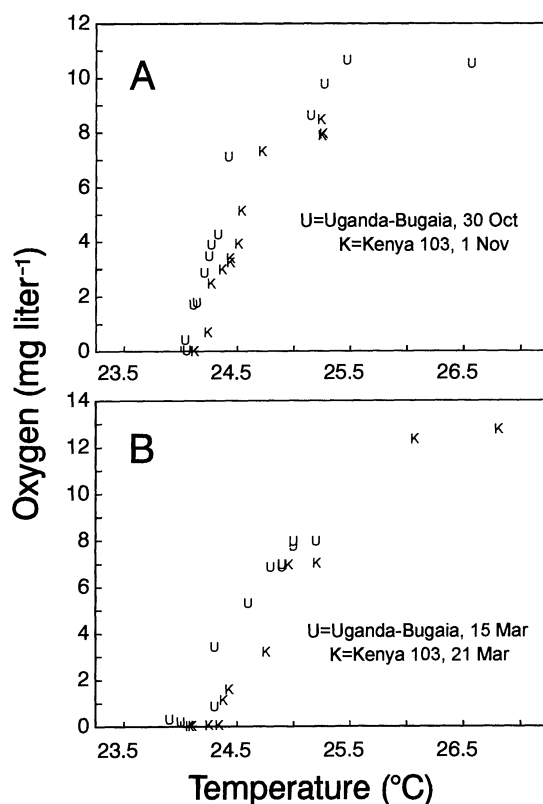

Fig. 2. Comparison of oxygen vs. temperature relations for the two profiles in Fig. 1.

closed for the immediate future the potential for a productive demersal fishery in the lake.

Definitive causes for the observed eutrophication of Lake Victoria and deoxygenation of its deep water are difficult to ascertain at present. Nutrient fluxes to the lake sediments have increased by a factor of at least two since 1960 (Hecky 1993), and the observed proportional increase in phytoplankton photosynthesis (Mugidde 1993) would be expected from eutrophication models developed for temperate lakes (Vollenweider 1976). The ultimate source of the increased nutrient flux is increasing human population and increasingly intensive land use. It is estimated that in 1992, the population of the Victoria basin was >20 million (>170 individuals km^{-2}) and the rate of increase was 3% per annum (Bootsma and Hecky 1993). However, other changes in the lake may have contributed.

The level of the lake rose by 2.5 m between 1960 and 1964 (Kite 1981) and has yet to re-

turn to its pre-1960 level. This rise in elevation nearly doubled the output of the Nile outlet over its mean annual discharge from 1900 to 1961 (Kite 1981). Hydrologic analysis has determined that the rise in level was due to natural causes and not to the imposition of a dam below the natural control cross-section (Kite 1981). Climatic changes or changes in water yield from the catchment must be invoked to account for this lake level rise. There is also evidence for a warming trend in East Africa since 1960 (Hastenrath and Kruss 1992). Earlier observers (Talling 1966; Fish 1959; Worthington 1930) commonly recorded deep-water temperatures as low as 23.5°C, although we have not observed temperatures below 23.8°C. Increased deep-water temperatures, increased stability of thermal stratification (Hecky 1993), and increased organic matter production would work in concert to reduce deep-water oxygen concentrations. More recent changes in the fish community may be, in part, the consequence of these physicochemical changes, but alterations in the fish community could also aggravate the low-oxygen conditions by altering nutrient flows and distributions within the lake (Kaufman 1992). Only future research can decide among these possible causes for the observed changes in the oxygenation of Lake Victoria.

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Iron limitation and the cyanobacterium *Synechococcus* in equatorial Pacific waters

Abstract—Iron enrichments in bottle experiments in high nutrient, low chlorophyll (HNLC) surface waters typically stimulate the net growth of nanophytoplankton (2.0–20 μm) but not picophytoplankton (<2.0 μm), suggesting either that picophytoplankton are not Fe limited or that any increased picophytoplankton growth is balanced by increased microzooplankton grazing rates. Using a novel approach in which we diminish iron availability in seawater with the fungal siderophore deferriferrioxamine B, we demonstrate that growth of the abundant picoplanktonic cyanobacterium *Synechococcus* is not strongly rate limited by Fe in the HNLC equatorial Pacific Ocean. However, experiments at the equator and 5°S show an unsuspected non-uniformity in iron nutrition within this HNLC region. Furthermore, our results indicate that a major portion of "dissolved" (<0.4 μm) iron in these waters is unavailable to *Synechococcus,* providing the first evidence that a significant fraction of dissolved iron occurs in forms other than the simple hydroxy species predicted by thermodynamic models. Deferriferrioxamine B affords a powerful new tool for probing the iron nutrition of marine phytoplankton and can provide unique insight into the role of iron in marine biogeochemical cycles.

The difficulty in demonstrating iron limitation by measuring changes in phytoplankton abundance in iron-*enrichment* experiments stems from the complicating effects of grazing. Specific rates of picoplankton growth may increase, but net rates may remain unaltered because of compensatory increases in grazing rates by microzooplankton which cannot be excluded from samples. Recognizing this problem, we instead investigated picoplankton iron nutrition by *diminishing* iron availability in seawater samples containing natural populations. The fungal siderophore deferriferrioxamine B (DFB), a strong Fe-complexing agent (Hudson et al. 1992), was added to cultures to "titrate" ambient reactive Fe, making it less available to the biota for uptake. In this way, we turned the complicating effects of grazing pressure to our advantage by sensitizing the bioassay to