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History and timing of human impact on Lake Victoria, East Africa

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Lake Victoria, the largest tropical lake in the world, suffers from severe eutrophication and the probable extinction of up to half of its 500+ species of endemic cichlid fishes. The continuing degradation of Lake Victoria's ecological functions has serious long-term consequences for the ecosystem services it provides, and may threaten social welfare in the countries bordering its shores. Evaluation of recent ecological changes in the context of aquatic food-web alterations, catchment disturbance and natural ecosystem variability has been hampered by the scarcity of historical monitoring data. Here, we present high-resolution palaeolimnological data, which show that increases in phytoplankton production developed from the 1930s onwards, which parallels human-population growth and agricultural activity in the Lake Victoria drainage basin. Dominance of bloom-forming cyanobacteria since the late 1980s coincided with a relative decline in diatom growth, which can be attributed to the seasonal depletion of dissolved silica resulting from 50 years of enhanced diatom growth and burial. Eutrophication-induced loss of deep-water oxygen started in the early 1960s, and may have contributed to the 1980s collapse of indigenous fish stocks by eliminating suitable habitat for certain deep-water cichlids. Conservation of Lake Victoria as a functioning ecosystem is contingent upon large-scale implementation of improved land-use practices.

Keywords: landscape disturbance; eutrophication; fish introduction; human impact; Lake Victoria; Nile perch

1. INTRODUCTION

Lake Victoria has in recent decades undergone a series of profound ecological changes, including strong increases in phytoplankton primary production (Hecky & Bugenyi 1992; Mugidde 1993), replacement of diatoms by cyanobacteria as the dominant group of planktonic algae (Kling *et al.* 2001), and the eradication of several hundred species of endemic cichlid fishes after the 1980s population explosion of Nile perch—an introduced piscivore (Barel *et al.* 1985; Ogutu-Ohwayo 1990; Witte *et al.* 1992). The observed changes in the phytoplankton community seem to be the logical consequence of excess nutrient loading that results from deforestation and greatly intensified agriculture throughout the drainage basin of Lake Victoria, which comprises portions of five countries (Hecky & Bugenyi 1992; Scheren *et al.* 2000). However, lack of long-term monitoring data and the complexity of ongoing ecosystem changes hamper full appreciation of the impact of catchment disturbance on the lake's present condition. Apparent coincidence in the timing of the first massive cyanobacteria blooms offshore (Ochumba & Kibaara 1989) with the collapse of indigenous fish stocks has tempted the question: to what extent does the decimation of phytoplanktivorous haplochromine cichlids by Nile perch contribute to increased algal production? (Goldschmidt *et al.* 1993). Also, invigorated algal growth may have resulted in part from the documented rise in average surface-water temperature and water-column stability in the 1960s, a possible regional manifestation of global climate warming (Hecky *et al.* 1994).

In the absence of adequate historical monitoring data that link observed ecological change to possible causative factors, we used the palaeolimnological record preserved in offshore sediments to reconstruct the succession and timing of these changes, and to elucidate the chain of cause and effect that led to today's conditions of severe eutrophication and restructured algal and fish communities. We describe the environmental history of Lake Victoria over the past 180 years as recorded in core V96-5MC from the deepest part of the lake, where rapid sediment accumulation and the absence of burrowing invertebrates combine to produce a high-quality sediment archive. This core is one of six intact cores recovered to date from the main offshore depositional basin of Lake Victoria (Hecky 1993; Verschuren *et al.* 1998; figure 1), and representative of three records from 67–68 m water depth.

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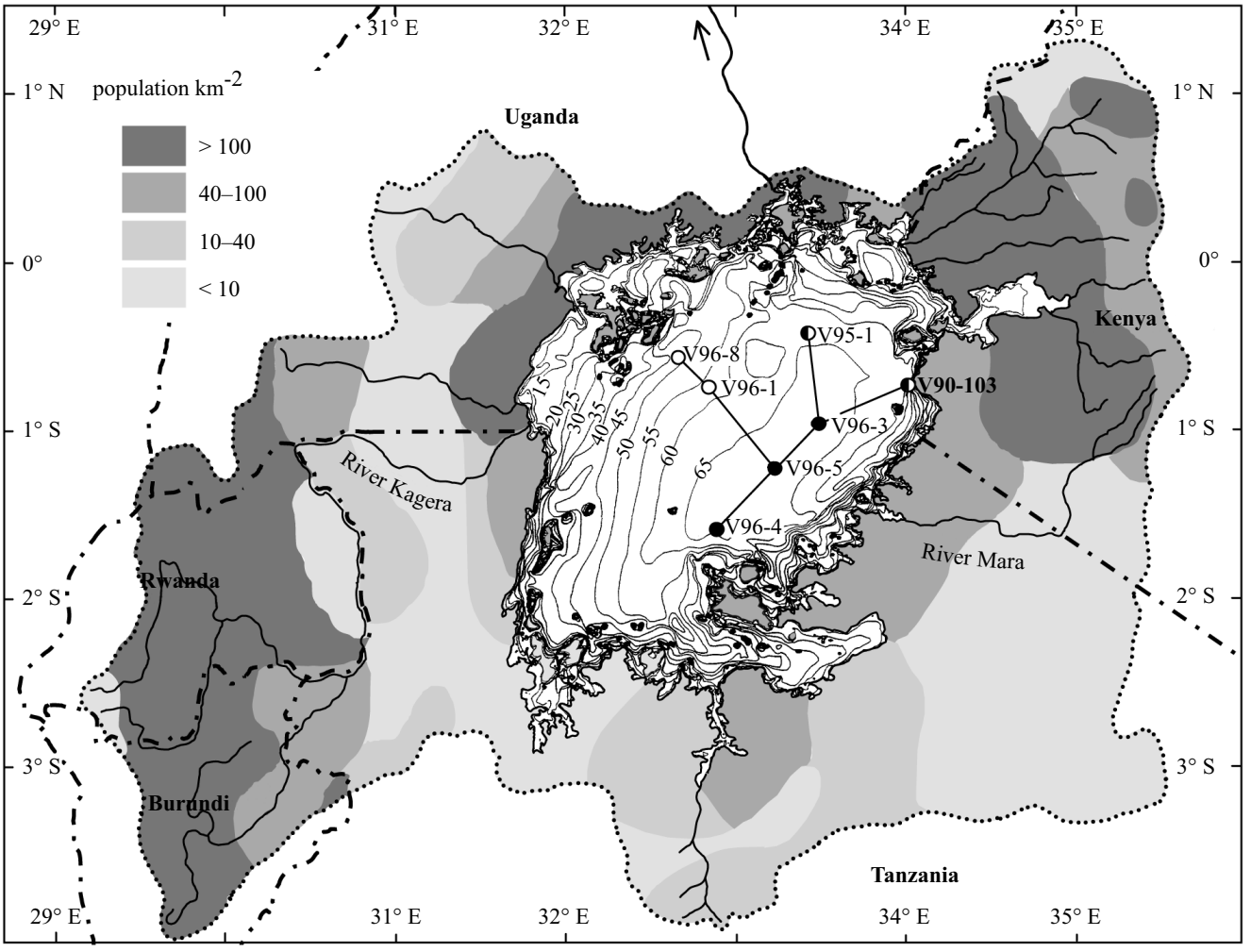

Figure 1. Lake Victoria, its drainage basin and coring stations. The 263 000 km^2 basin comprises portions of Uganda, Kenya, Tanzania, Rwanda and Burundi, with a 1995 population of 27.7 million (United Nations 1995). Highest population densities and agricultural activity occur in the drainages of Kenyan, Rwandan and Burundi rivers that together contribute *ca.* 90% of total river input to Lake Victoria (Balirwa & Bugenyi 1988). Core-site symbols reflect the relative quality of sediment records as determined by local bottom dynamics. Closed symbols, undisturbed sedimentation; half-open symbols, bioturbation; open symbols, both bioturbation and frequent wave turbulence. Depth contours are in metres. Lake Victoria bathymetry prepared at the Large Lakes Observatory, based on IDEAL project echosounding in 1995 and 1996 (mainly offshore areas) and British Admiralty maps (nearshore areas); river drainages from Crul (1993); and population data from Beck (1998).

2. MATERIAL AND METHODS

Fieldwork on Lake Victoria that was conducted by the IDEAL programme (International Decade for the East African Lakes) in 1995 and 1996 recovered surface-sediment cores from six offshore stations between 48 and 68 m water depth (Verschuren *et al.* 1998). The 1996 cores, including V96-5MC, were collected with a Hedrick–Marrs multi-corer (sampling area 4×71 cm^2), that provides hydraulically dampened sediment penetration after a support frame has come to rest on the lake floor. Of the four core replicates recovered at each site, two were extruded in the field in 0.5 cm increments near the top (0–10 cm), and 1 cm increments down-core. The third replicate was used for pore-water extraction at 2 cm (0–10 cm) and 4 cm intervals; the fourth replicate was capped and stored intact.

Water content and dry mass (dry weight ml^{-1} wet mud) were determined by drying for 20 h at 105 °C. Sediment age at depth and accumulation rates were determined by ^{210}Pb dating (Robbins & Edgington 1975). Unsupported ^{210}Pb (the fraction of ^{210}Pb activity not supported by *in situ* decay of ^{226}Ra) was calculated as the difference between total ^{210}Pb and its constant value of 1.74 pCi g^{-1} below a core depth of 37 cm ($n = 3$). Unsupported ^{210}Pb was fitted to a nonlinear regression (Robbins *et al.* 1978), taking into account a disconformity at a core depth of 25–26 cm (see § 3). Solid-phase biogenic silica (Si) in the sediments was analysed by wet alkaline extraction (DeMaster 1981), using a 0.5 m sodium hydroxide solution at 80 °C for sample digestion. Dissolved Si in pore water was analysed by spectrophotometry, on aliquots extracted from successive core increments immediately upon recovery. Fossil diatom assemblages were analysed quantitatively in aqueous suspensions of undigested sediment (Kling 1998). Sample processing for fossil midge analysis followed standard techniques (Walker & Patterson 1985), using a 100 μm sieve to extract fossils from the sediment matrix.

3. RESULTS

(a) *Offshore sedimentation dynamics*

Deep-water sediments in Lake Victoria (figure 2*a*) are soft, dark-brown organic muds capped by a 1.5 cm

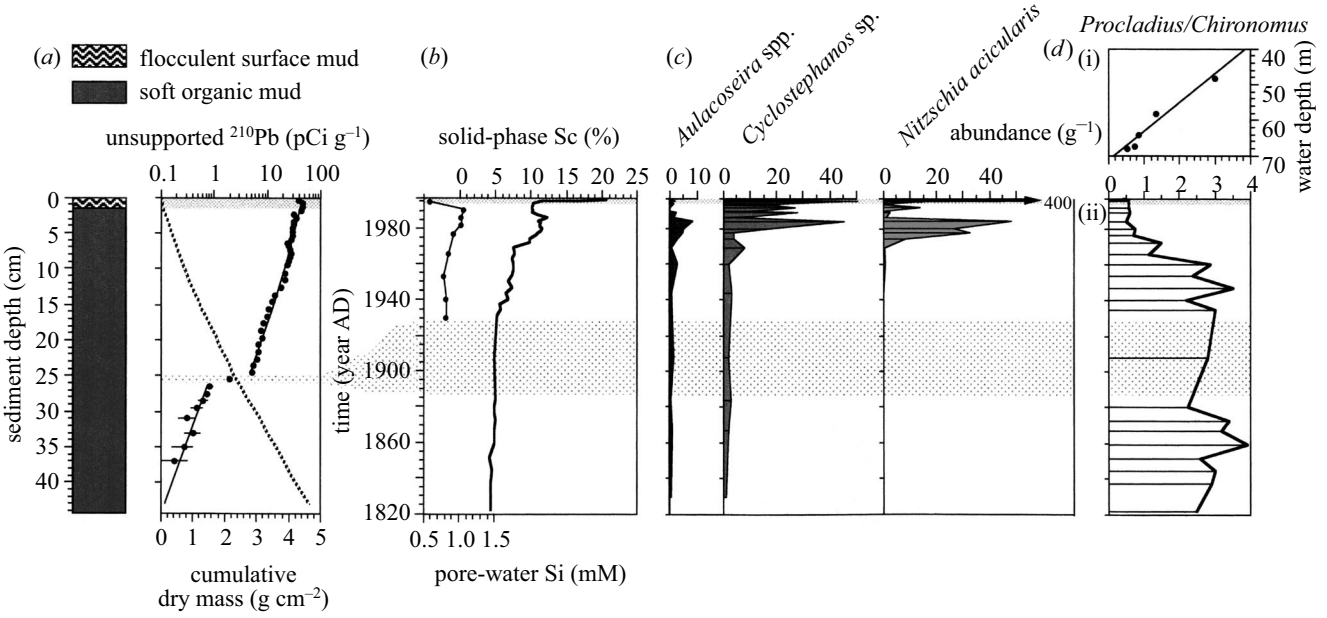

Figure 2. Palaeolimnological evidence for lake-wide ecosystem change in Lake Victoria. (*a*) Sediment stratigraphy, cumulative dry mass and ^{210}Pb activity of core V96-5MC from 68 m water depth. Black circles, data; solid line, model; dashed line, cumulative dry mass (g cm^{-2}). (*b*) Stratigraphy of biogenic Si in the solid phase (solid line) and dissolved in pore water (black circles); the stippled zone corresponds to the inferred disconformity, representing a hiatus of *ca.* 40 years (*ca.* 1885 to 1925). (*c*) Down-core distribution of the pelagic diatoms *Aulacoseira* spp., *Cyclostephanos* sp., and *Nitzschia acicularis*, reflecting changes in their absolute abundance over the past 180 years; peak concentrations in flocculent surface muds are diatoms subject to further dissolution before permanent burial. (*d*)(i) Abundance ratio of the midge taxa *Procladius* and *Chironomus* in Lake Victoria surface sediments between a water depth of 48 and 68 m, reflecting the modern-day gradient in the seasonal persistence of bottom anoxia from 0 to approximately 10 months ($r = 0.98$, $p < 0.01$); (ii) evolution of the *Procladius*/*Chironomus* abundance ratio at 68 m water depth over the past 180 years.

thick surface horizon of flocculent mud and a thin blanket of recently settled algae. Unsupported ^{210}Pb activity decreases exponentially with cumulative dry mass downcore, which indicates that sediments have accumulated at a relatively constant rate (0.032 ± 0.001 g cm^{-2} yr^{-1} or 2.3 mm yr^{-1}), and that both physical and biological mixing of recent deposits are insignificant (Robbins *et al.* 1978). A shift to lower ^{210}Pb activity at a core depth of 25–26 cm reflects a disconformity that we interpret to have resulted from sediment erosion during an exceptionally violent storm. The large wind fetch and relative shallowness of Lake Victoria make its entire offshore bottom susceptible to the wave turbulence generated by high-intensity storms (Johnson 1980; Dearing 1997). Only in the deepest part of the lake is wave-induced erosion a rare event, and has the sediment record been preserved sufficiently intact to reconstruct recent lake history (Verschuren *et al.* 1998). The effects of wave turbulence and bioturbation on the archival quality of the sediment record are increasingly evident at depths of less than 64 m (figure 1). In many offshore areas shallower than 50 m, frequent wave turbulence prevents the permanent deposition of fine-grained organic muds (Scholz *et al.* 1991).

(b) *Historical diatom production*

The record of biogenic Si in core V96-5MC (figure 2*b*) and other deep-water cores (Verschuren *et al.* 1998) documents the history of pelagic diatom production in Lake Victoria. Peak Si concentrations (21% of dry mass) in the flocculent top 1.5 cm are recently settled diatoms subject to further dissolution before permanent burial (Conley & Schelske 1989). Si concentrations below that level correlate strongly with the logarithm of total fossil diatom abundance ($r = 0.89$, $p < 0.001$, $n = 20$), implying that diatoms are the principal source of solid-phase biogenic Si in these sediments (Conley 1988). Low, constant Si concentrations (*ca.* 5% of dry mass) in the lower half of the profile are similar to those in the upper portions of Holocene records (Johnson *et al.* 1998), and reflect the moderate, fairly stable offshore diatom production in Lake Victoria before human impact became noticeable. Increasingly higher Si concentrations deposited from the 1930s to the mid-1980s reflect the greater diatom production that resulted from an increased supply of growth-limiting nutrients (Hecky 1993). Cumulative loss of this excess diatom Si to burial in deep-water sediments gradually depleted Lake Victoria's reservoir of dissolved Si. Concentrations in the upper water column during stratification have declined from 70–80 μM in 1960 to less than 8 μM in 1990 (Hecky 1993), and are now frequently below 1 μM—a concentration considered to severely limit diatom growth (Schelske *et al.* 1986). The slightly lower diatom-Si concentrations deposited since the late 1980s (figure 2*b*) reflect the current situation in which diatom production is limited by the dissolved-Si concentration that is realized through recycling of Si from shallow-water sediments and new inputs from the watershed through soil runoff.

Changes in the pelagic diatom flora of Lake Victoria over the past 60 years (figure 2*c*) provide further evidence for significant historical changes in nutrient loading. The thinly silicified species *Nitzschia acicularis* comprises 94%

of total diatom abundance in recently settled algae, consistent with live plankton data (Kling *et al.* 2001) that show this species to be the most common pelagic diatom in Lake Victoria today. A 30-fold decrease in its fossil abundance immediately below the flocculent surface muds (as compared with *ca.* 1.5 times *Cyclostephanos* sp. and *ca.* 1.2 times for *Aulacoseira* spp.) points to strong differential dissolution of *Nitzschia* frustules before permanent burial. This is supported by the depth profile of dissolved Si in pore water (figure 2*b*), which indicates significant Si dissolution and diffusion to the overlying water column from the uppermost few centimetres of sediment only. Differential diatom dissolution implies that the species abundances in fossil assemblages are not quantitatively comparable with live floral composition (Flower 1993); however, species abundance trends in permanently buried assemblages (i.e. those below the flocculent surface muds) can be considered to reflect real changes in the pelagic-diatom community through time (Haworth 1980; Leavitt *et al.* 1994). The fossil diatom data (figure 2*c*) show that the pelagic-diatom community of Lake Victoria was stable between about 1820 and 1940, with *Cyclostephanos* and *Aulacoseira* co-dominant at *ca.* 80% and *ca.* 15%, and *Nitzschia acicularis* absent, or too rare to be preserved. The abundance of all three diatom taxa started to increase between about 1940 and the early 1960s, with *Nitzschia acicularis* achieving *ca.* 50% of fossil assemblages deposited in the late 1970s and early 1980s; a level of dominance not observed at any previous time during the past 12 400 years (Stager & Johnson 2000). Consistent with the biogenic-Si data, the fossil-diatom record then indicates a reduction of diatom production in the late 1980s, with declines in all three major diatom taxa. The ^{210}Pb-inferred timing of this reduction matches the increased occurrence of massive cyanobacteria blooms after 1987 (Ochumba & Kibaara 1989). This indicates that restructuring of the algal community to cyanobacteria dominance in the mid-1980s was influenced by Si limitation of diatom growth, due to seasonal depletion of a diminished dissolved-Si reservoir. Our fossil data also agree with long-term plankton surveys (Kling *et al.* 2001) that show the virtual elimination of *Aulacoseira* spp. over the past 20 years. In Lake Victoria today these diatoms are out-competed because of their high-Si needs and high sinking rate through the water column (Talling 1966; Kilham 1990).

(c) *Development of deep-water anoxia*

Fossil assemblages of midge larvae (Insecta: Chironomidae) in offshore surface sediments are a spatially integrated reflection of modern benthic communities across a large area of the offshore lake bottom (Frey 1988). In Lake Victoria they are rather poor in species diversity, and reflect today's principal environmental gradient in mud-bottom habitat from adequate year-round oxygenation at shallow depths to persistent seasonal anoxia (up to 10 months) in deep water. Abundance ratios of the anoxia-intolerant *Procladius brevipetiolatus* to the anoxia-tolerant *Chironomus imicola* among core stations correlate strongly with water depth (figure 2*d*(i) $r = 0.98$, $p < 0.01$, $n = 5$), and with the intensity of seasonal anoxia ($r = 0.91$, $p < 0.01$, $n = 5$), which is measured as the ratio between the duration of bottom anoxia (< 1 mg O_2 l^{-1}; in months) and deep-water oxygen content during the mixing season (data from Hecky *et al.* 1994; Ochumba 1996). Changes in the *Procladius*/*Chironomus* ratio of fossil midge faunas deposited through time at V96-5MC (figure 2*d*(ii)) indicate that, after at least 140 years of adequate year-round bottom oxygenation, the deep-water oxygen regime of Lake Victoria started to deteriorate in the early 1960s. Seasonally persistent deep-water anoxia appears to have reached its current spatial extent by the late 1970s. These fossil data agree with fragmentary historical dissolved-oxygen data from the 1920s, 1960s and 1990s (Hecky *et al.* 1994), and imply that the intermittent deep-water anoxia first observed in 1960–1961 (Talling 1966) represented the earliest stage of eutrophication-induced deep-water oxygen loss in Lake Victoria.

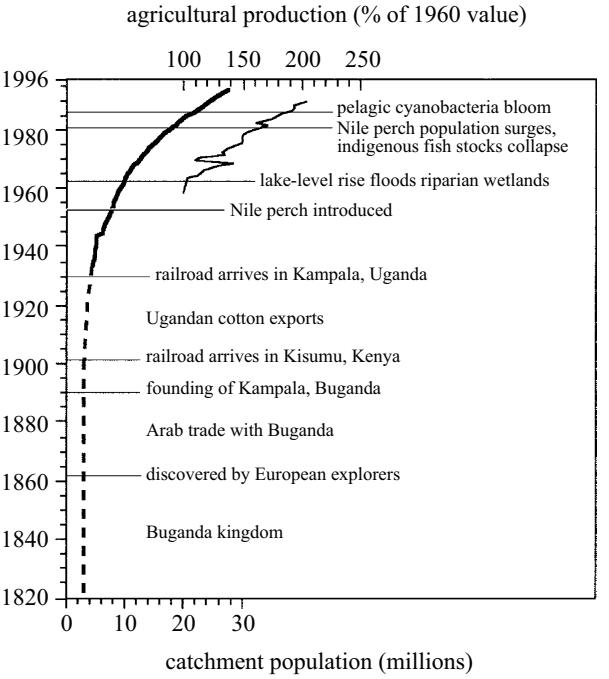

Figure 3. Principal events in the recent environmental history of Lake Victoria, in relation to human-population growth and agricultural production in its drainage basin.

4. DISCUSSION

The combined fossil evidence indicates that historical changes in phytoplankton productivity and composition of Lake Victoria have been caused mainly by bottom-up effects of excess nutrient loading, and less so by food-web alterations after the 1980s upsurge of Nile perch. Timing and progress of the inferred productivity increase match human-population growth and agricultural activity in the Lake Victoria basin (figure 3). Quantitative estimates of total historical and current nutrient exports to the lake do not exist (Scheren *et al.* 2000), but strong correlation of population size with agricultural production over the past 40 years (1965–1991: $r = 0.97$, $p < 0.001$, $n = 27$) justifies the use of historical population size as a proxy indicator for anthropogenic soil disturbance and its effect on nutrient fluxes in catchment runoff (Meybeck 1982; Caraco 1995). The population of the Lake Victoria basin has grown from 4.6 million in 1932 to 27.7 million in 1995 (United Nations 1995). Between 1900 and *ca.* 1930 it had not increased appreciably beyond pre-colonial levels

because of high natural mortality under early colonial rule, exacerbated by the toll of exotic diseases (Kuczynski 1949). Completion of the Uganda railroad by 1930 opened the Lake Victoria region to settlement by stimulating plantation agriculture for the export of commercial crops (Maxon 1990). Rapid population growth through immigration and improved health conditions then started the pattern of large-scale deforestation and agricultural conversion that continues to the present day.

The occurrence of seasonally persistent deep-water anoxia since the late 1970s that is inferred from our data supports the hypothesis (Kaufman & Ochumba 1993; Hecky *et al*. 1994) that deep-water oxygen loss in Lake Victoria may have facilitated the decimation of demersal haplochromine fish stocks by Nile perch, by eliminating the deep-water refugium that had protected these fishes from such excessive predation until then. This idea is attractive because it might potentially explain why the Nile perch population exploded suddenly, some 25 years after its introduction from lakes Albert and Turkana (Lowe-McConnell 1987). However, the evolution of fish species composition in experimental trawls since the early 1970s (Witte *et al*. 1995) does not show evidence that expansion of seasonal deep-water anoxia caused characteristic deep-water haplochromines to migrate to shallower depth ranges and augment the food base of Nile perch. Also before the Nile perch upsurge, haplochromine densities at depths of more than 30 m had been significantly lower than in shallower areas (Kudhongania & Cordone 1974). Hence, although the development of deep-water anoxia must have contributed to the demise of certain haplochromine fish taxa that were dependent on the deep-water mud habitat, it probably did not 'trigger' the 1980s population explosion of Nile perch.

Our palaeolimnological data establish a strong chronological link between historical land use and algal production in Lake Victoria, which indicates that landscape disturbance rather than food-web alterations or climate change is the dominant cause of the ongoing eutrophication. With current estimates projecting a doubling of the regional human population to 53 million by the year 2020 (United Nations 1995), further degradation of the Lake Victoria ecosystem can be countered only if land-management strategies that severely restrict nutrient input to the lake and its tributaries are implemented on a multinational, basin-wide scale.

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