

Multiple stressors cause rapid ecosystem change in Lake Victoria

R. E. HECKY*, R. MUGIDDE[†], P. S. RAMLAL[‡], M. R. TALBOT[§] AND G. W. KLING[¶]

*Large Lakes Observatory, University of Minnesota Duluth, Duluth, MN, U.S.A.

[†]Fisheries Resource Research Institute, Jinja, Uganda

[‡]Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, MB, Canada

[§]Geological Institute, University of Bergen, Bergen, Norway

[¶]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, U.S.A.

SUMMARY

1. Lake Victoria endured multiple stresses over the past century including population growth, increased cultivation of land, meteorological variability, resource extraction, intensive fishing, introduction of exotic species and more recently climate warming. These stressors became manifest through a fundamental and rapid change in the fish community and fishery in the early 1980s and visible eutrophication. However, the relation of these two phenomena and the possible interaction of the multiple stressors have been difficult to establish because of the temporally fragmented nature of the environmental data.

2. Comprehensive limnological observations from the 1960s were repeated in the 1990s and established the eutrophication of the lake, but these do not provide insight to the time course of when changes in trophic state occurred. Comprehensive fishery catch data from 1965 to the present provide a time course of the change in community composition and yield but cannot be correlated in time with discontinuous and sparse limnological data to determine possible cause–effect relationships.

3. Palaeolimnologic studies were conducted on three cores, two offshore and one nearshore, to establish a time course for the eutrophication of the lake that can be related to time-based data on the fishery. In the 1920s, the cores recorded an increase in nitrogen content of the sediments, but there was no significant response in the paleo-productivity indicators of biogenic Si deposition and change $\delta^{13}\text{C}$ of deposited organic matter. Phosphorus deposition began to increase in the 1940s in all three cores after which biogenic Si deposition increased steadily over time. Responses in $\delta^{13}\text{C}$ of organic matter begin in the 1960s at the coring sites. In the 1970s, the $\delta^{13}\text{C}$ of organic matter at the nearshore site increased nearly 3‰ in a 10-year period likely as a response to a dramatic increase in internal P loading caused by spreading anoxia.

4. Nile perch, the large predatory fish introduced in 1954, had become established through much of the lake at low abundances by the 1970s. In 1980, the catch of this fish began to increase, and by the end of the decade, the Lake Victoria fishery was the largest lake fishery in the world; and Nile perch dominated the catch. While catches of some other fishes also increased, the endemic haplochromines suffered a catastrophic decline in abundance and loss of biodiversity.

5. The detailed chronostratigraphies for these sediment cores established that the major changes in the trophic condition of the lake were accomplished prior to the change in the fish community and that the increased primary productivity of the lake likely contributed

to the increased fish catches after 1980. The increased algal abundance also would have greatly reduced visibility and facilitated the emergence of Nile perch as the dominant top predator.

6. *Thematic implications:* multiple stresses were present in Lake Victoria over several decades, but transition to a new ecosystem state with a transformed food web and highly productive algal community may have been triggered by a period of low wind stress and then generally warming climate since the 1970s. Unless phosphorus loading is stabilised or reduced, the ecosystem's diversity and balanced productivity will not recover, and other state transitions may occur to the detriment of the lake and its riparian populations.

Keywords: eutrophication, fisheries, multiple stressors, paleolimnology, stable isotopes

Introduction

Lake Victoria is the world's largest tropical lake by area (68 800 km²) and has been transformed over the last 30 years into the largest freshwater lake fishery in the world with annual catches of over 500 000 tonnes since the late 1980s and with most recently reported catches exceeding one million tonnes (Kolding *et al.*, 2008). Catches increased dramatically in the early 1980s because of a fundamental change in the fish community (Witte *et al.*, 1992a; Fig. 1). Prior to 1980, the fish community consisted of hundreds of endemic species of trophically specialised haplochromine (Cichlidae) fishes (Kaufman, 1992), which dominated the biomass while the commercial fishery focused on native tilapiines, catfishes and riverine species (Kudhongania, Twongo & Ogutu-Ohwayo, 1992). Beginning in the early 1980s, there was a rapid transition to a greatly simplified fish community in which three species of fish dominated the biomass and the commercial catch (Kudhongania *et al.*, 1992; Kolding

et al., 2008). Two of the current three dominant species, the Nile perch (*Lates niloticus* L.) and the Nile tilapia (*Oreochromis niloticus* L.), had been introduced in the period 1954–64. The native *Rastrineobola argentea*, a small zooplanktivorous cyprinid (known as dagaa) has thrived along with the two introduced species (Fig. 1). These introduced species, although broadly distributed with the Nilotic fauna across Africa including Lake Albert downstream of Lake Victoria, did not occur in Lake Victoria because it has been separated from the Nile River by the Murchison Falls, an impassable barrier to upstream fish migration, since the lake was desiccated during the Pleistocene (Johnson *et al.*, 1996). In the late 1970s and early 1980s, a rapid increase in the Nile perch population led to the development of a valued export fishery on the lake following a major expansion of fishing effort. Today, catch and effort continue to expand on Lake Victoria leading to concern about the sustainability of this valuable fishery (Kolding *et al.*, 2008).

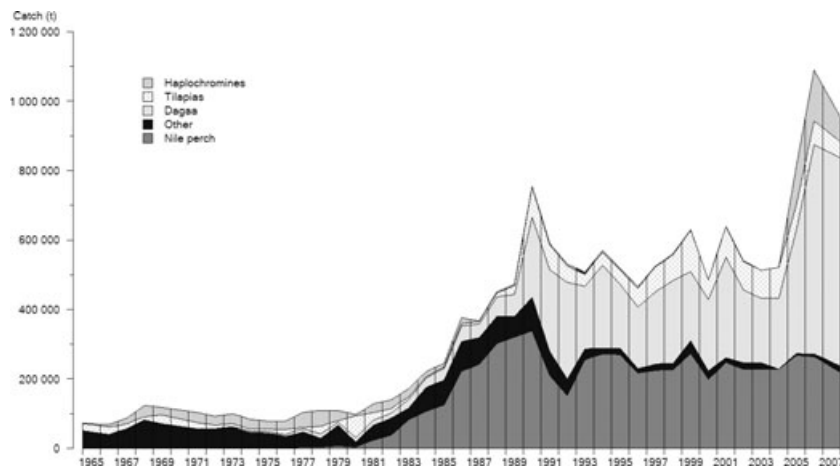


Fig. 1 Total catch of major species and groups of species in Lake Victoria, 1965–2007, recording the rapid increase in fish catch after 1980.

By the late 1980s, after a prolonged period of little or no systematic observation of water quality, the lake in Kenyan waters was thought to be exhibiting evidence of a eutrophic condition (Ochumba & Kibaara, 1989). Eutrophication since the 1960s was increasingly substantiated as more recent data on water quality, phytoplankton abundance and primary productivity (Hecky, 1993; Mugidde, 1993; Silsbe, Guildford & Hecky, 2006) were compared with the earlier, extensive observations of Talling (1965, 1966). Palaeolimnological studies established that nutrient loading had begun increasing as early as the 1930s (Hecky, 1993; Verschuren *et al.*, 2002). The algal populations, as represented by subfossil diatoms and other microfossils in sediment cores from offshore areas of the lake, had responded to that increased nutrient loading through shifts in the algal community composition and abundance resulting in increasing deoxygenation of the hypolimnion (Hecky *et al.*, 1994; Verschuren *et al.*, 2002). The growing population of the basin, currently among the most rapidly increasing in Africa (Kolding *et al.*, 2008), and the resulting pressures on the land for agricultural production were inferred to be responsible for the increasing nutrient loading. These palaeolimnologic studies established that the lake was already on a eutrophication trajectory by the time of Talling's studies, well in advance of the introduction of Nile perch and Nile tilapia and well before the Nile perch population explosion of the early 1980s.

Initial observations on transparency, elements of chemistry and zooplankton and the fishery had been made in 1927–28 by Graham (1929) and Worthington (1930). Talling (1965, 1966) provided the first comprehensive characterisation of Victoria's limnology including measurements of primary production, nutrients and algal populations over a complete annual cycle in 1960–61. Talling's studies were carried out just prior to a rapid rise in lake level during 1961–62. Lake levels continued upward over two subsequent exceptionally wet years during which the lake reached its historic recorded high level, nearly two metres above the annual mean levels of the previous 60 years of systematic observation. Since attaining those historic high annual lake levels in 1964, the lake has not returned to the levels that characterised the first half of the 20th century (Kite, 1982) initially raising concern that the construction and operation of the Owen Falls dam that flooded Ripon Falls at the outlet of Victoria in 1954–56 may have altered the

hydrological balance of the lake. However, hydrological studies over the past decades have concluded that the high lake levels were the product of an unusually wet phase in the East African climate (Nicholson, 1998) and that the Owen Falls dam has not had any significant effect on lake levels (Kite, 1982). However, the recent construction of increased outlet and generation capacity at Owen Falls (Phase 2) and a deviation from long observed operating rules did contribute to a rapid decline in level during the first years of the 21st century (Mwanuzi *et al.*, 2005; Swenson & Wahr, 2009) although the lake still remains above levels of the first half of the last century.

Arguably over the past 50 years, no large lake, and certainly no Great Lake, in the world has exhibited the magnitude of change that Victoria has because of the imposition of the multiple stresses of intensive fishing, eutrophication, species introductions, species loss, water level change and climate variation. Overfishing and falling catches of the valuable tilapia fishery had been reported as early as Graham (1929) and was at least in part the motivation for the introduction of Nile perch and four species of tilapiines (Pringle, 2005). Since the introductions, hundreds of the endemic species have been lost (Snoeks, 2000). However, there remains debate and uncertainty as to the direct and indirect causes of their demise; and its relation to the Nile perch population boom over just a few years in the early 1980s (Kudhongania *et al.*, 1992; Goudswaard, Witte & Katunzi, 2008; Kolding *et al.*, 2008). Today, concern remains that overfishing and continuing unchecked eutrophication could lead to a catastrophic loss of productivity in this now immense fishery. The lake has become the most eutrophic of the world's largest lakes as measured by nutrient concentrations or algal abundance (Guildford & Hecky, 2000) and has become light limited (Mugidde, 1993; Silsbe *et al.*, 2006) because of self-shading by the higher algal biomasses generated by the high phosphorus concentrations and the highest rates of nitrogen fixation known for any large lake (Mugidde *et al.*, 2003). A profound shift in its phytoplankton community from diatom and chlorophyte dominance through much of the year (Talling, 1966) to near-continuous dominance by filamentous and colonial cyanobacteria (Kling, Mugidde & Hecky, 2001) has occurred as a result of the enrichment in P (and N from N fixation) and depletion of Si (to limit many diatom species).

The successful invasion and establishment of water hyacinth, first observed in Lake Victoria in 1990 (Twongo, 1996), was likely facilitated by the eutrophication of the lake (Williams & Hecky, 2005) because it had been introduced into the Lake Victoria catchment as an ornamental pond plant much earlier in the last century. Once established in Lake Victoria, the plant spread rapidly and covered extensive lengths of shoreline in protected embayments and created substantial economic disruption of fishing, lakeshore access and transport. The introduction of the weevil *Neochetina* has led to effective control (Williams, Duthie & Hecky, 2005) although seed populations of *Eichornia* in inflowing rivers and seed banks in sediment maintain a potential for local eruptions of hyacinth populations. The potential for major outbreaks of water hyacinth remain because of high and increasing nutrient concentrations which are yet to be addressed (Mwanuzi *et al.*, 2005; Williams *et al.*, 2005).

A less appreciated stress on the Victoria ecosystem is the warming climate over Africa (Hulme *et al.*, 2001), and the effect that regional warming may have had on events in Lake Victoria and the other African Great Lakes especially since 1980 (Verburg, Hecky & Kling, 2003; Lorke *et al.*, 2004; Vollmer *et al.*, 2005). Increasing physical stability and shallower mixing depths observed in Lake Victoria (Hecky, 1993) would contribute to the more extensive anoxic and hypoxic conditions that now occur (Hecky *et al.*, 1994) compared to the conditions described by Talling (1966). Lehman, Mugidde & Lehman (1998) have suggested that a shoaling of the mixed layer in the offshore could in itself have caused higher algal biomasses by relieving light limitation in the deeply mixed offshore pelagic. However, in shallower inshore areas (e.g. <20 m) where mixing depth is determined by the bottom depth, the large changes in algal biomass could only be accomplished by increasing nutrient concentrations, by relieving grazing effects or by alteration of diurnal dynamics because these shallow water columns still mix to the bottom daily. In these shallower inshore areas, self-shading by high phytoplankton biomasses that now limits primary productivity (Silsbe *et al.*, 2006) cannot be accounted for by significant changes in seasonal mixing depths, but a period of decreasing wind strengths might change the diurnal dynamics, e.g. shallower diurnal stratification, to reduce mixing intensity and favour one phytoplankton group, e.g. a more buoyant taxa over a

rapidly sinking taxa (Reynolds, 2005, Fig. 2.16). The possible role of complex interactions among climate warming, physical mixing dynamics, rising nutrient concentrations and loss of endemic species in causing the dramatically changed Lake Victoria ecosystem, with its increased algal productivity and dramatically altered fish community, requires a continuous record of phytoplankton abundance and primary productivity over time to compare with historical changes in the fish community. Unfortunately, such continuous direct observational records with annual resolution do not exist for Lake Victoria.

There have been multiple stresses acting upon the Lake Victoria ecosystem especially over the last half of the 20th century, and fundamental changes have taken place both at the top and bottom of the food webs. It has been difficult to compare these changes over time because the direct observations are quite discontinuous, or non-existent for water quality and biological productivity, over the period during which the most dramatic observed changes occurred between the 1960s and the early 1990s. The only continuous historic records of variations in the lake ecosystem are from the recorded fish landings and for water levels. Fortunately, it is possible to recreate a temporal record for lower food web changes by using high resolution palaeolimnological techniques to relate changes in primary productivity and attendant water chemistry which can be compared to the changes in the fish community.

Palaeolimnological studies in Lake Victoria to date have focused on the deep offshore depositional basin to elucidate changes in the areally extensive pelagic zone. At two different coring sites, paleorecords provide a temporal record of offshore changes in nutrient deposition, diatom communities and biogenic silicon deposition, a measure of diatom paleoproductivity (Hecky, 1993), as well as chironomid community change, as a metric for oxygen depletion over time (Verschuren *et al.*, 2002) at two different coring sites. However, the location of these cores in the deeper areas of the lake (both cores >55 m depth; lake maximum depth 79 m; mean depth 40 m) limits the inferences that can be made about limnological changes in the shallower inshore areas of the lake where primary productivity is now highest (Mugidde, 1992), fish densities are greatest (Getabu, Tumwebaze & MacLennan, 2003) and fishing activities are most intense. We here report results from an inshore core

taken in Itome channel inside the archipelago of islands along the Ugandan northern coast in an area of frequent limnological observation over the last two decades (Mugidde, 1992; Kling *et al.*, 2001; Ramlal *et al.*, 2001; MacIntyre, Romero & Kling, 2002; Guildford *et al.*, 2003; Mugidde *et al.*, 2003). This core enables direct temporal comparison of changes in magnitude and timing of significant limnological changes in shallower waters to compare with changes in offshore areas as well as with documented rapid changes in fish community composition and fishery landings.

Previous paleoproductivity studies in Victoria have focused on the changes in the diatom community composition and its productivity as measured by relative depositional rates of biogenic Si. However, these subfossil diatom data may present an incomplete view of the phytoplankton community which is known to have changed dramatically in composition from diatoms to cyanobacteria over the past century. Carbon stable isotopic composition of sedimentary organic matter has been shown to be a reliable indicator of phytoplankton production in the Laurentian Great Lakes (Schelske & Hodell, 1991, 1995; Hodell & Schelske, 1998) and are applied here to the new core from Itome channel as well as to the two previously published deep water cores (Hecky, 1993; Verschuren *et al.*, 2002) to establish a continuous record of relative change in algal abundance and primary production in Victoria. This record can be related to the timing and magnitude of phosphorus (P) enrichment and also to the temporal record of fish landings. Modern observations on the C and N isotopic composition of suspended organic matter is also reported here to demonstrate how these isotopic signatures reflect the current spatial patterns of algal abundance, primary productivity and N fixation in the lake. Because the current spatial gradients for primary productivity (Mugidde, 1992) and nitrogen fixation (Mugidde *et al.*, 2003) are from highest rates inshore to lower offshore, the modern spatial variation in stable isotopic composition of suspended particulate matter can be used to validate the use of isotopic variation in sedimentary organic matter to interpret past changes in primary productivity in Victoria.

Methods

Campbell *et al.* (2003) presented the Pb-210 dating profiles of the V96-5MC and the Itome cores and the

dating models used to establish the chronostratigraphy of the cores. Hecky (1993) presented all data reported here for the 103 core (Fig. 2). These two investigations used the same methods (Stainton, Capel & Armstrong, 1977) for sedimentary total P, biogenic Si, organic C and total N as well as suspended particulate C (PC; carbonate-free) and N (PN) measured along a cross lake transect sampling surface waters in October 1995 (Fig. 2). Here, we add stable isotopic C and N signatures of the suspended particulate organic matter and the lake sediments that were performed at the Freshwater Institute Laboratory (Winnipeg, Canada) using methods of Hecky & Hesslein (1995). The stable isotope signatures of the 103 and Itome cores were performed at the Environmental Isotope Laboratory of the University of Waterloo (Waterloo, Canada). The carbon and nitrogen isotope analyses for the V96-5MC core were performed at the Geological Institute, University of Bergen (Bergen, Norway). All the carbon isotopic signatures from the cores have been corrected for the decreasing $\delta^{13}\text{C}$ of atmospheric CO_2 over the past 200 years, the Suess effect, by applying the algorithm of Verburg (2007). Schelske & Hodell (1991, 1995) demonstrate and discuss the necessity of making this correction when comparing carbon isotopic signatures

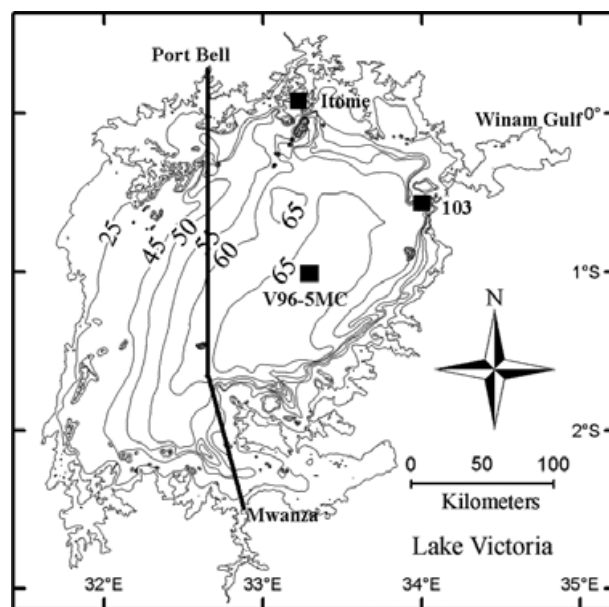


Fig. 2 Location of three sediment cores, Itome, 103 and V96-5MC (triangles), on Lake Victoria and the transect from Mwanza to Port Bell (solid line).

through significant periods of time, especially over the last 100 years when the isotopic signature of atmospheric CO₂ has changed markedly.

Limnological changes

Talling's classic studies of Lake Victoria in 1960–61 provide an invaluable baseline for comparing many properties of the lake over time (Table 1). Since his studies, total P concentrations have more than doubled both inshore and offshore as has gross primary productivity. Chlorophyll concentrations increased remarkably both inshore and offshore, but maintained the pattern of higher chlorophyll concentrations inshore observed by Talling likely as a consequence of reduced mixing depth inshore. Transparency inshore and offshore at Talling's locations has declined as a result of the increase in chlorophyll. Silsbe *et al.* (2006) found that chlorophyll concentrations explained 88% of the variance in transparency (vertical extinction coefficient) using both historic and modern data. The relationship between chlorophyll and extinction was a decreasing exponential relationship likely as a result of the change in the taxonomic composition of the Victoria phytoplankton from diatoms and green algae to dominance by cyanobacteria as chlorophyll concentrations have increased (Kling *et al.*, 2001). Chlorophyll concentrations in Victoria are now limited by self-shading and controlled by mixing depth (Mugidde, 1992; Silsbe *et al.*, 2006), and so shallow inshore locations achieve much higher chlorophyll concentrations than offshore stations where the deeper mixing depth is controlled by seasonal thermal stratification. Dissolved Si concentrations have also declined dramatically with greater declines

recorded at inshore stations compared to the offshore (Table 1). In the 1960s, there was not a strong differentiation between inshore stations in total phosphorus (TP) or Si with both being somewhat higher at inshore stations. In the 1990s, both parameters had lower concentration inshore with Si being strongly depleted inshore. The decline in dissolved Si has likely played a role in the shift from large diatoms dominating phytoplankton abundance to the current dominance by N-fixing filamentous and colonial cyanobacteria along with thinly silicified diatoms (Kling *et al.*, 2001). The decline in dissolved Si also has left a clear record in the lake sediments through increased burial of biogenic Si (Hecky, 1993; Verschuren *et al.*, 1998).

Oxygen concentrations have been affected by the increased productivity and algal biomass in Victoria. Surface waters are now supersaturated with oxygen at midday while deep waters are now anoxic for several months of the year (Hecky *et al.*, 1994). In 1960–61, surface waters were slightly undersaturated through much of the year, and deep water hypoxia was ephemeral (Talling, 1966). Although the doubling of primary productivity and a >fivefold increase in chlorophyll (Table 1) has most likely increased organic sedimentation into deep water, climate change and stratification dynamics may also have played a role in lowering deep water oxygen concentrations. Hecky (1993) found the lake warmer and more stably stratified (compared with 1960–61) with a thermocline at 30–40 m depth for much of the year although it still fully circulated in July and August when the deep waters were oxygenated during the coolest months. In contrast, Talling (1966) generally observed a well-mixed water column through much of the year with only occasional deep and ephemeral occurrence of thermal stratification. Changes in deep water oxygen conditions earlier in the last century were inferred from changes in the deep water chironomid microfossil assemblages in a sediment core (Verschuren *et al.*, 2002), which indicated that the coring site at 68 m depth was suffering increasing anoxia and became similar to modern conditions at that depth by 1980. Hecky *et al.* (1994) suggested that climate warming may have played a role in the deoxygenation of the deep water as well as eutrophication, and Verburg *et al.* (2003) noted that the African climate began a general warming trend about 1980. Although modern conditions of prolonged anoxia were

Table 1 Comparison of historic nutrient and primary productivity data for Lake Victoria. Total phosphorus (TP), chlorophyll (chl), primary productivity (PPr) and transparency (k) data from Mugidde (1992, 2001) and Talling (1965) while Si from Talling and Hecky (unpublished data)

	1960–61		1990s	
	Inshore	Offshore	Inshore	Offshore
TP ($\mu\text{moles L}^{-1}$)	1.2	1.1	2.8	3.0
Si (μM)	74	66	10	25
Chl a ($\mu\text{g L}^{-1}$)	13	3	71	13.5
PPr ($\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$)	11	7.4	22	14
k ($\ln \text{ m}^{-1}$)	0.60	0.25	1.1	0.6

established by 1980 at the 96-5MC site, Verschuren *et al.* (2002) indicated a general decline to the modern condition was initiated around 1960. Both Hecky (1993) and Verschuren *et al.* (2002) in their separate cores reported palaeolimnological evidence of changing diatom community structure and increased biogenic Si deposition suggesting that the eutrophication of the lake was well underway as early as the 1940s.

Spatial patterns

Lake Victoria in 1960–61 had only slight gradients in TP and Si with inshore stations (<20 m) having somewhat higher dissolved Si and TP on average compared to offshore deep water stations (Table 1). Talling did not measure total fixed nitrogen (TN) and made relatively few dissolved inorganic fixed nitrogen concentration measurements, but noted that dissolved fixed N concentrations were very low, at and near the detection limit of his colorimetric methods. These low concentrations of fixed N suggested to him that dissolved inorganic N was most likely to limit algal growth and abundance, especially as dissolved inorganic P was easily measured with concentrations up to 0.2 μM (Talling & Talling, 1965; Talling, 1966). Inshore stations, although less frequently sampled by Talling than his offshore station, did have substantially higher chlorophyll concentrations compared to offshore as well as higher primary productivity rates while light extinction was also higher in inshore. By the 1990s, these spatial patterns had been dramatically amplified as chlorophyll increased by a factor of >4 and primary productivity had doubled both inshore and offshore (Table 1).

In the modern lake, the inshore to offshore gradients for chlorophyll and primary productivity are still present; and, while TP is still relatively spatially homogenous, its concentrations have more than doubled. In parallel with the chlorophyll gradients and light extinction gradients but inverse to the dissolved Si gradient, particulate C, N and P (PC, PN and PP) and TN all decline from inshore to offshore (Table 2) while dissolved inorganic N remains low both inshore and offshore (Mugidde *et al.*, 2003). Talling did not measure TN or the particulate nutrient concentrations. However, he did observe much lower algal biomass compared to the 1990s (Kling *et al.*, 2001) while also reporting low concentrations of inorganic fixed N. When dissolved fixed N concentrations remain low

Table 2 Mean nutrient concentrations $\mu\text{moles L}^{-1}$ of total fixed nitrogen (TN), total phosphorus (TP), particulate C (PC), particulate N (PN), particulate P (PP), TN : TP molar ratios and $\delta^{15}\text{N}$ in PN for samples taken between 1994 and 1998 (Mugidde, 2001). Concentrations are for upper mixed layer depths at inshore stations in water depths between 5 and 25 m while offshore samples are primarily from Bugaia Island (station O of Talling, 1965). Nitrogen fixation (N fix) from Mugidde *et al.* (2003) for same stations with offshore at station Bugaia likely over-estimating rates farther offshore (Mugidde *et al.*, 2003). Number of months sampled is *n*

	Nearshore	<i>n</i>	Offshore	<i>n</i>
PC	232	104	138	24
PP	1.4	205	0.5	24
TN	98.1	46	37.1	25
PN	33.2	97	10.6	24
TN : TP molar	35.0	23	12.4	15
N fix g N m ⁻² year ⁻¹	14.0	62	7.3	18
$\delta^{15}\text{N}$ (PN)	2.8	13	8.9	25

(Mugidde *et al.*, 2003), the much higher algal biomasses indicate that the amount of N cycling in Lake Victoria certainly increased and TN concentrations, on average, would also be higher in the upper mixed layer than in the 1960s.

The source of much of the increase in TN compared to the 1960s arises from N fixation in the lake. Inshore regions have much higher rates of N fixation and therefore much lower $\delta^{15}\text{N}$ in particulate organic matter compared to offshore (Mugidde, 2001; Table 2). The filamentous diazotrophic cyanobacteria that are now dominant in the Lake Victoria phytoplankton (Kling *et al.*, 2001) fix atmospheric N with a $\delta^{15}\text{N}$ of near zero; therefore, the $\delta^{15}\text{N}$ of PN declines in proportion to the ratio of fixed N to recycled N which has a much higher $\delta^{15}\text{N}$. Nitrogen fixed from the atmosphere now dominates the sestonic N inshore while isotopically heavy recycled N dominates offshore available dissolved inorganic nitrogen (DIN). The offshore PN has an enriched $\delta^{15}\text{N}$ because denitrification in the hypoxic metalimnion/hypolimnion preferentially removes the lighter N isotope, and offshore N fixation is light limited (Mugidde *et al.*, 2003), so there is a net enrichment in $\delta^{15}\text{N}$ in PN offshore.

The spatial patterns in algal biomass and composition with distance from shore (and depth) are demonstrable along a transect from Mwanza on the southern shore to Port Bell on the northern shore (Fig. 2). This transect was accomplished overnight (15–16 October 1995) taking surface water samples every 20 km from the trans-lake ferry MV Bukoba.

Algal biomass was highest near the coast and fell rapidly to lower values offshore as measured as particulate organic carbon and nitrogen (POC and PON) (Fig. 3a). The POC and PON were highly correlated along the transect ($r = 0.96$) with a mean molar C : N ratio of 7.2 with higher ratios near shore (up to 8.4). These low, near Redfield Ratios, values for C : N are characteristic of Lake Victoria (Guildford & Hecky, 2000) and are indicative that the particulate matter sampled was of algal origin. Isotopically depleted PC occurred offshore, and $\delta^{13}\text{C}$ was increasingly enriched nearer the coasts as depth shoaled (Fig. 3b). The $\delta^{15}\text{N}$ of the PN showed an inverse pattern with highest $\delta^{15}\text{N}$ values observed offshore. Consequently, there was a strong inverse relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with the former decreasing at high algal abundances and the latter increasing as PC increased (Fig. 4). The scatter of the isotopic signatures with increasing algal abundances indicates that these relationships are dynamic in

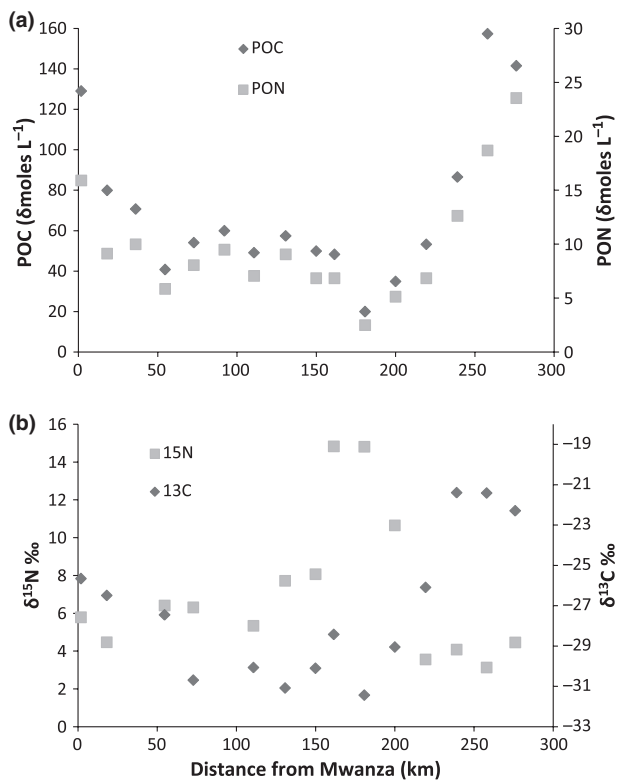


Fig. 3 Top panel: concentration of particulate organic carbon and nitrogen in surface waters along a transect from Mwanza, Tanzania to Port Bell, Uganda on 15–16 October 1995 (see Fig. 2). Bottom panel: stable isotopic signatures $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of particulate organic matter along the transect.

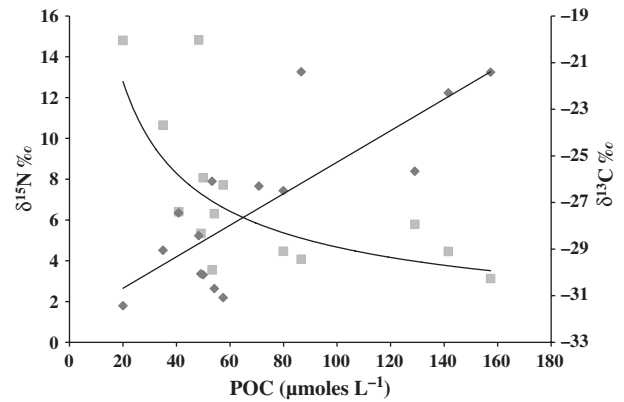


Fig. 4 Relationships between particulate organic carbon (POC) concentrations and the $\delta^{13}\text{C}$ (diamonds) and $\delta^{15}\text{N}$ (squares) signatures of particulate organic matter along the Mwanza to Port Bell transect (Fig. 2). Fitted lines are linear between POC and $\delta^{13}\text{C}$ ($r^2 = 0.65$) and a power function between POC and $\delta^{15}\text{N}$ ($r^2 = 0.54$).

nature responding to the availability and demand for CO_2 and DIN.

The N fixation which creates the isotopically light $\delta^{15}\text{N}$ PN in diazotrophic cyanobacteria relieves the N limitation that more generally may control the biomass of phytoplankton that cannot fix N. Consequently, the cyanobacteria increase in abundance inshore and achieve levels of primary productivity and biomass that reduce isotopic fractionation of CO_2 fixation and results in enriched $\delta^{13}\text{C}$ of PC (Hecky & Hesslein, 1995). For the N-fixing cyanobacteria, biomass can increase until light (through self-shading) or another nutrient, most likely P (Hecky, 1993), becomes limiting (Mugidde *et al.*, 2003). Although there is little difference in TP concentration between inshore and offshore areas (Table 1), the PP concentrations are much higher in inshore (Table 2) and constitute a much higher fraction of the TP as a result of dissolved P being incorporated into PP as N fixation overcomes N limitation inshore (Hecky *et al.*, 1996). As a result of the high rates of N fixation inshore, TN concentrations are much higher inshore, and TN : TP ratios increase by a factor of 3 inshore (Table 2) while TP does not change.

Increasing TP concentrations since the 1960s have enabled the accomplishment of higher algal biomasses because the N-fixing cyanobacteria cannot be limited by low dissolved inorganic N. The twofold increase in PP both inshore and offshore is proportional to the increase in TP while the higher algal biomass

(chlorophyll) inshore is a result of light-limiting algal biomass and productivity, but at higher chlorophyll concentrations, at the shallower inshore stations. Just as the pattern of enriched $\delta^{13}\text{C}$ of PC in the modern lake indicates higher productivity and biomass in inshore areas (Fig. 3b), it would be expected that $\delta^{13}\text{C}$ of sedimentary organic matter would reflect the increasing primary productivity of the lake over time (Table 1), and the $\delta^{13}\text{C}$ sedimentary organic matter in sediment cores may provide a detailed record revealing the rate and timing of increased algal productivity in Lake Victoria.

Sediment cores

The ^{210}Pb dating results for the three cores that are the subject of this study were previously reported by Hecky (1993) for core 103, Verschuren *et al.* (2002) for V96-5MC and Campbell *et al.* (2003) for the Itome core (core locations in Fig. 2). All three cores are rich in biogenic sediments as their composition is dominated by organic C and biogenic Si (Table 3). Such organic and Si-rich sediments are characteristic of many other cores from the depositional basins in Victoria (Johnson *et al.*, 1998), reflecting the relatively low rates of detrital inputs from the catchment in proportion to the enormous surface area of this Great Lake. Non-biogenic detrital components (mineral matter) account for only 30% of the content of the offshore cores and 40% of the inshore core on a dry weight basis. Despite the similarity in composition between the offshore cores, the sedimentation rate of core 103 was much lower, less than one-third the rate of that of V96-5MC suggesting that sediment transport may have been winnowing the fine materials from the shallower 103

core (56 m) to the deeper offshore sites such as V96-5MC. The lake still mixes completely annually restoring oxic conditions to the hypolimnion in July and August, but the high organic content of the sediments likely imposes a strong oxygen demand on the hypolimnion and maintains anoxic conditions within the sediment. These highly organic sediments, therefore, likely escape strong bioturbation. A discontinuity in the radioisotope profile for V96-MC5 was attributed to a storm event that removed a section of the record prior to 1925 (Verschuren *et al.*, 2002), so physical processes can still episodically affect even the deepest part of the basin. Neither the 103 core nor the Itome core had evidence of this storm event as their ^{210}Pb profiles declined smoothly and exponentially over their length to background activity (Campbell *et al.*, 2003). The offshore core V96-5MC and the inshore Itome cores had remarkably similar rates of sedimentation (Table 3) that were nearly three times higher than the 103 core. This higher rate of sedimentation in these two cores allows greater temporal resolution per equivalent sampling interval than in the 103 core and also facilitates direct stratigraphic comparison of temporal sequences between them. As a consequence of their high content of biogenic materials and good preservation engendered by anaerobic conditions, sediment cores from Victoria are ideal for detailed palaeolimnologic reconstructions (Hecky, 1993; Verschuren *et al.*, 2002).

The precision and accuracy of the chronostratigraphy created by ^{210}Pb chronologies of these cores is critical to their interpretation especially when comparing the palaeolimnologic reconstruction with other environmental historic records, such as fisheries data. Pb-210 dating relies on the decay of ^{210}Pb , which originates in the atmosphere, falls on a lake's surface bound to particles and rapidly settles to the sediment (Binford, 1990). Normally, any contribution of particle-bound Pb-210 from the catchment is minor except in small waterbodies with high erosion rates. Lake Victoria with its huge surface area and relatively small catchment loading of inorganic detritus is an ideal candidate for Pb-210 dating. The detailed profiles of ^{210}Pb activity in the Itome and V96-5MC cores, given in Campbell *et al.* (2003), have remarkably smooth log-linear decay of ^{210}Pb and indicate essentially linear mass sedimentation rates over the available record. Also, the sedimentation rates of these two cores are remarkably similar (Table 3), which

Table 3 Coring depths, sedimentation rates (SR) of dry matter and mean composition for major constituents sediment cores 103 recovered in 1990 (Hecky, 1993), V96-5 MC5 recovered in 1996 (Verschuren *et al.*, 2002) and Itome recovered in 1995 (Campbell *et al.*, 2003). Per cent biogenic sediment is based on weight conversion of C to organic matter (CH_2O) and Si to silica (SiO_2). Mean is for all depths sampled over the total core length

	103	96-5MC	Itome
Site depth (m)	56	68	25
SR ($\text{g m}^{-2} \text{ year}^{-1}$)	100	320	276
Organic C ($\text{mg g}^{-1} \text{ d.w.}$)	168	204	184
Biogenic Si ($\text{mg g}^{-1} \text{ d.w.}$)	133	86	59
% Biogenic sediment (d.w.)	70	69	58

facilitates comparison of their stratigraphies and gives them similar resolution in time. Both cores were subsampled at equivalent depth intervals of 0.5 cm. In these two cores, such a sampling interval results in a resolution of 1–2 years per 0.5 cm sampling interval back to 1950 and 2–3 years from 1950 to 1930. At deeper sampling intervals, sediment compaction further reduces dating resolution. Core 103 with a lower sedimentation rate and a coarser (1 cm) sampling interval will have a lower resolution in its age assignments, and we will use it primarily to confirm long-term trends and when those trends were initiated.

Binford (1990) gives a relationship for estimating the 95% confidence interval (CI in years) on an age assignment. The CI increases with age from <2 years from 0 to 20 dating years up to 3 years at 40 dating years. Because the last 20 years of the stratigraphic and historical record (mid-to-late 1970s to the present) are a primary focus for our historical comparisons, we will assume a CI of 2 years for the last 20 years of assignment increasing to a CI of 3 years at sediment age of 40 years.

Accuracy in the dating assignments depends on the precision of the estimate as well as the certainty with which the surface of the core reflects the current rate input of ^{210}Pb . Dates are assigned assuming the surface of the core can be dated to the time it was taken, and all dates are based on the time required to reduce the radioactivity of the ^{210}Pb from the modern (surface) concentration. If the very surface layers of the core are lost in sampling, then the core top is not modern (it is older) and all dates assigned relative to that surface activity will be artefactually too young. The cores we are using have been dated by two independent laboratories, and the age model applied was determined in previous publications cited above. Here, we adopt the age models as published, and assume that the core surfaces were modern as stated by the original authors. If this assumption is false, then our age assignments would be erroneously younger than they should be when comparing it with an historical archive where no error is assumed in the date (if not the data). Because we will argue that certain events in our palaeolimnological reconstruction preceded archival historical events, we are confident in our conclusion especially when those events preceded historical events by more than the CI of our assigned date. To be conservative, we will only

invoke a reconstructed chronological event to precede an historical record when 4 years or more separate a reconstructed age event or trend and an historical event.

Palaeolimnologic changes in P deposition

All three sediment cores demonstrate nearly constant sedimentary P concentrations in the early part of the last century up until the 1940s when rising trends begin first in Itome and then in the offshore cores (Fig. 5). Itome had the highest deposition rates ($\text{mg P m}^{-2} \text{ year}^{-1}$) initially, nearly double the rate at V96-5MC which had a similar mass sedimentation rate. Itome also had a higher P deposition rate than the 103 core which had similar P concentrations to Itome (Fig. 5) but a much lower mass sedimentation rate (Table 3). Although Itome P concentrations start to increase somewhat before the offshore cores and had an initially higher P deposition rate than the other two cores, the trends once initiated continue unabated to the present in all three cores and actually show some upward acceleration as the modern day is approached. Greatest rate of change in P concentration in the three cores occurred in the offshore core V96-5MC indicating a rapid acceleration of sedimentary P deposition at this deepest site in the early 1980s. This dramatic increase in P deposition occurs only at the deepest core site and not at the expense of contemporaneous P deposition rates that are not altered at the other coring locations. This increase in P at the V96-5MC core occurred entirely within the organic P fraction (R.E. Hecky, unpublished data). Even

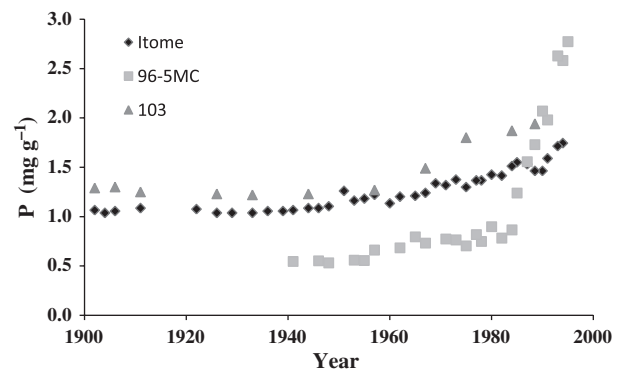


Fig. 5 Weight concentration of phosphorus (TP) in sediments deposited over the past century in three cores from Lake Victoria. TP, total phosphorus.

without considering the post-1980 dramatic rise in sedimentary P at V96-5MC, all three cores exhibit monotonic increases in P inputs of 60 to >500% from 1960 to the 1990s in general agreement with the >100% increase observed for TP concentrations in lake water (Table 1).

Change in deposition of biogenic Si

Biogenic Si concentrations began to increase in the 1930s at Itome and 96-5MC and underwent an approximate doubling over the past century from stable baseline values observed in the earliest part of the 20th century (Fig. 6). At Itome, Si deposition declined somewhat in the early 1950s before undergoing a strong and apparently accelerating increase in deposition post 1980. In the two offshore cores, Si deposition was more continuously rising over time but with evidence of a leveling off of Si deposition from 1950 to 1970 at 96-5MC. After 1970 at V96-5MC, Si concentrations undergo a rapid increase prior to 1980. After 1980, Si deposition at 96-5MC leveled off and did not respond to the subsequent rapid increase in P deposition at this site (Fig. 5). The 103 Si record also shows some indication of leveling off post 1980, but the temporal resolution is too coarse in this core to appreciate shorter-term changes in Si deposition. The Si deposition rates at 103 are quite similar to those at V96-5MC once the difference in mass sedimentation rate is taken into account. The increase in biogenic Si content of the sediments in all three cores especially

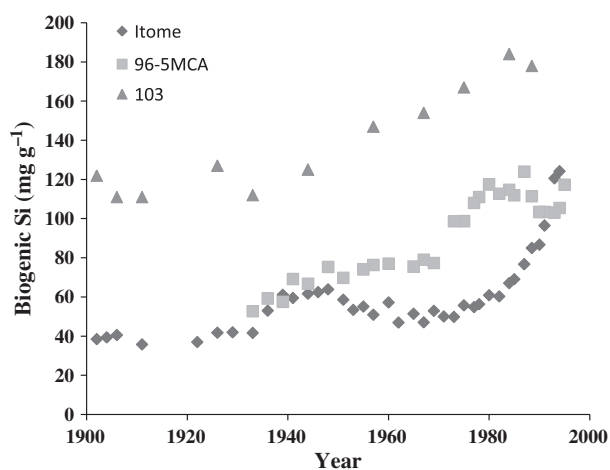


Fig. 6 Weight concentrations of biogenic silicon (Si) in sediments deposited over the past century in three cores from Lake Victoria.

since 1960 is consistent with the decline in dissolved Si concentrations in the lake as sedimentation of Si increased. This pattern of dissolved Si depletion with increased nutrient loading has been observed in other large lakes (Schelske *et al.*, 1986) and is consistent with the directly observed changes in the trophic status and productivity over this time period (Table 1; Hecky, 1993; Verschuren *et al.*, 2002). However, the inshore areas of the lake, at least near Itome, followed a different and partly delayed Si deposition response to nutrient enrichment compared to the offshore response. From 1950 through 1980, the Itome core lagged well behind the offshore cores in its Si deposition trend. By the 1970s, Si deposition rates were nearly twice as high at V96-5MC as at Itome. But, while the offshore Si deposition rates are nearly constant post 1980, the Itome core exhibits a rapid increase even surpassing the deposition rates in the offshore post 1980.

Chronology of changes in carbon isotopic signatures

All three cores recorded increases in the isotopic signature of the sedimentary organic matter (Fig. 7). The deepest and farthest offshore core, 96-5MC, shows a subdued upward trend as early as 1950s, from baseline $\delta^{13}\text{C}$ signatures of -22‰ , with a somewhat more rapid increase around 1980 before stabilising at values of -21‰ , but the overall increase in $\delta^{13}\text{C}$ is less than $+1\text{‰}$ over the last century. The increase in $\delta^{13}\text{C}$ at the 103 site was perhaps later but clearly rising after 1960 with an increase of nearly 2‰ relative to the values of the 1940s and 1950s. By the

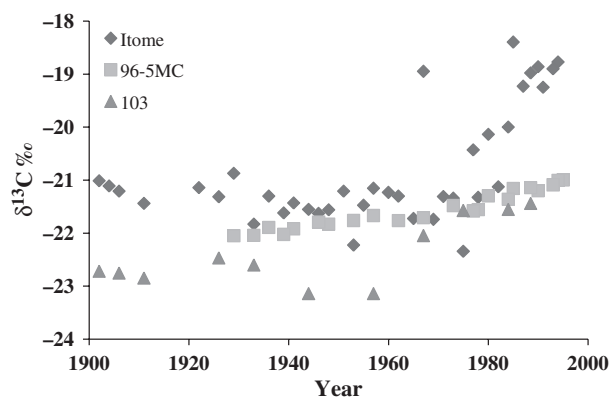


Fig. 7 The $\delta^{13}\text{C}$ signature of sedimentary organic matter (Suess corrected) deposited over the past century in three cores from Lake Victoria.

1990s, both offshore cores had similar isotopic signatures. At the inshore core, there is no clear upward trend in the $\delta^{13}\text{C}$ until the late 1970s when there is a substantial change of approximately 2.5‰ achieved by 1990 after which values appear stable. The most recent isotopic signatures in sedimentary organic matter at these sites are consistent with modern spatial patterns in the lake with the inshore site, Itome, being significantly enriched in its $\delta^{13}\text{C}$ compared to the offshore cores. The range of 2‰ in $\delta^{13}\text{C}$ values between surface sediments of offshore cores and the nearshore core is not as great as was observed on our single transect, -21 to -31‰ (Fig. 3); but the sediments integrate spatially through sediment transport and deposition as well as over seasons and will tend to reduce the range in values observable at any particular time. The degree of influence of inshore isotopic signatures on the offshore values is a function of both the higher productivity of the inshore regions of the lake (Table 1) and the difference in the $\delta^{13}\text{C}$ between inshore and offshore regions (Fig. 3b). In the Itome stratigraphic record, the $\delta^{13}\text{C}$ of sediments was quite similar to the 96-5 MC core prior to 1980; therefore, a higher contribution of organic C from inshore areas would not have altered the offshore values as much as they would have after 1980 when the inshore $\delta^{13}\text{C}$ was much enriched relative to the offshore sedimentary C.

Transport and sedimentation of particulate organic matter will integrate the instantaneous $\delta^{13}\text{C}$ values observed in PC, spatially and temporally; and so a reduced range in organic matter in lake sediments compared to the range in PC might be expected. However, the most recent sediment deposited at Itome is, in fact, as enriched in its $\delta^{13}\text{C}$ as the modern seston. This suggests that the reduction in the range between inshore and offshore sediments compared to modern PC is a result of transport of isotopically enriched inshore PC to the offshore resulting in offshore sediments that are more enriched in $\delta^{13}\text{C}$ than would be expected from sedimenting PC produced in offshore waters (Fig. 2b). MacIntyre *et al.* (2002) demonstrated that differential heating and cooling between inshore shallow waters and bays and deeper waters leads to active horizontal transport in the upper mixed layer which would lead to offshore transport of PC from these productive inshore areas. The record of change in the $\delta^{13}\text{C}$ of sedimentary organic matter is consistent with the

evidence for changes in primary productivity in the lake over time, both inshore and offshore (Table 1) and over spatial gradients in the modern lake. Therefore, the $\delta^{13}\text{C}$ stratigraphic record may be accepted as a reliable estimate of relative changes in productivity at the respective coring sites with the caveat that offshore sites will also reflect productivity changes at inshore sites because of the much higher rates of organic production at inshore sites and the general offshore transport to deeper waters of particulate organic matter isotopically heavier than that produced in the offshore. The most dramatic change in $\delta^{13}\text{C}$ of all the cores is clear in the inshore Itome core beginning around or before 1980 when a substantial and rapid increase in $\delta^{13}\text{C}$ occurred. This indicates that there was an increase in C demand for photosynthesis most likely associated with a substantial increase in algal biomass, and the modern levels of algal biomass and primary productivity were achieved lakewide by the mid-to-late 1980s.

Both the $\delta^{13}\text{C}$ of sedimentary organic matter and the biogenic Si deposition may be indicators of primary productivity in lakes with the carbon signatures reflecting the integrated carbon demand of all phytoplankton while the biogenic Si primarily tracks the production of one component of the phytoplankton, the diatoms. In the Lake Victoria cores, these two indicators of primary productivity are highly correlated, with correlation coefficients all highly significant at $P < 0.001$ (Table 4). This suggests that,

Table 4 Pearson's correlation coefficients among total phosphorus, $\delta^{13}\text{C}$, biogenic Si and TN in Lake Victoria cores 103, 96-5MC and Itome

	P	Si	$\delta^{13}\text{C}$	N
Core 103 ($n = 11$)				
P	–	0.91	0.93	0.76
Si	0.91	–	0.82	0.89
$\delta^{13}\text{C}$	0.93	0.82	–	0.63
N	0.76	0.89	0.63	–
96-5MC ($n = 20$)				
P	–	0.47	0.83	0.82
Si	0.47	–	0.88	0.86
$\delta^{13}\text{C}$	0.83	0.88	–	0.95
N ($n = 16$)	0.82	0.86	0.95	–
Itome ($n = 38$)				
P	–	0.81	0.74	0.51
Si	0.81	–	0.68	0.59
$\delta^{13}\text{C}$	0.74	0.68	–	0.35
N	0.51	0.59	0.35	–

TN, total fixed nitrogen.

although dissolved Si has become depleted in Lake Victoria (Hecky, 1993; Verschuren *et al.*, 2002), diatom productivity has, in general, kept pace with total phytoplankton production during the period of eutrophication. This implies a shift to diatom species more efficient at accomplishing growth at lower dissolved Si concentrations and is consistent with the shift, observable in all three of our cores, over the latter part of the last century from heavily silicified *Aulacoseira* as the dominant diatom to the current dominance by thinly silicified and smaller *Nitzschia* spp. (Hecky, 1993; Kling *et al.*, 2001; Verschuren *et al.*, 2002).

Nitrogen, phosphorus and primary productivity

Correlations among sedimentary $\delta^{13}\text{C}$, biogenic Si, N and P content of sediments are all significant. With the exception of the correlations between N and $\delta^{13}\text{C}$ in the Itome and 103 cores and Si and P in 96-5MC which are only significant with $P < 0.02$, all the other correlations are very highly significant ($P < 0.001$; Table 4). The reduced Si : P correlation at 96-5MC is likely attributed to a saturation of the Si (diatom productivity indicator) response as P exceeds 0.8 mg P g⁻¹ d.w. (Fig. 8a), which occurs about 1977 (Fig. 5) and prior to the rapid increase in P deposition that subsequently occurred at this offshore site. The $\delta^{13}\text{C}$ at V96-5MC also shows a saturation response to increasing P (Fig. 8b) although the correlation coefficient between P and $\delta^{13}\text{C}$ is less affected than the Si : P correlation (Table 4). This saturation response in Si deposition (Fig. 6) to the rise in sedimentary P concentrations at this deepest station (Fig. 5), which receives both inshore and offshore organic matter, indicates that the primary productivity enhancement stimulated by the increasing P concentrations in Lake Victoria was largely accomplished by the mid-1980s. It is possible that this P saturation response was a result of the lake becoming light limited at a level of primary production set by the self-shading of the chlorophyll crop (Mugidde, 1992; Silsbe *et al.*, 2006). This interpretation would predict that the inshore areas also became light limited at this time because these areas are the most productive areas of the modern lake (Table 1) and are major contributors to organic sediments accumulating offshore. The inshore Itome core also shows evidence of saturation of the $\delta^{13}\text{C}$ sensitivity to P. Since 1989, $\delta^{13}\text{C}$ has been essentially invariant at Itome (mean of -18.95‰ ,

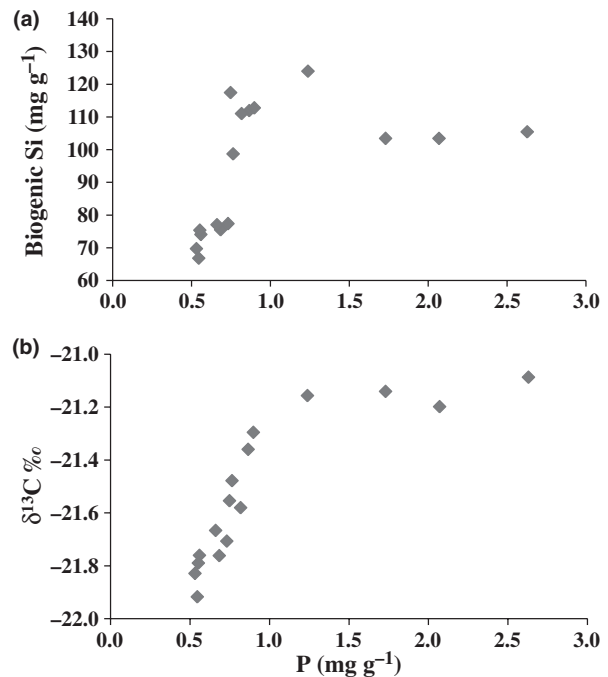


Fig. 8 (a) Relationship between biogenic Si and TP in sediments of core V96-5MC deposited since 1929. (b) Relationship between $\delta^{13}\text{C}$ signature of sedimentary organic matter (Suess corrected) and TP in sediments of the same core. TP, total phosphorus.

$\text{SD} = 0.18\text{‰}$, $n = 5$) even though P continued to rise (Fig. 5). At Itome, the paleoproductivity indicators, $\delta^{13}\text{C}$ and biogenic Si, both exhibit a dramatic upsurge beginning in the late 1970s, with the rise in $\delta^{13}\text{C}$ completed by 1989 while the Si deposition continued to increase (Fig. 9). The stabilisation of $\delta^{13}\text{C}$ by 1989 indicates that the transition in primary production of

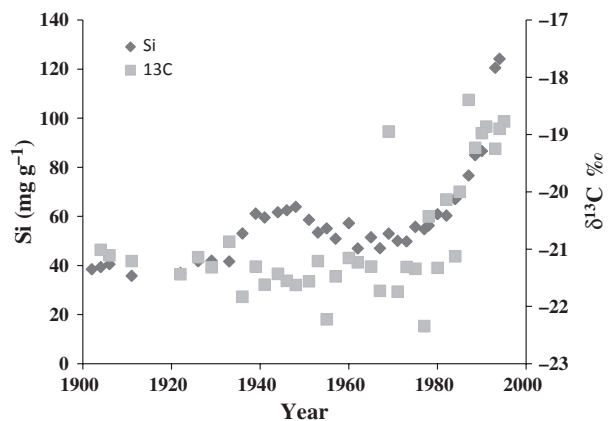


Fig. 9 Relationship between two paleoproductivity indicators, biogenic Si content and $\delta^{13}\text{C}$ signature (Suess corrected) of sedimentary organic matter, in the Itome core.

the phytoplankton community was accomplished in a relatively brief period starting in the late 1970s and completed by the late 1980s after which light availability became limiting on the algal crop. This upsurge in inshore productivity occurred after initiation of the longer-term, but more subdued, change in the paleo-productivity indicators in the offshore cores (Figs 6 & 7). The deeper mixed layer offshore would become light limited at lower chlorophyll concentration and photosynthetic carbon demand than the inshore site (Silsbe *et al.*, 2006). By 1980, offshore phytoplankton were already light limited and could not respond to the rapid increase in P availability that is recorded at V96-5MC, but the inshore regions were responding with increased productivity and algal biomass as recorded at Itome.

The rapid increase in P concentrations at the V96-5MC core is not evident at the shallower 103 or the inshore Itome cores, and it occurs as a dramatic and quick onset after a prolonged period, after 1950, of steadily rising P concentrations in all three cores (Fig. 5). Verschuren *et al.* (2002) used oxygen sensitivities of chironomids that leave identifiable head capsules in lake sediments to reconstruct a chronology of the deoxygenation of the deep water. A steady decline in oxygen concentrations was observed at the V96-5MC site beginning about 1960 and stabilising at minimum inferred oxygen concentrations by the late 1970s. By the 1990s, the deep waters below 40 m were enduring prolonged seasonal anoxia (Hecky *et al.*, 1994). We hypothesise that the rapid increase in sedimentary P at V96-5MC resulted from a substantial increase in the availability of P liberated from internal sedimentary sources under increasingly prolonged anoxia. This apparently rapid rise in internal P loading recorded at V96-5MC stimulated inshore productivity as recorded in the Itome $\delta^{13}\text{C}$ and biogenic Si stratigraphies (Fig. 9). Much of this increased productivity was likely accomplished by N-fixing cyanobacteria that were able to overcome increasingly severe N limitation. These cyanobacteria would eventually form P-rich low density organic detritus with slow sedimentation rates that would be translocated to the deeper offshore sites before final burial accounting for the P enrichment of sediments deposited at V96-5MC after 1980. Scholz *et al.* (1990) mapped the sediments of the open portions of Lake Victoria and concluded that much of the fine grained sedimentation in the open lake (excluding protected

embayments and channels) was occurring at depths >50 m depth, primarily in the northeast sector of the lake. Above 50 m depth, there were extensive areas of sands and coarser sediments especially in the relatively shallower southwestern portion of the main basin (Fig. 1). This extensive area of oxidised coarser sediments would be able to provide remobilised P when exposed to reducing conditions. Subsequent to its mixing into the euphotic zone and incorporation into phytoplankton, this organic P would then be eventually sedimented in the depositional zone to the northeast. In the highly biogenic sediment of our cores (Table 3), largely organic P is present; and this P would not have been mobilised by the imposition of reducing conditions. Consequently, the shallower cores show no sign of a loss of P while the deep core 96-5MC underwent a dramatic increase in organic P deposition.

Nitrogen in sediments increased over time in all three cores and was significantly correlated with P concentrations as well as with the paleoproductivity indicators, $\delta^{13}\text{C}$ and biogenic Si (Table 4). Although highly correlated with $\delta^{13}\text{C}$ and biogenic Si and with a higher significance than P in V96-5MC, N was much more weakly associated with $\delta^{13}\text{C}$ and biogenic Si than P in the 103 and Itome cores. In the V96-5MC core (Fig. 10a), sedimentary N exhibited a monotonic increase after 1960 as does $\delta^{13}\text{C}$, biogenic Si and P although P accelerated rapidly after 1980 (Figs 5, 6 & 7). As P concentrations rose rapidly in sediments after 1980, N concentrations did not keep pace; and the sedimentary TN : TP ratio fell sharply as TP increased at V96-5MC. In the other two cores with weaker association between N and $\delta^{13}\text{C}$, N concentrations varied more over time exhibiting both increases and decreases prior to 1960. In both the Itome (Fig. 10b) and 103 cores (Hecky, 1993), sedimentary N underwent an early rise in concentration starting as early as 1920 as did sedimentary C as indicated by the nearly constant C : N ratio (Fig. 9b). Hecky (1993) hypothesised that this early rise in C and N (but not P) was a response to deforestation and land clearance as dissolved N release from terrestrial catchments is significant following vegetation removal (Likens *et al.*, 1970).

Although the increase in N concentration and TN : TP ratio is easily measured in the sediments (Fig. 10b), there was muted or no response by either of the paleoproductivity indicators, $\delta^{13}\text{C}$ and biogenic Si,

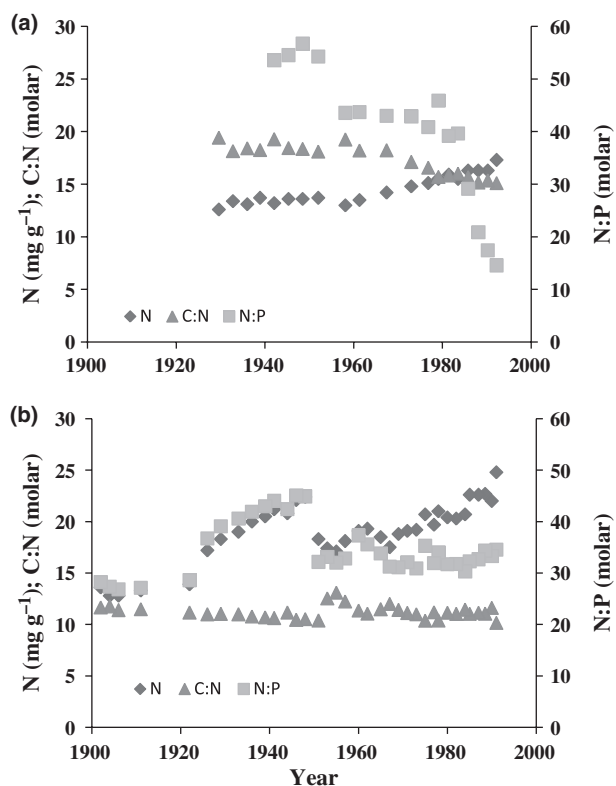


Fig. 10 (a) Trends over the past century in nitrogen content (N) and the organic C : TN and TN : TP ratios of sediments deposited at offshore coring site, V96-5MC and (b) the inshore core, Itome. TP, total phosphorus; TN, total fixed nitrogen.

in the Itome and 103 cores (Figs 6 & 7) to this early N enrichment. Much stronger responses were expressed with regard to rising P concentrations which began in these cores after 1960. After the initial rise in the 1920s in N concentrations in sediments, they subsequently fell during the 1950s and 1960s and did not recover to the 1940s high concentrations until the early 1990s (Fig. 10b). The reduced correlation between N and $\delta^{13}\text{C}$ compared to the P correlation in Itome and 103 is likely because of the lack of a strong productivity response to this early nitrogen enrichment between 1920 and 1940. Both the Itome and 103 cores also cover a longer period than the V96-5MC record which starts later and cannot completely reflect these early changes.

Talling (1966) observed barely detectable dissolve nitrate while phosphate was readily measurable in 1961–62 and suggested that N might be more limiting than P for algal growth. In the late 1990s, phosphate was still readily measurable at Talling's station, and N concentrations were still low (Mugidde *et al.*, 2003).

Although many phytoplankton may have been N limited by the early 1960s, the N-fixing cyanobacteria were able to respond to the increasing P inputs to become increasingly persistent and dominant (Kling *et al.*, 2001) and drove up the primary productivity as reflected in the paleoproductivity indicators. By the 1990s, the algal biomasses in the lake were much higher than in 1961–62 (Table 1) and inshore rates of primary production and N fixation were especially high and affecting the isotopic composition of the phytoplankton (Fig. 3).

Talling & Talling (1965) and Talling (1966) suggested that nitrogen was most likely to limit algal production in Lake Victoria. They based their hypothesis on the readily measurable concentration of inorganic dissolved P relative to the very low concentrations of nitrate (generally near or below detection with their methods). Nitrogen-fixing cyanobacteria cannot be limited by N alone since they can meet their requirements for N by drawing on atmospheric N. There is little doubt that Victoria is an N deficient system compared to many freshwaters (Guildford & Hecky, 2000). In addition to Talling's observations about the availability of inorganic P relative to inorganic fixed N sources that remain true today, offshore TN : TP ratios in surface waters are also low, mean 12.4 (Table 2) and below 8 in hypolimnetic waters (Hecky, 1993; Hecky *et al.*, 1996), all well below the Redfield Ratio indicative of a balanced nutrient supply for growth of most phytoplankton. These low TN : TP ratios favour heterocystous filamentous cyanobacteria (Guildford & Hecky, 2000), which now are dominant in the lake phytoplankton through much of the year (Kling *et al.*, 2001). These cyanobacteria are capable of meeting their own N demands through N fixation, and their decomposition in surface waters will seasonally build up a fixed N reserve which then allows other non-fixing phytoplankton to meet their N requirement.

In the early 1960s, Talling observed heterocystous cyanobacteria (*Anabaena* and *Anabaenopsis*) that were briefly dominant in October–November after restratification of the lake from deep mixing in July–August. The prominence of these heterocystous cyanobacteria then likely indicated a mild seasonal N deficiency after deep mixing that was relatively quickly overcome through N fixation by these cyanobacteria. The increasing anoxic/hypoxic condition of the hypolimnion since 1960, as inferred by Verschuren *et al.* (2002)

and measured by Hecky *et al.* (1994) in the early 1990s, would aggravate the N deficiency because of greater denitrification loss of fixed N in increasingly extensive hypoxic waters (Hecky *et al.*, 1996). While losses to denitrification would increase under spreading and annually more persistent anoxia and hypoxia, the liberation of internally stored P from formerly oxidised sediments would not only drive up P concentrations as evident in the V96-5MC core, but also would increase the degree and duration of N deficiency. The sedimentary organic C : TN and TN : TP ratios are more strongly affected at the V96-5MC site compared to the inshore region at Itome; however, both cores exhibited declines in these ratios since the 1960s (Fig. 10a,b). The greater decline offshore may be a consequence of differential settling and transport of primarily organic detritus from cyanobacteria to permanent burial in the deepest parts of the lake while shallower nearshore cores continue to be retentive depositional sites for denser diatomaceous debris (Fig. 6).

The evidence for N enrichment in the 1920s and 1930s without evidence of an increase in the paleoproductivity indicators suggests that Victoria phytoplankton was co-dependent on both N and P and their availability in near balance to their growth requirements in the first half of the last century. Increasing N alone could not increase productivity because it would only shift community limitation to P. Species with high N : P ratios for growth (Hecky & Kilham, 1988) would tend to be favoured by the N enrichment and the shift in the TN : TP ratio in the sediments at Itome (Fig. 9b) and 103 would record that N enrichment. However, there is no evidence from the chironomid head capsule record (Verschuren *et al.*, 2002), nor a P response in the stratigraphic record that this N enrichment led to altered oxygen conditions or increased productivity (Figs 6 & 7) at that time. In contrast, the onset of increased P loading in the 1950s continuing on to modern days (Fig. 5) eventually resulted in significant changes in the ecosystem. Increasing P loading would initially shift the nutrient balance to favour phytoplankton species with lower N : P optimum ratios for growth, and eventually N-fixing cyanobacteria would be increasingly favoured. Because the N-fixing cyanobacteria could not be limited by N, the frequency and duration of high algal biomasses and cyanobacterial blooms began and continues until today.

Coastal Kenya waters contributing sediments to the 103 site responded to P enrichment by the 1960s with increased productivity. The paleoproductivity indicators also clearly show a consistent rise at V96-5MC throughout the available record up until the 1980s, and this core also records declining deep water oxygen concentrations post 1960 at 96-5MC (Verschuren *et al.*, 2002). In contrast to the period of N enrichment earlier in last century that increased P limitation in all phytoplankton with little effect on productivity, the response to P enrichment set off a positive feedback that was well underway by the mid-1970s. The positive feedback was initiated by increased P loading from the atmospheric (Tamata-mah, Duthie & Hecky, 2005) and land catchment (Hecky, Bootsma & Kingdon, 2003), which led to higher productivity and gave a selective advantage to N-fixing cyanobacteria. The higher productivity increased organic loading to the hypolimnion, leading to falling year over year oxygen concentrations. Spreading hypoxia and anoxia would then selectively liberate and regenerate P relative to N increasing the lake's N deficiency and increasingly favouring the persistence of the N-fixing cyanobacteria (Hecky *et al.*, 1996). In this P-rich lake, the upper limit to algal productivity is set by light limitation through self-shading when nutrients and grazing (see Lehman & Branstrator, 1993) are not limiting biomass accumulation, and the modern lake is now light limited over much of its area much of the year (Silsbe *et al.*, 2006). Highest phytoplankton biomasses are now dominated by cyanobacteria (Kling *et al.*, 2001) and occur in the shallowest coastal embayments with the shallowest mixing depths (Silsbe *et al.*, 2006; Tables 1 & 2).

Through the processes of accelerated P loading to Victoria and the compensatory increases in nitrogen fixation that increased TN concentrations, diatom productivity rose over the past century along with total phytoplankton productivity (Figs 6 & 7). However, Si loading from the land catchment has not increased in response to P loading and compensatory N fixation. Consequently, Si concentrations were drawn down over time as more biogenic Si was buried by diatom sedimentation (Fig. 6). The falling Si concentrations likely favoured smaller, more thinly silicified diatom species with a lower Si requirement than the formerly dominant *Aulacoseira* spp., a large, filamentous and heavily silicified species (Kilham, Kilham & Hecky, 1986). All three of these cores exhibit

a successional sequence from *Aulacoseira* spp. dominant in the 1950s and 1960s (Talling, 1966) through an increasing and then decreasing contribution of *Cyclotella* to an apparent climax community of *Nitzschia* in the modern lake (Hecky, 1993; Verschuren *et al.*, 2002). Although the proportional contribution of *Aulacoseira* to the diatom community begins falling as early as the 1950s (Hecky, 1993) as other diatoms become more productive, there is a very rapid absolute decline of *Aulacoseira* from all three cores around 1980 (H. J. Kling, personal communication). Falling dissolved Si annual mean concentrations would have been accompanied by even greater seasonal declines in dissolved Si concentrations, which may have driven the succession of the proportions of these three species contributing to the total community over time (Killham *et al.*, 1986). However, the rapidly deteriorating light environment around 1980 may have led to the abrupt demise of *Aulacoseira* at that time.

Fish yields and primary productivity

Commercial fishing became viable on Lake Victoria in the early 1900s after the arrival of the railway to Kisumu and eventually Kampala. The endemic tilapia, *Oreochromis esculentus*, was the primary focus of this emerging commercial fishery with lesser demands on other native fishes, e.g. species of *Bagrus*, *Clarias*, *Barbus* and others. Graham (1929) conducted the first scientific assessment of the fishery in response to concern about declining catches of tilapia. Thirty years after Graham, when systematic catch data began to be recorded (Fig. 1), the fishery had much the same species composition although catch per unit effort was even lower (Kudhongania *et al.*, 1992). Although the highly diverse haplochromines composed approximately 80% of the demersal ichthyomass in the lake, they were only a minor component of the commercial catch as the gears used for tilapia did not efficiently capture the predominantly small haplochromines. Graham (1929) contemplated, but did not recommend, the introduction of a piscivore to transform the abundant haplochromines to fish biomass more harvestable and valuable; but eventually an (initially) unauthorised introduction of *L. niloticus*, the Nile perch, was performed in 1954 (Pringle 2005) with some subsequent further official introductions (despite concern and controversy, e.g. Fryer, 1960) of Nile

perch and exotic tilapiines. By 1961, mature Nile perch were found in Ugandan waters, by 1968, mature Nile perch, in low abundances, were reported from all sectors of the lake by an extensive stock assessment survey (1968–70; Kudhongania *et al.*, 1992), and by 1975, Nile perch were considered fully established in Ugandan waters (Kudhongania *et al.*, 1992). The Nile perch population began to be seen as problematic in Kenya in the late 1970s. Within just a few more years (by the mid-1980s), its biomass had become dominant throughout the lake (Fig. 1; Kolding *et al.*, 2008). The dramatic upsurge in its biomass to dominate the fishery was credited with driving hundreds of species of haplochromines to extinction or near extinction (Witte *et al.*, 1992b) and raising international concern for the future of the fishery (Barel *et al.*, 1985).

The demise of the haplochromines is clearly temporally linked to the surge in the Nile perch population, but the causation is less clear. Although there is no doubt that the haplochromines have always been a preferred diet for the Nile perch (Kudhongania *et al.*, 1992), perch had been present throughout the lake at low and apparently stable populations for nearly 20 years. So, what changed in the late 1970s and early 1980s that caused the dramatic shift in community composition? The surge in Nile perch at that time has recently been attributed to a decline in haplochromine predation on Nile perch eggs, larvae and juveniles (Goudswaard *et al.*, 2008). Goudswaard *et al.* propose that haplochromine densities were reduced first in Kenya in the late 1970s by heavy fishing pressure from fine meshed nets and beach seining that drove down haplochromine densities leading to increased survival of Nile perch young. Then, this is hypothesised to have caused a rapid population increase of sub-adult Nile perch that migrated away from Kenya resulting in increased predation on the haplochromines all over this large lake and causing the transition to a new fishery in less than a decade (Fig. 1). The hypothesis of Goudswaard *et al.* suggests that there may be a role for eutrophication in the transition from haplochromines to Nile perch through its impact on water clarity and visibility:

“With respect to eutrophication, especially increased turbidity may have had a strong impact, as cichlids are highly dependent on vision for feeding and reproduction...Because the Nile perch upsurge in Lake Victoria and the increase of eutrophication both occurred in about the same period (Verschuren *et al.*,

2002), it is difficult to establish the relative impact of these phenomena separately."

The establishment of the chronostratigraphy of primary productivity both inshore and offshore allows new insight into the relative importance of these processes based on the premise that causation requires a time dependence in response, i.e. cause precedes effect.

The fish yield for the whole lake underwent a rapid increase above recent (post 1960) baseline catches beginning after 1980 (Fig. 1). Specifically in Uganda waters, experimental trawl catches from inshore waters (<40 m depth (Okaromon, 1994) deeper trawls returned few or no fish because of low oxygen) date the upsurge in Nile perch abundance to post 1982 (Kolding *et al.*, 2008). Experimental trawl catch per unit effort in 30-min trawls for haplochromines fell dramatically from approximately 200 kg in 1981 to approximately 5 kg by 1985 with the greatest rate of decline between 1983 and 1984 (Kolding *et al.*, 2008). The reconstructed record of inshore primary productivity in Uganda (Fig. 11a) exhibited an increase in the isotopic indicator of productivity, well above the long-term baseline productivity (Fig. 7) underway prior to 1980, in advance of the increase in whole lake fish yields (and the decline in Ugandan trawl catches in the early 1980s). In Tanzanian trawl surveys, the upsurge in Nile perch abundance was initiated in 1983 (Goudswaard *et al.*, 2008). There is a remarkable synchrony between the dramatic increases in sedimentary P recorded at the offshore coring site and whole lake catches (Fig. 11b). The fishery captures adult fishes, and so changes in abundance reflect changes in Nile perch larval and juvenile survival 2–3 years earlier. Similarly, the offshore coring site receives sediments from inshore areas with some, unknown, time delay as inshore generated particulate matter is focused to deeper offshore waters. The changes in inshore primary productivity and algal abundance preceded the transition to Nile perch dominance and loss of haplochromines as recorded in both experimental trawls and the catches in the fishery.

We agree with Goudswaard *et al.* (2008) and Seehausen, van Alphen & Witte (2003) that an increase in inshore turbidity would alter inshore predation dynamics favouring release of young Nile perch from haplochromine predation as well as increased advantage to Nile perch sub-adults and

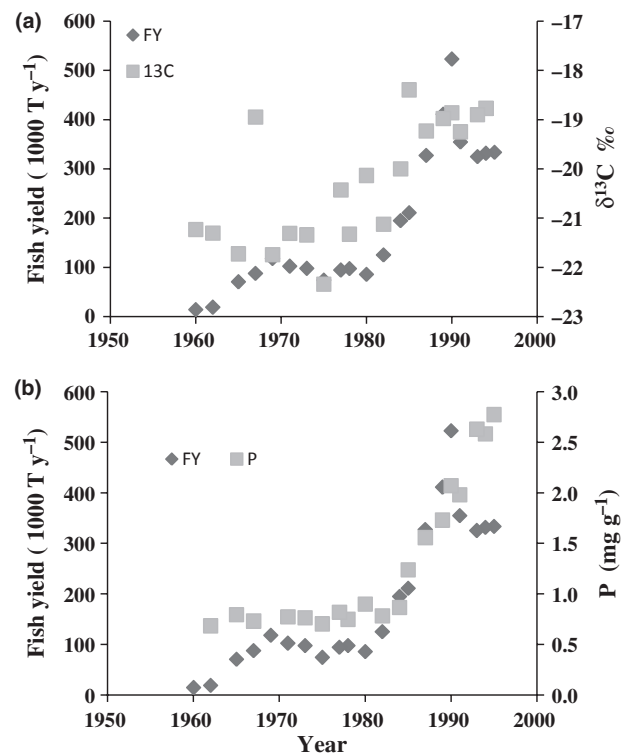


Fig. 11 (a) Temporal relationship between $\delta^{13}\text{C}$ signature of sedimentary organic matter (Suess corrected) at Itome site and recorded total fish catches on Lake Victoria. (b) Temporal relationship between TP content of dated sediments at V96-5MC and recorded total fish catches of Lake Victoria. TP, total phosphorus.

adults feeding on haplochromines under the low light and turbid conditions following the increase in algal growth and abundance inshore. The independent chronostratigraphies from the Itome and V96-5MC cores indicate that there was a major change in P availability, inshore algal abundance and therefore related visibility that preceded and could have facilitated the transition in the fish communities. The 103 core just off the Kenya coast and south of the Rusinga Channel connecting Winam Gulf to Lake Victoria (Fig. 2) indicates that such changes in primary productivity, as recorded by $\delta^{13}\text{C}$ and biogenic Si changes, occurred earlier in coastal Kenya waters (Figs 6 & 7). Goudswaard *et al.* (2008) conclude that the Nile perch upsurge was recorded in fish catches first in Kenya waters, but they attribute the Nile perch increase to fishing pressure depressing the haplochromine stocks and their predation on young Nile perch. The earlier shift in fish community composition in Kenyan waters compared to the other regions would

also be expected because algal productivity and associated declines in transparency also increased earlier in Kenyan waters.

Although precedence does not necessarily establish causation between changes in primary productivity and the consequent change in the fish community, it does establish that the change in the fish community cannot be responsible for the increase in algal abundance or productivity. An increase in primary productivity over time and especially in the late 1970s would also be expected to result in an increase in secondary productivity including the fishery (Melack, 1976). However, the increase eventually realised in fish yield was disproportionate to the approximate doubling of primary productivity since the early 1960s (Table 1), and thus the increase in fish yield also responds to the greatly increased fishing effort on the lake as the fishery became more profitable to exploit after the dominance of the Nile perch was established (Kolding *et al.*, 2008). There seems little reason to doubt that the fishery today is more productive because of the increased energy flow from eutrophication than it would have been without increasing P loading and dependent primary production. Moreover, the increasingly productive lake since the 1960s had been priming for a rapid restructuring of its food web into an alternative stable state (Scheffer *et al.*, 2001). However, it must be noted that the putative positive response to increased P loading will not continue as the lake's primary productivity is now light limited rather than nutrient limited. This is illustrated by the saturation response of the productivity indicators (Fig. 8) at V96-5. Although sedimentary P concentrations continue to rise at Itome and V96-5MC, fish yields in the Nile perch fishery did not continue to rise in the early 1990s.

Interacting multiple stressors and the rapid ecosystem transition

Lake Victoria endured a suite of stressors over the past century each of which individually may have left the ecosystem relatively unaltered. The completion of the railroad to the lake at Kisumu and Kampala in the early 1900s opened the lake ecosystem to increasing human pressures and a trajectory of development. The rail link to Nairobi and the coast opened the market for a commercial fishery, which led to overfishing of the prime target species of tilapia as well as

perhaps other native species. Falling catch per unit efforts were experienced over the next half century that eventually was used to justify the introduction of Nile perch and other tilapiine species in the 1950s and early 1960s. The railheads on Lake Victoria opened the lake region for export of natural resource products as well as the importation of fishing nets and other technologies to accelerate the pace of resource extraction. Colonial administration also introduced medical and veterinary practices that led to increased human survival and growing livestock herds which both increased pressures for land occupancy and increased agricultural productivity to feed the growing populations that exceeded 30 million people in the basin (at an average density of over 100 persons per square kilometre) by the 1990s from initial populations estimated at one to two million. Subsistence agriculture had been a continuously growing pressure on the land, but there were also episodes of extensive forest clearance for conversion to plantation arboriculture and agriculture for other high-valued crops.

These early anthropogenic stresses prior to 1950 left their traces in the lake sediments as changing microfossil communities (Hecky, 1993) and altered sedimentary nutrient ratios but apparently had little historically reported, noticeable effect on the lake. However, the phytoplankton community and lake productivity were already in transition prior to Talling's studies in the early 1960s, which in turn were just before an unusual (within the last century) 3-year period of intense rainfall from 1962–64 that saw lake levels rise to nearly 2 metres above the previous highs recorded in the 20th century. This caused extensive coastal flooding, but had little detectable impact on lake sediments or at least on the paleo-indicators evaluated in this study. From the 1960s up to the 1980s, the lake sediments were continuing to record the increasing phosphorus loading of the lake as well as the changing diatom community, increasing primary productivity and declining hypolimnetic oxygen concentrations. During this time, Nile perch and the introduced tilapiines became established throughout the lake, but with little effect on fish yield and concerns about overfishing continued. During the 1970s, there was a significant increase in offshore biogenic Si deposition and inshore primary productivity as recorded in $\delta^{13}\text{C}$ signatures which was likely amplified by increasing internal loading of P from the now extensive and persistent hypolimnetic anoxia.

The increase in algal biomass directly reduced light transmission and visibility (Silsbe *et al.*, 2006). The changing light environment altered the predation dynamics in the lake favouring the success of Nile perch over the haplochromines. By the late 1970s in Kenya, there was transition in the fish community that was later observed in the early 1980s in Ugandan and Tanzanian waters. Within the short space of 10 years from the mid-1970s to the mid-1980s, the entire fish community as well as the supporting food web (Witte *et al.*, 1992a) was altered and simplified while fish yields skyrocketed. The lake had made a rapid transition to a new state consisting of a new trophic structure and new nutrient and trophic pathways that is still maintained today.

The current ecosystem state would not have been realised without the imposition of multiple stresses. If overfishing had not occurred, there would have been no justification for the introduction of exotic species to boost fish yields. If human populations had not grown, there would not have been the demand for fish and the land pressures would not have developed accelerating nutrient losses from the catchment. Without the fish introductions, there would not have been a possible alternative food web structure. If there had been an introduction without eutrophication, there may not have been the decline in visibility that changed the balance of predation from haplochromine dominance to Nile perch dominance with the fateful consequences for the biodiversity of the lake. Even without the Nile perch introduction, the declining visibility would have led to a decline in biodiversity as colour-based sexual selection would have been weakened and hybridisation increased (Seehausen, van Alphen & Witte, 1997). But haplochromine biomass dominance over the other native fishes may have still been maintained or perhaps even strengthened if their abundance could have responded positively to increased primary productivity.

Scheffer *et al.* (2001) suggest that the potential for a state transition can exist prior to its realisation and that a perturbation, often a randomly occurring meteorological event or trend, which may have limited consequences to the original state, can become a trigger for a rapid transition as the original ecosystem loses resilience. In Lake Victoria, it has been suggested that not only was the lake of the 1990s warmer than in the 1960s, but also it was physically different with a shallower, more stable and more

persistent thermocline (Hecky, 1993). Lehman *et al.* (1998) suggested that this shallower mixing depth in itself could have led to higher offshore productivity. Climate warming is now recognised to be affecting all the large tropical lakes (Verburg *et al.*, 2003; Lorke *et al.*, 2004; Vollmer *et al.*, 2005) with a recent strong warming trend initiated about 1980 based on instrumental records. Hecky *et al.* (1994) suggested that the increased rate of oxygen depletion in Victoria could in part be attributed to the more stable and persistent stratification that retards ventilation of the deep water compared to 1960s. Kolding *et al.* (2008) identify a period of low wind strengths over Lake Victoria in the late 1970s to early 1980s that were concurrent with the change in the fish community. Such a period of low wind strengths, and its affect on mixing depth, stability of stratification (Hecky, 1993) and deep water ventilation (Hecky *et al.*, 1994), may have provided a physical trigger that precipitated the state transition by enabling the mobilisation of the internal store of P being built up over decades. Earlier periods of similarly low wind strength, e.g. in the early 1960s, were apparent in the climate reconstruction of Kolding *et al.*, but these earlier periods did not lead to a rapid state transition because increased P loading was not advanced. The potential for the rapid state transition created by the imposition of multiple concurrent stresses may not have yet been fully developed in Lake Victoria in the early 1960s, but by the late 1970s, the ecosystem was vulnerable to the state transition ultimately realised.

Lake Victoria is now in a new stable state, and it may be difficult to return to the original state (Scheffer *et al.*, 2001). It will certainly be difficult to reverse if there is no agreement on causation. This palaeolimnological study using independently dated cores and chronostratigraphies demonstrates that changes in the productivity of the lake, and its transition to the modern condition of P saturation and light limitation, preceded the change in the fish community. There are two important conclusions from this observation. First, it has been suggested that the change in the fish community, and especially the loss of phytoplanktivorous and detritivorous fishes, may have caused the change in the trophic state of the lake (Goldschmidt, Witte & Wanink, 1993). The timing of changes established from our cores rejects this possibility as a later event cannot be invoked as a cause of a preceding event. Consequently, a top-down causation

for the change in trophic state and algal abundance can be rejected. This conclusion precludes the possibility that management of the fishery through increased fishing mortality on Nile perch alone (Schindler, Kitchell & Ogutu-Ohwayo, 1998; Balirwa *et al.*, 2003) can lead to reversal of the changes in water quality or recovery of the multitude of species that formerly occupied the lake. The second critical conclusion is that eutrophication alone can lead to loss of haplochromine biodiversity. Therefore, conservation efforts in the remaining bastions of haplochromine diversity, Lake Tanganyika and Lake Malawi, must focus on controlling the future eutrophication of those lakes as well as the prevention of species introductions. Preventing the introduction of exotic species alone will not guarantee the integrity of the endemic species flocks in those lakes. Similarly, there cannot be a broad recovery of the haplochromine stocks in Lake Victoria to their former abundance and even with reduced diversity without a return to more transparent waters. This will require reducing the phosphorus loading to Lake Victoria.

The future: restoration or hypereutrophication?

Recovery of the lake through reducing the phosphorus loading will require a major effort by the riparian states and likely international financing. But a more urgent matter may be preventing further degradation of the lake by currently unchecked phosphorus loading, perhaps to a third ecosystem state of hypereutrophication (Kolding *et al.*, 2008). The water hyacinth outbreak and its imposition of high organic loading and deoxygenation of shallow inshore waters in the mid-1990s may have been a preview of that possible future state. At that time, water hyacinth caused massive economic disruption and hardship as it prevented shoreline access for watercraft of all sizes, favoured the spread of water-vectoring diseases, such as schistosomiasis, and restricted access to water for domestic uses including hydroelectricity production (Twongo, 1996). If current hypoxic conditions continue to spread laterally from the hypolimnion and into shallow water under floating macrophytes, the presently lucrative Nile perch and tilapia fisheries may eventually become limited through excessive mortalities and reduced growth as a result of hypoxia (Kolding, Haug & Stefansson, 2008). Although water hyacinth is currently reduced

from its high abundances in the 1990s (Williams *et al.*, 2005), the conditions that favoured its successful establishment and extensive stands still exist, and other floating macrophytes will also be favoured by continued unabated loading of nutrients into Lake Victoria. Whereas it can be argued that the first ecosystem transition brought economic benefit from the resulting productive Nile perch fishery, the hypereutrophic state that may result from unchecked P loading would have substantial negative economic consequences for the riparian states and especially their lakeside populations.

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Conflicts of interest

The authors have declared no conflicts of interest.

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