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Research Paper

The Environment of Lake Victoria (East Africa): Current Status and Historical Changes

key words: temperature, oxygen, chlorophyll, transparency, conductivity, eutrophication

Abstract

Beginning in the mid-1980s Lake Victoria experienced severe eutrophication and it was suggested that deteriorating water quality might lead to a collapse of its fisheries. A series of lake-wide surveys carried out 1999–2001 and 2005–2009 revealed that the temperature of the lake had risen by >1 °C since 1927, with more rapid warming of the deeper waters reducing the thermal gradient in the water column and thus weakening stratification and the extent and severity of deoxygenation. The chlorophyll *a* concentrations in open water decreased since the 1980s, while Secchi disc visibility increased, indicating a reduced severity of algal blooms. Chlorophyll *a* was higher and Secchi disc visibility lower in inshore waters but there has been no deterioration in these areas since the 1980s. The conductivity remained unchanged, although it was about 50% greater in the semi-enclosed Nyanza Gulf than in the open lake. The water quality of the lake has therefore improved considerably despite the fact than concentrations of plant nutrients have not decreased and the reasons why this may be the case are discussed.

1. Introduction

Lake Victoria is the world's second largest freshwater lake (area = 68,800 km², mean depth = 35 m) and it supports one of the world's largest inland fisheries, yielding almost one million tons per annum (LVFO, 2009a). It has attracted much interest in recent years because of the extraordinary ecological changes that occurred in it over the last three decades, comparable in their magnitude to those in newly created man-made lakes. These changes were triggered in the mid-1980s by an introduced predatory fish, the Nile perch *Lates niloticus* (L.), and its subsequent destruction of the endemic haplochromine cichlids. These fishes, which formed a species flock with some 500 described forms (Witte *et al*., 2007), accounted for over 80% of the fish biomass in the lake (Kudhongania and Cordone, 1974) but they were small fish thought to be of little commercial value. Nile perch were therefore introduced with the specific intention of converting haplochromines into a more

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valuable fish product (ANDERSON, 1961), which they did so effectively that it was feared that most haplochromines were facing extinction (WITTE *et al*., 1992). As a result, food chains in the lake were greatly simplified with only three fish species dominating the biomass; Nile perch and Nile tilapia *Oreochromis niloticus* (L.) which were both introduced, and the native cyprinid *Rastrineobola argentea* (PELLEGRIN) (LIGTVOET and WITTE, 1991).

In addition, the lake became eutrophic following the extremely rapid growth of the predominantly rural human population, which is still increasing at more than double the global average (PRB, 2009). Land-based activities in the drainage basin, primarily deforestation and increasingly intensive agriculture, but with some contribution from urban runoff have increased nutrient loading to the lake and led to its progressive enrichment (SCHEREN *et al*., 2000). There is considerable evidence to show that eutrophication began as early as the 1950s in Kenyan waters, but rather later in Uganda and Tanzania, with the phytoplankton changing from a diatom flora to one dominated by cyanobacteria. Fossil assemblages of chironomids also provide evidence that deep water anoxia became more prevalent around that time (LEHMAN, 1998; VERSCHUREN *et al*., 2002; STAGER *et al*., 2009). The relationship between Nile perch and eutrophication is controversial, but the almost complete destruction of the endemic fishes, especially the phyto- and zooplanktivorous haplochromines, must have had significant ecological impacts and probably accelerated the process of eutrophication through cascading effects caused by the loss of phytoplanktivorous species (GOLDSCHMIDT *et al*., 1993).

The effects of eutrophication included a change in the composition of the phytoplankton with a shift from diatoms to cyanobacteria (GOPHEN *et al*., 1995) along with an increase in algal biomass, which resulted in fish kills and more severe deoxygenation of deeper waters (OCHUMBA and KIBAARA, 1989; OCHUMBA, 1990; MUGIDDE, 1993; HECKY, 1993; HECKY *et al*., 1994; BUGENYI and MAKUMBA, 1996). The transparency of the water also declined, partly because of the algal blooms and partly because of silt carried in by the rivers, and this has been implicated in the decline of the haplochromines by disrupting their mating behaviour, which relies heavily on visual cues (SEEHAUSEN *et al*., 1997). A further consequence of eutrophication was an explosion of the water hyacinth *Eichhornia crassipes* (MART.) SOLMS. This plant was first reported from Lake Victoria in 1989 and it began to increase in the early 1990s until it infested some 200 km^2 by 1998. Its spread was almost certainly a consequence of nutrient enrichment but the infestation was brought under control by weevils introduced for that purpose and the plant is now no more than a local nuisance (WILSON *et al*., 2007).

These environmental changes were reflected by changes in the fishery which, prior to 1980, amounted to about 100,000 t per annum and consisted primarily of haplochromines, tilapias and other native species. Catches increased dramatically from 1980 onwards to reach about 500,000 t by 1989 with Nile perch making up 70% of the total (REYNOLDS *et al*., 1995). By 2007 the total catch had risen to around 1,000,000 t with the Nile perch catch being around 240,000 t (25% of the total) with *Rastrineobola*, *Oreochromis* and haplochromines making up the balance. The decreased proportion of Nile perch in the catch led to concerns that the stock was becoming overfished (MATSUISHE *et al*., 2006; NJIRU *et al*., 2007; MKUMBO *et al*., 2007) and the biomass of Nile perch in the lake has indeed declined significantly over the last decade (LVFO, 2008). SIMONIT and PERRINGS (2005) asserted that landings of *all* [our italics] fish had declined since 1994 and, while recognising the contribution of overfishing, suggested that eutrophication was an important factor. This was taken further by KOLDING *et al*. (2008) who claimed that the Nile perch stock has not been affected by fishing but that environmental conditions in the lake may now limit its productivity. The increased intensity of deoxygenation during the stratified period, when >50% of the water column was said to become anoxic, was seen as a particular threat since Nile perch is sensitive to low oxygen concentrations (FISH, 1956; SCHOFIELD and CHAPMAN, 2000).

Because of these concerns, an assessment of the current condition of the lake is needed and is presented in this paper. Determining the physico-chemical changes that have taken

place and the environmental health of the lake have been hampered by the fact that most data have not been collected systematically or on a lake-wide basis. There has been a tendency to make assumptions about the lake on the basis of data from restricted localities, which has given rise to some misleading views of its condition. This paper presents data from two lake-wide investigations made during the course of acoustic fisheries surveys carried out as part of (1) the Lake Victoria Fisheries Research Project (LVFRP), 1999–2001, and (2) the Implementation of a Fisheries Management Plan (IFMP) project, 2005–2009. These results are placed in a historical context by comparison with data taken from the literature and other sources to assess both the present condition of the lake and the changes that have taken place over the last 50–80 years.

2. Methods

Data were collected from around 53 stations located across the lake (Fig. 1) during acoustic surveys carried out in February–March (when the lake was stratified) and August–September (when it was isothermal) each year in 2000–2001 and from 2005–2009. Not all stations were sampled on each occasion and the number depended on the track followed by the acoustic survey and other factors such as weather conditions. On average, 50 stations were sampled each time with 20 being 'inshore' stations ranging from 5–20 m depth and 30 being 'offshore' stations ranging from 21–70 m depth. A submersible Conductivity-Temperature-Depth profiling system (CTD, Sea-bird Electronics®, Sea Cat SBE 19) was used to determine depth, temperature, conductivity and the concentrations of dissolved oxygen and chlorophyll a. Measurement of these variables began at approximately 0.4 m depth and finished just 0.4 m above the lake bed. Before each survey, the CTD was checked for accuracy in the laboratory, and twice during the survey at the start and end of the cruise using the Winkler titration method for determining dissolved oxygen concentrations. Secchi depth was measured with a standard 20 cm diameter Secchi disc, with quadrants painted in black and white. The Secchi depth was calculated as the average of the depth at disappearance and that of reappearance of the disc in water. Systematic random sampling design was used in selecting the sites to be investigated throughout the entire lake and marked using a GARMIN Global Positioning System (GPS). Historical data were collected from the literature or unpublished sources.
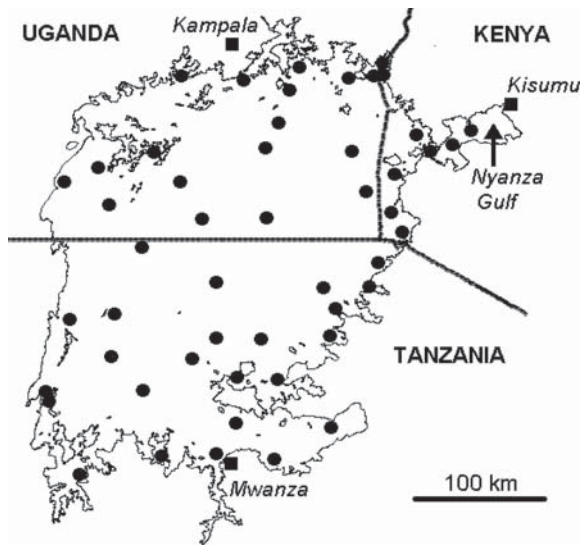

Figure 1.   Lake Victoria, East Africa, showing the location of the sampling stations (●) from which physico-chemical data were collected during lake-wide surveys in 2000–01 and 2005–08.

3. Results

3.1. Temperature

Temperature was first measured in Lake Victoria at 55 stations across the lake during a six-month survey which began in August 1927 and probably ended around February or March, although this is not specifically stated (GRAHAM, 1929). This made it possible to determine the long-term changes in temperature that have taken place. On average, the surface waters have warmed by almost 1.2 °C in 82 years while the temperature rose by 1.57 °C in water >50 m deep over the same time period (Table 1). The rate of increase was not uniform, however, being considerably faster between 2000 and 2008 (0.079 °C yr^{-1} at the surface and 0.094 °C yr^{-1} at >50 m) compared to 1927–2000 (0.005 °C yr^{-1} at the surface and 0.008 °C yr^{-1} at >50 m). From an analysis of GRAHAM'S data TALLING (1966) noted the presence of a lens-shaped mass of cool water (in September) with temperatures ranging from 22.85–23.10 °C at the bottom of the lake in water >60 m deep. There was no trace of this body of cool water during the later surveys; the water temperatures in August–September at depths >50 m ranged from 23.9–24.2 °C during the 2000–2001 surveys and 24.3–25.1 °C during the 2005–2009 surveys.

Table 1.   Mean temperature (°C) in Lake Victoria at the surface and at depths >50 m based on lake-wide surveys. Data from GRAHAM (1929) and LVFRP and IFMP surveys. *n* = number of stations sampled.

Year	Surface		>50 m deep	
	n	Mean ± *SD*	*n*	Mean ± *SD*
1927	55	24.69 ± 0.71	27	23.32 ± 0.29
2000	98	25.05 ± 0.71	35	23.91 ± 0.15
2009	108	25.88 ± 0.86	30	24.89 ± 0.23

Table 2.   The mean dissolved oxygen concentrations (mg l^{-1} ± standard deviation) at 0–5 m depth. 20–40 m depth and at depths >40 m in Lake Victoria. Data for stations >40 m deep only; 2000–01 are from LVFRP, data for 2005–08 are from IFMP.

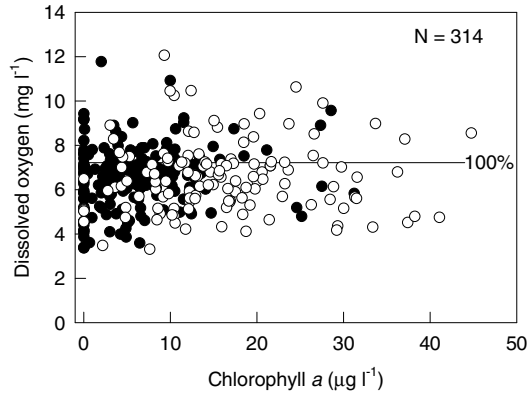|	February–March			August–September		
	0–5 m	>40 m	*n*	0–5 m	>40 m	*n*
2000	7.1 ± 0.6	1.8 ± 1.9	21	8.1 ± 1.6	6.3 ± 0.6	17
2001	8.1 ± 0.7	3.3 ± 1.8	15	7.8 ± 0.6	5.2 ± 0.9	14
Mean	7.80	2.55		7.85	5.75	
2006	6.4 ± 1.3	6.9 ± 3.8	8	6.6 ± 0.9	1.7 ± 2.0	18
2007	7.0 ± 0.7	4.1 ± 1.2	9	7.3 ± 0.5	7.0 ± 0.7	8
2008	7.6 ± 0.5	7.0 ± 1.1	10	7.1 ± 0.3	6.8 ± 1.0	16
2009	8.0 ± 0.7	6.5 ± 1.2	18	8.1 ± 1.0	7.7 ± 1.2	10
Mean	7.25	6.13		7.27	5.80	

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Figure 2. Dissolved oxygen concentrations in relation to chlorophyll *a* in the 0–5 m depth zone in Lake Victoria, 2005–08. ● = offshore stations (depth >20 m) and ○ = inshore stations (depth <20 m); the horizontal line labelled "100%" indicates 100% saturation.

3.2. Dissolved Oxygen

The relatively more rapid rise in the temperature of the deeper waters has weakened thermal gradients in the water column and reduced the intensity of stratification, which in turn has decreased the extent of anoxia in deeper waters. As a result, the differences between oxygen concentrations in the surface layer (0–5 m depth) and in deep water (>40 m) during the stratified period have diminished since 2001 (Table 2). The mean concentration of dissolved oxygen in February–March 2000–01 was 3.2 times higher in the 0–5 m zone than at depths >40 m but this had fallen to only 1.2 times higher in 2005–08. The differences between the surface and deep layers were less pronounced during the isothermal period (August–September) with oxygen concentration in the surface layer being 1.4 and 1.3 times higher in 2000–01 and 2005–08, respectively.

Most significantly, the average concentration of dissolved oxygen in the deep waters of the lake rose dramatically during the stratified period, from 2.55 mg l^{-1} in 2000–01 to 6.15 mg l^{-1} in 2005–09, thus marking a major reduction in deoxygenation at this time. Oxygen concentrations in the surface layer during the isothermal period were generally rather lower in 2005–08 which may reflect a decrease in algal populations in open water. There was little difference in the deeper waters, apart from a very low concentration noted in August–September 2006; the reasons for this low value were unclear as the water had a high oxygen concentration down to 40 m. Saturated or supersaturated concentrations of oxygen were recorded at only 78 out of 314 stations, or 25% of the total (Fig. 2).

3.3. Chlorophyll a

The concentrations of chlorophyll *a* in the surface layer (0–5 m) of the lake were similar in 2005–09 (mean = 10.6 µg l^{-1}) and 2000–01 (mean = 9.7 µg l^{-1}) but there were some spatial variations (Table 3). During both periods the concentration of chlorophyll *a* was higher in inshore waters (mean = 11.9 and 15.3 µg l^{-1} in 2000–01 and 2005–08, respectively) than in offshore waters (mean = 7.5 and 5.8 µg l^{-1}). There was little seasonal variation, either in offshore or inshore waters, and the mean chlorophyll *a* values were similar in both the stratified (February–March) and isothermal (August–September) periods (Table 3). The mean

Table 3. The mean concentrations of chlorophyll *a* (μg l^{-1} ± standard deviation) in the inshore (<20 m deep) and offshore (>20 m deep) waters of Lake Victoria. Values are for the upper layers of the lake (0–5 m deep). Data for 2000–01 are from LVFRP, data for 2005–08 are from IFMP.

| | February–March | | August–September | |
	Inshore	Offshore	Inshore	Offshore
2000	13.2 ± 4.4	4.9 ± 2.6	12.8 ± 11.3	8.8 ± 8.9
2001	10.8 ± 6.7	10.3 ± 15.8	10.9 ± 7.0	5.8 ± 3.2
Mean	12.00	7.60	11.85	7.30
2006	14.8 ± 10.9	2.1 ± 3.0	16.2 ± 8.0	4.9 ± 3.5
2007	15.7 ± 8.5	6.5 ± 8.0	14.4 ± 8.4	4.6 ± 4.7
2008	16.8 ± 8.6	9.3 ± 7.1	14.5 ± 11.2	7.4 ± 4.0
2009	12.7 ± 12.5	5.9 ± 7.1	14.8 ± 6.1	7.4 ± 4.3
Mean	15.00	5.95	14.98	6.08

concentrations at inshore stations was about two to three times higher. This is in contrast to the situation in the 1960s when TALLING (1966) found that chlorophyll *a* in the entire water column was twice as high in January–February as it was in May–June.

Chlorophyll *a* concentrations have changed considerably since the 1960s and an increase in chlorophyll concentrations was one of the principal indicators of eutrophication (Fig. 3). Early data indicated that chlorophyll concentrations were low (3.0–4.6 μg l^{-1}) in both inshore and offshore waters but the concentrations rose rapidly from 1980 onwards to reach average values of 40 μg l^{-1} and 60 μg l^{-1} in offshore and inshore waters, respectively, while maximum concentrations reached 650 μg l^{-1}. Since then, chlorophyll concentrations have fallen with offshore concentrations being only slightly higher than those recorded in the 1960s. The concentrations in inshore waters were still relatively high and some high values were record-
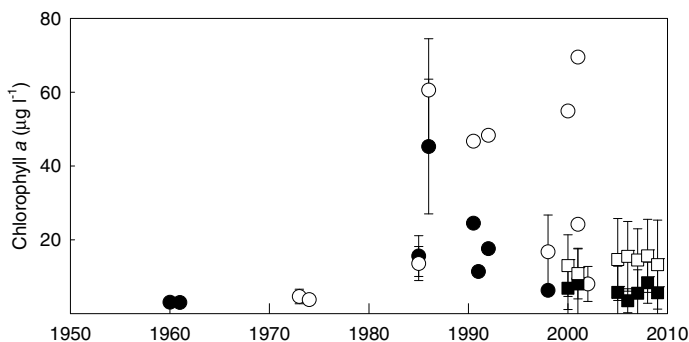

Figure 3. Historical changes in chlorophyll *a* in Lake Victoria, 1960–2008. Where possible, data are shown as means ± standard deviation; ■ = offshore waters (lake-wide), ● = offshore waters (single localities), □ = inshore waters (lake-wide), ○ = inshore waters (single localities). Data from TALLING (1966), AKIYAMA *et al*. (1977), OCHUMBA and KIBAARA (1989), MUGIDDE (1993), LEHMAN and BRANSTRATOR (1993, 1994), KENYANYA (1999), MBONDE *et al*. (2004) and SILSBE *et al*. (2006), as well as LVFRP and IFMP surveys.

ed in localised areas; an example is the values of 55 and 70 µg l^{-1} reported by SILSBE et al. (2006) from bays in northern Uganda that tend to have high concentrations of chlorophyll.

3.4. Transparency

The earliest Secchi disc readings on Lake Victoria were made in 1927 (GRAHAM, 1929) when transparency in the offshore waters was high (mean = 7.5 m) but relatively low in inshore waters (mean = 2.2 m). A marked decline in transparency in the mid-1980s was recognised as a significant consequence of eutrophication and transparency has been measured more regularly since then. Secchi disc visibility was significantly higher in offshore than in inshore waters in both the 2000–01 (t-test, $P < 0.05$) and 2005–09 (t-test, $P < 0.001$) surveys (Table 4) but there were some differences between the two periods. In 2000–01 inshore readings were higher, in both February–March and August–September, than they were in 2005–09 but the opposite applied to offshore readings, which were higher in the later samples. There was a slight seasonal variation in transparency with Secchi disc readings being rather higher in August–September than in February–March but in neither case were these differences significant (t-test, $P > 0.05$). As with conductivity, this is probably because the latter period is in the main rainy season (BALIRWA et al., 2004) and the inflowing rivers would be carrying more silt into the lake.

Water transparency has changed considerably since 1927 (Fig. 4) although the gap in the record up to 1972 means that it is not possible to determine when these changes took place. Secchi disc transparency decreased dramatically in both inshore and offshore waters in the 1980s, falling to one and two metres respectively in 1986. This coincided with the most severe algal blooms and the highest concentrations of chlorophyll a and was considered to be one of the main indicators of eutrophication. Transparency remained low until about 1995 since when there appears to have been a steady improvement in offshore waters with mean Secchi disc visibility reaching about 3.5–4.0 m. This coincides with a decline in chlorophyll a concentration in offshore waters (Fig. 3) and indicates some improvement in water quality. Secchi disc visibility in the inshore waters, in contrast, have not changed much and remain at about 1.5–2.0 m which is close to some of the values obtained in 1927.

Table 4. The mean Secchi disc visibility (metres ± standard deviation) in the inshore (<20 m deep) and offshore (>20 m deep) waters of Lake Victoria. Values are for the upper layers of the lake (0–5 m deep). Data for 2000–01 are from LVFRP, data for 2005–08 are from IFMP.

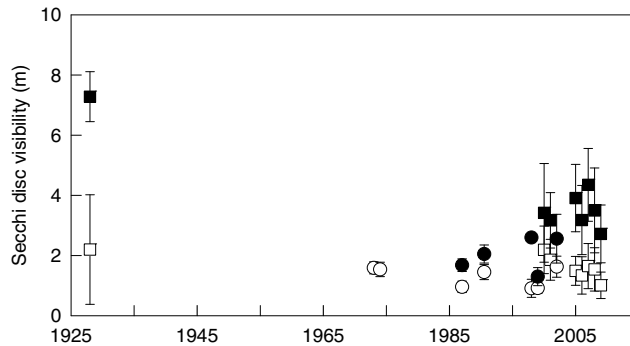|	February–March		August–September	
	Inshore	Offshore	Inshore	Offshore
2000	1.6 ± 0.7	2.7 ± 0.8	2.5 ± 0.6	4.2 ± 2.0
2001	2.2 ± 0.7	3.2 ± 0.8	1.5 ± 0.5	3.2 ± 1.1
Mean	1.90	2.95	2.00	3.70
2006	1.3 ± 0.4	3.1 ± 1.1	1.5 ± 0.9	3.3 ± 1.2
2007			1.7 ± 0.8	4.4 ± 1.2
2008	1.7 ± 0.7	3.3 ± 1.1	1.4 ± 0.8	3.7 ± 1.6
2009	1.0 ± 0.4	2.8 ± 0.9	1.2 ± 0.4	3.5 ± 1.4
Mean	1.33	3.07	1.45	3.73

Figure 4. Historical changes in Secchi disc visibility in Lake Victoria, 1927–2008. Wherever possible, data are shown as means ± standard deviation; ■ = offshore waters (lake-wide), ● = offshore waters (single localities), □ = inshore waters (lake-wide), ○ = inshore waters (single localities). Data from GRAHAM (1929), AKIYAMA *et al*. (1977); DE BEER (1989), GOPHEN *et al*. (1993), and SEKADENDE *et al*. (2005), as well as LVFRP and IFMP surveys.

The standard deviation of the mean in 1927 (± 1.8 m) was much greater than those obtained since 2000 (± 0.4–0.8 m), which suggests a much greater degree of variability in the early samples; this reflects both the higher concentrations of chlorophyll *a* in inshore waters and the increased quantities of silt being carried into the lake at the present time.

The link between chlorophyll *a* and transparency was evident in Figures 3 and 4 and there was a significant correlation between the two variables (Fig. 5). Transparency at the inshore stations rarely exceeded 2.5 m, even at low concentrations of chlorophyll *a* which probably reflects higher turbidity resulting from silt. The correlation between the two variables was therefore lower than at the offshore stations which were likely to have lower silt concentrations.
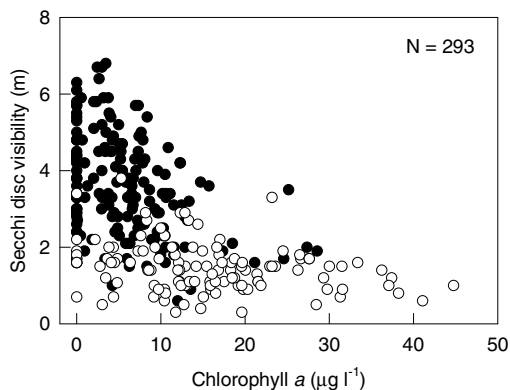

Figure 5. The relationship between chlorophyll *a* in the 0–5 m zone and Secchi disc visibility in offshore (●) and inshore (○) waters of Lake Victoria, 2005–08. Significant correlations were obtained for both inshore ($r = 0.389$, $P < 0.001$, $n = 173$) and offshore stations ($r = 0.275$, $P < 0.01$, $n = 120$).

Table 5.   The mean conductivity ($\mu S\ cm^{-1} \pm$ standard deviation) at 0–5 m depth and at depths >40 m in Lake Victoria. Data for 2000–01 are from LVFRP, data for 2005–08 are from IFMP.

	February–March		August–September	
	0–5 m	>40 m	0–5 m	>40 m
2000	98.4 ± 11.7	94.8 ± 3.8	99.8 ± 16.4	92.9 ± 0.6
2001	97.2 ± 9.3	94.7 ± 4.7	92.9 ± 10.3	93.2 ± 1.4
Mean	97.8	94.8	96.4	93.1
2006	107 ± 13	101 ± 1	104 ± 12	99 ± 1
2007	110 ± 11	99 ± 1	101 ± 9	99 ± 1
2008	101 ± 3	99 ± 1	103 ± 12	98 ± 1
2009	106 ± 13	100 ± 1	103 ± 11	99 ± 1
Mean	106.0	99.9	102.8	98.8

3.5. Conductivity

The conductivity of the water in Lake Victoria is relatively low and the lake falls into Category I, defined by TALLING and TALLING (1966) as lakes with a conductivity of less than 600 $\mu S\ cm^{-1}$ and which includes most African lakes. During the period 2000–01 the mean conductivity was 95.5 $\mu S\ cm^{-1}$ and it was slightly higher (101.8 $\mu S\ cm^{-1}$) during 2005–08. There was a slight seasonal variation with conductivity being rather higher in February–March than in August–September (Table 5). Neither of these were significant differences (t-test, $P > 0.05$). This may be accounted for by the fact that the former is in the main rainy season when rivers would be flowing most strongly and carrying dissolved ions into the lake (BALIRWA et al., 2004).

Conductivity did not vary much in relation to water depth except at some very shallow (<2 m) inshore stations where it rose to around 120 $\mu S\ cm^{-1}$ (Fig. 6). These were either in
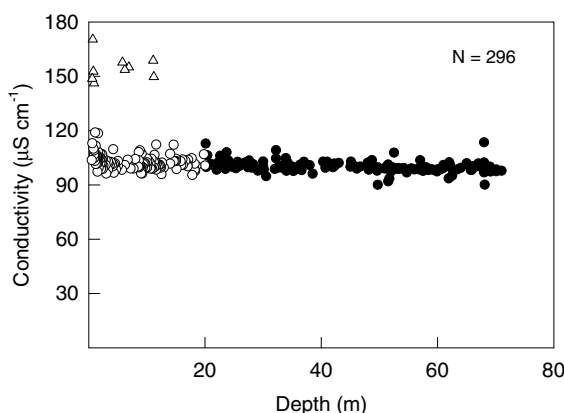

Figure 6.   Conductivity in the 0–5 m zone in relation to depth, 2005–08. ● = offshore stations, ○ = inshore stations, △ = Nyanza Gulf stations.
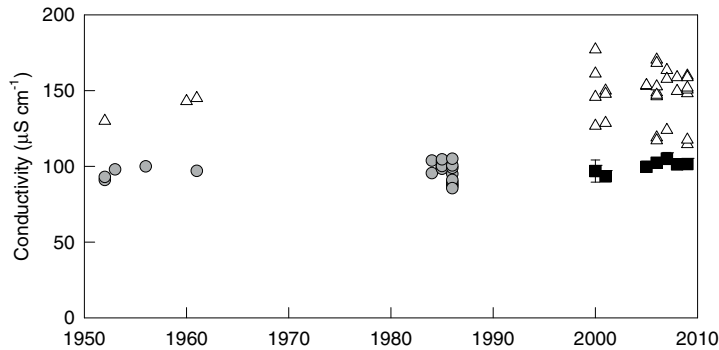
Figure 7. Historical changes in the conductivity of Lake Victoria, 1952–2008. ■ = mean values from lake-wide surveys (standard deviations mostly too small to be visible), ○ = records from single or restricted localities, △ = Nyanza Gulf stations. Data from FISH (1952, 1953), BEAUCHAMP (1956), TALLING and TALLING (1966), OCHUMBA and KIBAARA (1989), as well as LVFRP and IFMP surveys.

river mouths where they were influenced by the inflowing rivers or in very shallow areas where evaporation rates may have been more influential than in open water. Stations in the Nyanza Gulf (Fig. 1) were an exception to the general pattern with conductivity values ranging from 148–175 $\mu S\ cm^{-1}$ and therefore around 50–75% higher than in the open lake.

The conductivity of the lake's water has not changed appreciably over the last 50 years, remaining at around $100\ \mu S\ cm^{-1}$ throughout the period in most of the lake and around $150\ \mu S\ cm^{-1}$ in the Nyanza Gulf (Fig. 7). It might have been expected to increase as a result of eutrophication but conductivity is a conservative variable determined largely by the concentrations of dissolved cations and an increased supply of these ions from the land has probably been matched by increased losses through the outflow since the discharge of the Nile is approximately equal to that of the inflowing rivers (TATE *et al*., 2004).

4. Discussion

The eutrophication of Lake Victoria represents a major ecological change and numerous investigators have described the events that occurred and explained the reasons for them (*e.g.* KAUFMAN, 1992; HECKY, 1993; MUGIDDE, 2001; LUNG'AIYA *et al*., 2001; VERSCHUREN *et al*., 2002). The general conclusion from these investigations is that eutrophication is a major problem which could detrimentally affect ecosystem functioning and fish productivity. The most extreme expression of this view came from KOLDING *et al*. (2008) who argued that nutrient concentrations in the lake will continue to rise, stimulating the growth of increasingly dense algal blooms that would decrease primary productivity by limiting light penetration. This, in turn, would cause a loss of fish production through something they termed the "productivity-nutrient continuum" and the process would be reinforced by increasingly severe, extensive and possibly permanent deoxygenation of the deeper waters. Data from the lake-wide surveys presented here discount this view and it is likely that KOLDING *et al*. were influenced by the situation in the Nyanza Gulf where light-limitation has been reported (GIKUMA-NJURU and HECKY, 2005) and fish catches have indeed declined dramatically − but through overfishing; the gulf is the most intensively fished part of the lake with >10 fishermen km^{-2} compared to about 2 km^{-2} in the rest of the lake (LVFO, 2008).

There is now clear evidence that the condition of Lake Victoria has improved considerably since its nadir in the 1980s. Thermal gradients within the water column have decreased, thus weakening stratification and reducing deoxygenation. This may be a consequence of the rapid warming of the deeper waters that occurred over the last decade, assisted by a general increase in wind speeds over the lake that would contribute to increased circulation (STAGER et al., 2009). There is little evidence of permanent deoxygenation at present and in this respect the lake now seems to be close to its condition in the 1960s, before the Nile perch population explosion. At that time TALLING (1966) found that the concentration of oxygen in the surface layers of the lake was generally below saturation (7.2 mg l^{-1} at Lake Victoria's altitude of 1135 m and mean temperature of 25 °C). In the 1990s the upper 20 m of the water column was likely to be saturated or supersaturated with oxygen (HECKY, 1993; HECKY et al., 1994; WANINK and KASHINDYE, 1998) as a result of photosynthetic activity by dense algal blooms but the incidence of supersaturation seems to have declined since then (Fig. 2).

The algal blooms that developed in the mid-1980s were reflected by a ten-fold increase in the concentrations of chlorophyll a in both open and inshore waters but these concentrations have decreased since 1990 (Fig. 3). KOLDING et al. (2008) asserted that chlorophyll a values of 15–35 µg l^{-1} made Lake Victoria one of the most eutrophic water bodies in the world but this claim seems exaggerated. The chlorophyll a values from Lake Victoria lie well within the range of values given by HUSZAR et al. (2006) who obtained a mean value of 34.2 µg l^{-1} from 192 tropical lakes (median = 11.0, range = 0.9–556.0 µg l^{-1}). The mean concentration of chlorophyll a in offshore waters is now close to the values recorded in the 1960s (TALLING, 1966) while the concentrations in inshore waters, although higher, have decreased considerably over the last decade. Although there were significant correlations between chlorophyll a and Secchi disc transparency it is not clear to what extent photosynthesis is light-limited. GIKUMA-NJURU and HECKY (2005) reported a strong correlation between the two variables and inferred that light-limitation was occurring, but without giving any data on primary productivity. SILSBE et al. (2006) showed that primary production was reduced when chlorophyll a concentrations exceeded 40–50 µg l^{-1}. This suggests that light-limitation is likely to be infrequent in both inshore and offshore waters where chlorophyll a concentrations rarely exceeded 30 and 50 µg l^{-1}, respectively (Fig. 5).

The decline in chlorophyll a in offshore waters has been matched by an increase in transparency (Fig. 4) although current Secchi disc visibility is still well below that recorded in 1927 (GRAHAM, 1929). The role of silt in determining water transparency still needs further investigation as silt loads in the lake are likely to have increased as a result of more intensive subsistence farming and deforestation in the lake basin. Although transparency decreased in the inshore waters, which are most likely to be affected by silt, the values lie within the lower range of those determined in 1927 (Fig. 4). Decreased transparency in inshore waters was proposed as a factor contributing to the decline of haplochromine species (SEEHAUSEN et al., 1997), and it could be argued that improved transparency may be contributing to the recovery that has taken place in recent years. The contribution of low transparency to the decline of the haplochromines has not been quantified and it may have been relatively small in relation to Nile perch predation and the decreased population of this predator may now be driving the recovery of some haplochromine species.

The most striking feature of conductivity is the high values recorded in the Nyanza Gulf (Fig. 6), which has been attributed to an increased supply of nutrients from fertilizers used on sugar estates in the catchment and urban effluents from the town of Kisumu (LUNG'AYIA et al., 2001; GIKUMA-NJURU and HECKY, 2005). Conductivity has not, however, increased substantially since the 1950s and 60s (Fig. 7) while the concentrations of nitrogen and phosphorus in the gulf tend to be lower than in the open lake (Table 6) so this may not explain its high conductivity. Its physical and hydrological conditions may be more important determinants as it is a shallow (mean depth = 10 m) arm of the lake about 70 km

Table 6.   Concentrations of nitrate-nitrogen and soluble reactive phosphorus ($\mu g\ l^{-1}$) in Lake Victoria (Nyanza Gulf and open lake), 1960–2009. Data from (1) Talling and Talling (1966), (2) Ochumba and Kibaara (1989), (3) Gophen et al. (2001), (4) Lung'ayia et al. (2001), (5) Gikuma-Njuru and Hecky (2005) and (6) L. Sitoki and C. Ezekiel (unpublished).

Period	NO$_3$–N		PO$_4$–P		Source
	Nyanza Gulf	Open lake	Nyanza Gulf	Open lake	
1960–61	15–29	0–10	4	9–50	1
1985–86		0.2 ± 0.2		11.3 ± 8.2	2
1989	24.8 ± 21.8	2.3 ± 2.0	43.5 ± 82.0	33.9 ± 18.9	3
1998	66.6 ± 44.0		59.7 ± 38.5		4
2000–02	48.2 ± 21.4		29.7 ± 19.1		5
2004	81.2 ± 12.3	81.3 ± 7.2	24.9 ± 8.3	41.3 ± 1.8	6
2008	98.7 ± 36.4	132.0 ± 7.0	57.0 ± 7.4	69.8 ± 3.8	6

long and 15–30 km wide connected to the main lake by the narrow Rusinga Channel. There is said to be a relatively limited circulation of water between the gulf and the main lake (Calamari et al., 1995) although Worthington (1930) noted that strong afternoon winds caused a regular diurnal flow of water up and down the gulf. It is also affected by several rivers which carry heavy silt loads and they may be primarily responsible for its conductivity, which decreased progressively from 171 $\mu S\ cm^{-1}$ at the head of the gulf to 99 $\mu S\ cm^{-1}$ where it enters the main lake (Gikuma-Njuru and Hecky, 2005) thus reflecting a dilution effect brought about by the exchange of water, however limited, between the gulf and the lake.

How can the improvements in Lake Victoria's condition be explained given the fact that the concentrations of plant nutrients have not decreased (Table 6)? It may not be possible to answer this question fully with the currently available data but it is evident that eutrophication is not a simple linear sequence of nutrient accumulation and environmental degradation as implied by Kolding et al. (2008) but a much more complex process. Events in the lake may perhaps be understood by regarding them as analogous to those that occur in newly-created man-made lakes. These are typically eutrophic as a result of the sudden release of nutrients from the drowned terrain and exhibit algal blooms, the explosive growth of floating macrophytes, oxygen depletion and rapid changes in the populations of fish and invertebrates. These decrease over time as the lake matures until an ecological equilibrium is reached (McLachlan, 1974). Lake Victoria may now also be reaching some kind of ecological equilibrium, in part because intense fishing of Nile perch has allowed species from lower trophic levels to increase (Balirwa et al., 2003).

The ecosystem disruptions brought about the population explosion of Nile perch and the destruction of the haplochromines may have contributed to a sudden release of nutrients, manifested in algal blooms, deoxygenation and the proliferation of water hyacinth. The fish population was dominated by a top predator and even as late as 1999 Nile perch accounted for 80% of the fish biomass in the lake (Getabu et al., 2003). The proportion of Nile perch in the fish stocks began to decline, falling to 46% in 2001, 31% in 2006 and 15% in 2009 with species lower on the food chain, notably *Rastrineobola* and some haplochromines, increasing proportionately (LVFO, 2009b). The decline of Nile perch was probably both a result of fishing pressure and a natural adjustment since a population consisting primarily of a top predator was unlikely to be sustainable over the long term. The effect of its decline may have been the restoration of some degree of ecological equilibrium with primary productivity

being more effectively utilised by consumers at lower trophic levels, thereby mitigating the impacts of eutrophication.

Localised pollution has not been discussed in this paper but there is evidence of pollution and water-borne diseases at fishing villages and sewage and industrial effluents from towns in Uganda (Oguttu *et al*., 2008; Muyodi *et al*., 2009). The Nyanza Gulf in Kenya is also subjected to pollution by domestic and industrial wastes from Kisumu (Gikuma-Njuru and Hecky, 2005) while gold mining in Tanzania is a source of mercury contamination in the southern part of the lake (Campbell *et al*., 2003). These types of pollution may not have affected the water quality in the lake as a whole but they have caused problems in specific areas and will need to be monitored and quantified in future so that steps to control them can be taken before their influence spreads.

5. Acknowledgements

6. References

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