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Some aspects of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East Africa)

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While this paper was in press, Peter B. O. Ochumba passed away. We dedicate this paper to his memory.

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Abstract

Dramatic changes in the Lake Victoria (East Africa) environment were observed after the introduction of the Nile perch (*Lates niloticus*) in the 1950s. An extraordinary spectrum of endemic haplochromine fishes, a result of intralacustrine adaptive radiation was reduced by massive species extinctions (ca. 65%) due in part to predation by Nile Perch. Such an abrupt destruction of natural diversity has never before been documented by scientists. Lake Victoria's haplochromine species flock comprised upwards of 400 species (5% of the world's known freshwater fishes), encompassing a remarkably wide trophic spectrum and constituting 83% of the lake's total fish biomass. The lot evolved in an isolated part of the Nile system since the formation of the lake basin about 750×10^3 years ago, but quite possibly as recently as 14×10^3 years ago, when most of the lake dried up. More than 50% of the haplochromine species (by number) were phytoplankton-zooplankton-detritus consumers; 55% of their biomass were detritivores and 27% zooplanktivores. The piscivore Nile perch (*Lates niloticus*) was first introduced into Lake Victoria in 1954. It underwent rapid population expansion in the 1980s, accompanied by haplochromine decline. Consequently, phytoplankton and detritus consumption by fishes was reduced. The biomass of the endemic Cyprinidae *Rastrineobola argentea* increased, as did its fishery, and predation pressure on zooplankton was therefore intensified. The population of the prawn *Caridina niloticus* became very dense, mostly in deep waters. The fishery and fish industry were altered fundamentally. Limnological changes suggesting eutrophication have been observed since 1960: hypolimnetic anoxia increased and the period of extensive vertical mixing was restricted to about one month per year; phytoplankton productivity increased and shifts from diatom to blue-green dominance occurred. Increased inputs of N (from the 1920s) and P (from the 1950s), induced through precipitation and human activity in the catchment area (agricultural and urban developments, deforestation, etc.) and high water levels accompanied by decline of available silicon, have persisted. Both top-down (Nile perch piscivory) and bottom-up (nutrient changes) influences enhanced eutrophication. The concurrent system changes in nutrient dynamics may have contributed an additional impact to the extinctions of haplochromine fishes.

Keywords: Aquatic communities, foodwebs, diversity, ecosystem, freshwater lake, eutrophication, nutrient cycles, *Lates niloticus*, Lake Victoria, East Africa.

Quelques aspects de perturbation dans la structure et la biodiversité de l'écosystème du lac Victoria (Afrique de l'Est).

Résumé

Suite à l'introduction dans les années 1950 de la perche du Nil (*Lates niloticus*) dans le lac Victoria, des changements importants ont été observés. Un grand nombre de poissons endémiques Haplochromines, résultat d'une radiation adaptative lacustre importante, a disparu par extinction massive (près de 65% des espèces) due en partie à la prédation exercée par la perche du Nil. Une telle destruction de la diversité naturelle n'avait jamais été observée auparavant par des scientifiques. Le groupe des Haplochromines du lac Victoria comprend plus de 400 espèces (5% des poissons d'eau douce connus dans le monde), formant un remarquable réseau de relations trophiques constituant ainsi 83% de la biomasse totale en poissons du lac. Le « species flock » a pu évoluer dans un système isolé du reste du bassin du Nil il y a environ 750 000 ans, mais aussi plus récemment il y a 14 000 ans lorsque le lac s'est retrouvé dans une période d'assèchement. Le prédateur *Lates niloticus* a été introduit la première fois en 1954. La population se développa rapidement dans les années 1980 accompagnée par un déclin du nombre des Haplochromines. Consécutivement, la consommation de détritus et de phytoplancton par les poissons s'est réduite. La biomasse du Cyprinidae, *Rastrineobola argentea*, a augmenté ainsi que sa pêche, et par conséquent la prédation sur le zooplancton s'est intensifiée. La population de crevettes, *Caridina niloticus*, devint dense, en particulier en eau profonde. La pêche et ses filières industrielles furent gravement altérées. Des modifications limnologiques, souvent liées au problème d'eutrophisation, ont été observées depuis 1960 : l'anoxie dans les couches d'eau les plus profondes du lac augmenta et la période de mélange vertical entre couches d'eau se limita à un mois par an : la productivité phytoplanctonique augmenta et un changement d'occurrence des diatomées vers des algues bleues et vertes se produisit. L'augmentation de l'azote (depuis les années 1920) et du phosphore (depuis les années 1950) provoquée par les précipitations et l'intensification des activités humaines dans la zone du lac (agriculture, développement urbain, déforestation...) ainsi que le haut niveau des eaux du lac accompagné d'une baisse des silicates disponibles ont persisté. La conjonction d'éléments comme la prédation exercée par la perche du Nil et les modifications dans la composition des éléments nutritifs ont nettement influencé le phénomène d'eutrophisation. Les modifications dans la dynamique des éléments nutritifs pourraient aussi avoir contribué à l'extinction des poissons Haplochromines.

Mots-clés : Écosystème lacustre, diversité, eutrophisation, sels nutritifs *Lates niloticus*, lac Victoria, Afrique de l'Est.

INTRODUCTION

Africa's Lake Victoria is by area the second largest freshwater body in the world. Lake Victoria is a unique ecosystem, presently separated from the other parts of the Nile River system by waterfalls. Therefore, a very high level of fish endemism was developed in this lake (Kaufman, 1992). More than 300 endemic species of cichlid fishes (Haplochrominae) were known from the lake (Greenwood, 1981; HEST, 1989); more were identified in recent years and yet others await scientific description (Kaufman and Ochumba, 1993).

During the 1950s the piscivorous Nile perch (*Lates niloticus*) was introduced to Lake Victoria. After twenty years the *Lates* had invaded the entire lake, with rapid population increases in the 1980s. Fisheries changed dramatically, reflecting changes in the lake's fish community structure (*figs.* 1, 2). The native haplochromine densities declined from 83% of total biomass prior to the Nile perch upsurge to currently almost zero (Goldschmidt *et al.*, 1993). Nile perch and the native zooplanktivorous species *Rastrineobola argentea* became the most abundant fishes in Lake Victoria (Ochumba *et al.*, 1992). *Lates niloticus* is a very efficient predator which very successfully feeds on cichlids (mostly haplochromines) of various sizes and also eats other organisms (HEST, 1989). The *Lates* partly destroyed the lake ecosystem by reducing the haplochromine biomass and diversity. The reduction of haplochromines resulted in a decline of the biomass of consumers of phytoplankton, zooplankton and detritus in the pelagic and bottom layers. The concentration of organics in the water was enhanced, and its decomposition greatly reduced the oxygen content. An increase of nutrient loads was also indicated (Hecky, 1993): N input enhancement began in the 1920s as did influx of P during the 1950s. Additionally, Si availability declined after the 1970s (*table* 1). Consequently, the eutrophication process in Lake Victoria was enhanced. The destruction of fish biodiversity together with nutrient dynamics resulted in changes in the ecosystem structure (Kaufman, 1992). Chlorophyll content measured in the late 1980s and early 1990s (Hecky, 1993: 11-23 mg.m^{-3} during March and December) was approximately 6 times higher than in 1960-1961 (Talling, 1966: 2-4 mg.m^{-3} during December, February and March) (*table* 1). These deleterious effects have now spread

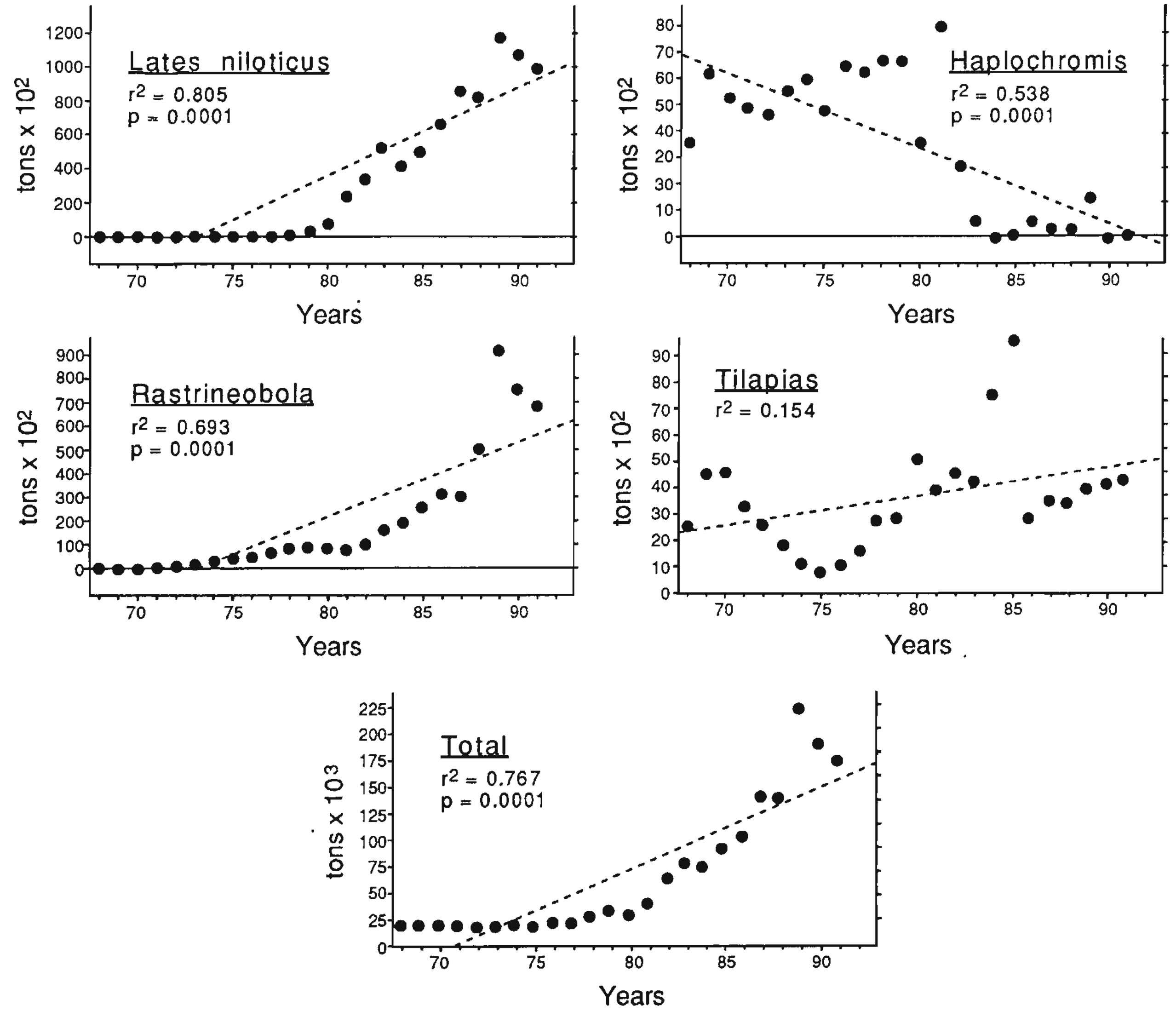

Figure 1. – Fisheries in Kenyan part of Lake Victoria: total and species annual catches (metric tons) vs. year regressions (Ochumba *et al.*, 1992; Greboval, 1990).

throughout most of the lake. Moreover, trees and shrubs are cut in large numbers (deforestation) for processing of the Nile perch as food (smoking, frying), and large areas in the catchment are exposed to water runoff and soil erosion with enhanced nutrient supply to the lake. The substantial and dramatic changes in the fish community and in the lake's trophodynamics have been accompanied by other system changes: nutrient dynamics, algal densities and species composition, thermal stratification and oxygen distribution and other factors (*table* 1). In this paper, the limnological conditions (plankton, temperature, pH, dissolved oxygen, nutrients) of Lake Victoria and feeding habits of tilapiine as we recorded during a 1989-1992 survey are compared with those of the period before the Nile perch invasion, and the eutrophication status of the lake is considered.

MATERIALS AND METHODS

Phytoplankton and zooplankton

Samples for zooplankton and phytoplankton analysis were collected by 5 l sampler (Van Dorn) during 1988-1990 in the Nyanza (= Kavirondo) Gulf, Rusinga Channel, and open water stations in the Kenyan part of Lake Victoria (*fig.* 3). Zooplankters were separated by sieving (100 μm mesh size) 1-3 litre water samples (preserved in 10% formalin); all organisms that were retained were counted under a

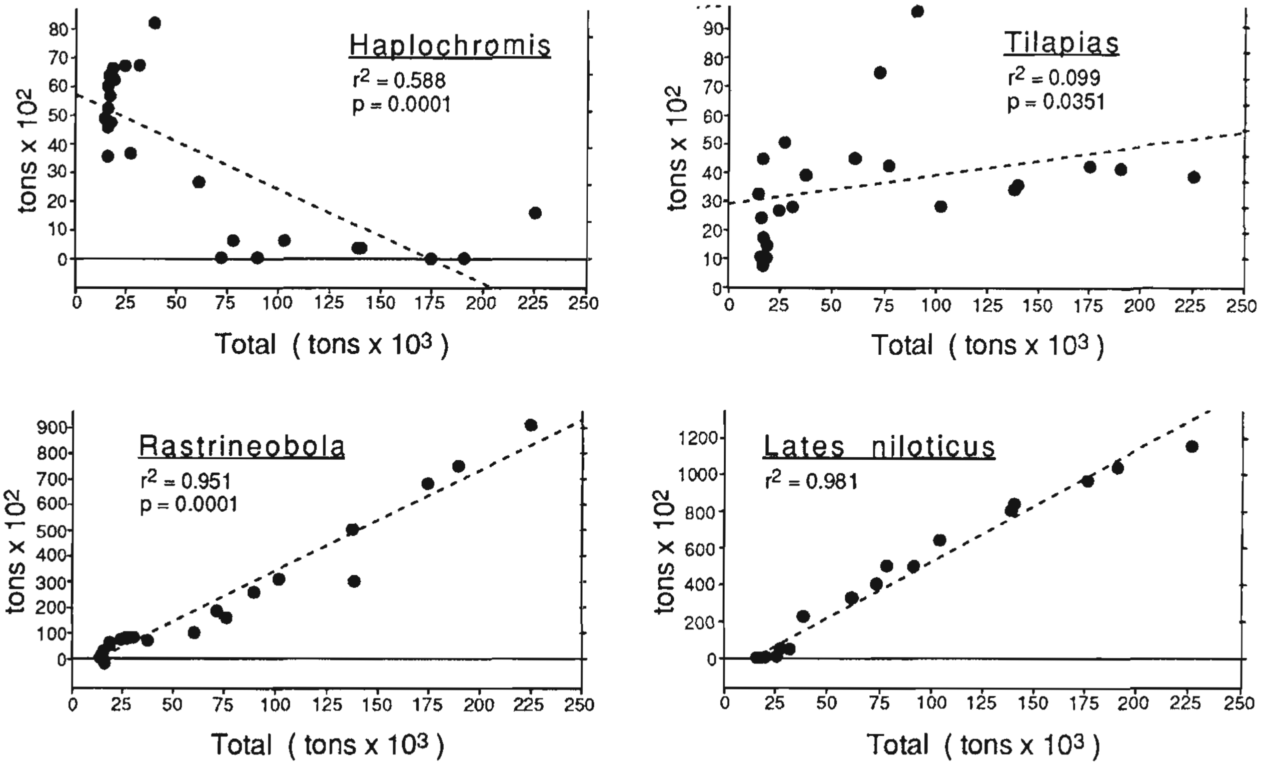

Figure 2. – Fisheries in Kenyan part of Lake Victoria: species annual catches (tons) vs. total landings (metric tons) (Ochumba *et al.*, 1992; Greboval, 1990).

wild model M7 dissecting-microscope. Phytoplankton samples (100 ml, preserved in Lugol's solution) and taken from the same sampler as for zooplankton, were analyzed by using Utermohl's sedimentation method with 5 to 10 ml chambers on a Wild M40 inverted microscope. Several net-tow samples on each date were analyzed for relative density counts.

Fish gut content analysis

The tilapiine fishes *Oreochromis niloticus* (n=70), *O. variabilis* (n=46), and *Tilapia zillii* (n=24), were collected from fishermen's catches, measured, immediately dissected and the viscera removed into small jars with 10% formalin. The following measurements were taken: total (TL) and standard (SL) lengths, total fresh weight (TW), and viscera (VW) fresh weight (stomach, intestines and related fatty tissues). Value variations: SL: 9-50 cm; TL: 10-55 cm; TW: 100-600 g; VW: 0.2-2.0 g.

Gut contents were analyzed (flood items counted) as follows. The intestine of each individual was gently dissected under a dissecting microscope and the content was scraped and squeezed out and dispersed in 300-400 ml 10% formalin and mixed on Vortex. Then: (1) ten, 20 ml subsamples were taken, while mixing, and analyzed under a dissecting microscope and (2) ten, 2 ml subsamples were taken while mixing and analyzed under a compound microscope (Dialux 20). The components of food of fishes were classified by biomass estimation into 5 quantitative levels (% of the total): 1) 5-15%; 2) 15-30%; 3) 30-50%; 4) 50-70% and 5) 70-90%. Results presented in *table* 4 include all major classes of identifiable food item groups comprising 30-90% of the total.

Nutrients

Samples (300 ml) were collected by Van Dorn 5 l sampler and kept in ice on board, frozen in the Mbita-Point and the Kisumu Institute the same day as collected, and shipped frozen in dry ice (CO_2) to the Kinneret Limnological Laboratory where they were thawed and analyzed within 4-5 days after being collected. The methods were as follows: Total P-persulfate digestion method (APHA, 1989); P-(soluble P) molybdate reactive reduction by ascorbic acid (APHA, 1989); total N-peroxidisulfate oxidation of total nitrogen in water (Nydahl, 1978); ammonia-phenolhypochlorite method (Solorzano, 1969); nitrate-cadmium reduction method (APHA, 1989).

Physico-chemical monitoring

Temperature, dissolved O_2, pH, and depth were recorded monthly in shallow and deep stations (*fig.* 3)

Table 1. – Comparative data from the offshore zone of Lake Victoria: 1960-Uganda-(Talling, 1965, 1966, 1987); 1990-Uganda-(Hecky, 1993); 1990-Kenya-(Gophen *et al.*, 1993).

	Uganda		Kenya
	1960	1990	1990
N-NH$_4$ (mg/l), Epilimnion		0.028	0.008-0.013
N-NH$_4$ (mg/l), Hypolimnion		0.056-0.12	0.021-0.152
N-NO$_3$ (mg/l)	0-0.01	0.011-0.084	0.01-0.03
SRP (mg/l)	0.09-0.50	0.012-0.043	0.004-0.073
Total-P (mg/l)		0.062-0.124	0.07-0.103
Total-N (mg/l)		0.336-0.448	0.44-1.16
TN/TP (Wt/Wt)		3.2-9.0	4.7-18.5
Upper depth of 4.0 mg/l DO isopleth	45 m	23 m	23 m
Silica (mg/l)	4.2-8.4	0.01-2.5	
Chlorophyll (μg/l)	2-4	11-23	
Dominant alga	Diatoms	Cyanophicae	Cyanophicae
Primary production (mgO$_2$.m^{-3}.day^{-1})	100-130	180-600	
Secchi depth		1.2 m	1.8 m
Euphotic zone	0-15 m	0-7.5 m	

(280 profiles) during 1989-1992 by the Hydrolab probe system (calibration: Hydrolab manual, 1991) (^{1}). Secchi depths were measured (n = 155).

RESULTS

Phytoplankton (*table* 2)

Phytoplankton densities (number/ml) are given in *table* 2 for the regions: 1: Winam (Kavirondo, Nyanza) Gulf (mean depth- 8±4 m) (stations K, 1, 2, 3, 17, 30, 31, 37, 38); 2: Rusinga Channel: a- shallow part (stations 5, 7, 8; mean depth- 8±2 m); b- deep part (stations 6, 34; mean depth- 47±5 m) and 3: offshore (mean depth- 40±8 m) (stations 32, 33, 55, 99, 100, 103) (*fig.* 3).

Kavirondo (=Nyanza, Winam) Gulf

During June and December 1989, and January-February 1990, coccoid coenobial cyanophytes dominated. Filamentous forms (*Lyngbya circumcreta* and *Anabaena flos-aquae*) were present in low numbers. The Chlorophyta were present in low densities and high diversity. The Cryptophyta were found during the whole period, and dinoflagellates were recorded in June, January and February.

At station 2 in May 1989 the highly abundant green algae showed a particularly high diversity but all other major groups were also recorded. In May 1990 the phytoplankton composition was considerably different, with a major bloom of *Anabaena flos-aquae*. Coenobia of *Microcystis* and filaments of *Melosira* (=*Aulacoseira*) sp. were rare, and other algae were not found at this time.

On the same day at station 3, *Melosira* sp. were dominant and *Anabaena* was common; also recorded were coenobial cyanophytes, as well as the chlorophytes *Scenedesmus* sp., *Pediastrum* sp., *Oocystis* sp., *Cosmarium*, cryptophytes and dinoflagellates.

In stations 31, 36, 37, 38 (March 1989) coccoid coenobial cyanophytes dominated and *Lyngbya circumcreta* was common. The diatoms were represented by *Nitzschia acicularis* and *Melosira* sp.; chlorophytes, cryptophytes, dinoflagellates and euglenoids were also recorded. In February 1990, a high density of coenobial cyanophytes (composed of very small cells), accompanied by filamentous forms, was recorded at stations 17 and 31. At stations 36 and 38, coenobial cyanophytes were common, but the diatom *Synedra cunningtonii* dominated. At stations 36 and 38 the diversity and abundance of the green algae were lower than at stations 17 and 31.

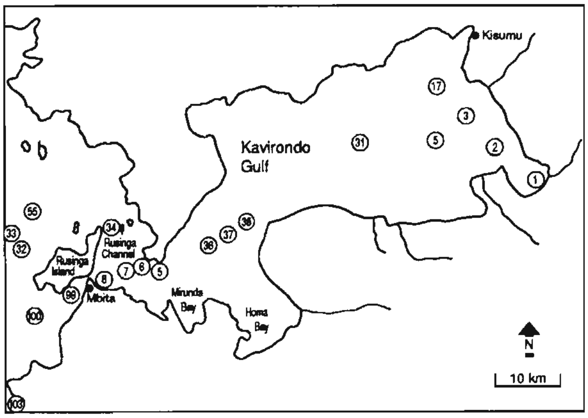

Figure 3. – The Kenyan part of Lake Victoria with sampling stations (circled numbers).

(^{1}) Hydrolab, 1991. Operating manual hydrolab corporation. All rights reserved, 28 p.

Table 2. – Algal density (cells, filaments or coenobia/ml) ranges and/or individual counts in Kavirondo Gulf (0, 1, 5, 7, 10 m depths) (1989-1990), Rusinga Channel (2, 3, 5, 20 m depths) (1990), and offshore (0, 1, 1.5, 5, 16, 20 m depths) (1990) stations. Only densities above 200/ml are presented.

Taxa	Densities		
	Kavirondo	Rusinga	Offshore
Aphanocapsa sp.	1 225-1 775	1 610	
Aphanocapsa delicatissima	3 480		
Lyngbya sp.	265-4 040	7 415-16 990	9 000 → 10 000
Lyngbya bipunctata	533-2 210	2 880-3 525	3 932 → 5 000
Merismopedia sp.	210-780		
Merismopedia punctata	1 010		
Microcystis sp.	355-1 150	600	
Anabaena flos-aqua	1 025		
Anabaena sp.	305-480		
Chroococcus sp.	225-915	410	
Other Coenobial cyanophytes	> 3 000		
Cylindrospermopsis sp.	465	590-4 120	2 724 → 4 000
Melosira nyassensis* var. *Victoriae*	1 385		
Melosira granulata var. *angustissima*	600		
Synedra cunningtonii	220-3 275	2 400-4 780	1 958 → 3 000
Navicula rynchocephala	340		
Rhodomonas sp.	335	470	
Chlamydomonas sp.	250		
Scenedesmus sp.	220-345		
Crytpomonas sp.	320-430	400	

* Aulacoseira

In April and May 1990 the relative abundance of phytoplankton was studied on net tow samples. During this period *Melosira* sp. dominated at stations 17, 30, 31 and 37, whilst at station 36 *S. cunningtonii* was the dominant alga and in April and May was accompanied by *Melosira* sp. The coccoid coenobial cyanophytes and *Anabaena flos-aquae* were common at all stations, as well as the green algae and the cryptophytes.

Rusinga Channel (February-May 1990)

In February-March the filamentous cyanophytes dominated and were accompanied by *Synedra cunningtonii* at stations 7, 8, 34, whereas at station 6 *S. cunningtonii* was more abundant than the filamentous cyanophytes. Coccoid cyanophytes and cryptophytes were recorded; all densities of other taxonomic groups were very low. In April-May (net tow samples, relative abundance) *S. cunningtonii* dominated at all stations and was accompanied by filamentous and coccoid cyanophytes, which became more abundant. Green algae were present but as a low number of species.

The offshore zone stations

In March 1989 at stations 99, 100, 103 *Lyngbya circumcreta* dominated. It was accompanied by *Nitzschia acicularis*; coccoid coenobial cyanophytes were present; green algae appeared sporadically. The filamentous cyanophytes also dominated in February 1990, and high numbers of *Synedra cunningtonii* were recorded, but chlorophytes were not found. A month later (20 March) the filamentous cyanophytes continued to dominate, *S. cunningtonii* became more abundant, and a few chlorophytes, dinoflagellates and cryptophytes appeared. In April-May *S. cunningtonii* increased in relative abundance and dominated together with the filamentous cyanophytes (*Lyngbya* sp., *Cylindrospermopsis*). Coccoid cyanophytes were present. The other taxonomic groups were present as a few species at relative low densities (*Oocystis solitaria, Scenedesmus quadricauda, Glenodinium pulvisculus*).

Zooplankton (*table* 3)

Samples collected in March 1989 at stations 6, 34, 36, 100, indicated zooplankton distribution as follows. High densities of cyclopoids were measured at 6 m, 11 m, 20-25 m and 39-40 m and nauplii and copepodites were also abundant at 1 m depth. Most of the cladocerans were found in deep layers (11-40 m) while *Moina* and *Bosmina* also were abundant at 1 m. The highest densities of rotifers were observed at shallow depths of 1-11 m (except 39 m, at st. 34). Calanoida were abundant in deep layers (6-40 m) and low densities of all their life-cycle stages were observed at 1 m depth.

Table 3. – Zooplankton density (No./L) ranges in Kavirondo Gulf (0, 1, 2, 3, 4, 5, 6, 9, 11 m depths), Rusinga Channel (0, 1, 3, 4, 5, 7, 8, 10, 20, 25, 39, 40 m depths) and offshore (0, 1, 3, 4, 5, 10, 17, 20, 40 m depths) stations (1989-1990).

	Density		
	Kavirondo	Rusinga	Offshore
Copepoda:			
Cyclopoida (all stages)	1-83	1-88	4-84
Calanoida (all stages)	0-46	0-15	0-56
Cladocera	0-25	0-28	0-14
Rotifera	0-56	0-27	0-13

A check-list of the zooplankton species recorded (1989-1990).

1. *Thermocyclops neglectus*
2. *Thermocyclops hyalinus*
3. *Mesocyclops leuckarti*
4. *Microcyclops minutus*
5. *Tropodiaptomus neumaniia*
6. *Diaphanosoma excisum*
7. *Ceriodaphnia rigaudi*
8. *Daphnia Longispina*
9. *D. lumholtzi* (*F. monacha*)
10. *Moina macrurus*
11. *Bosmina longirostris*
12. *Chydorus sphaericus*
13. *Brachionus caudatus*
14. *Brachionus calyciflorus*
15. *Keratella tropia*
16. *Polyarthra remata*
17. *Filinia longispina*
18. *Asplanchna brightwelli*

others: *Collotheca* sp., *Trichocerca* sp., *Ascomorpha* sp.

During 1990, high densities of cyclopoids were recorded at stations 36, 31, 100, 32, 5, 33 and 30 at shallow depths (0-4 m). These high values were mostly due to small-bodied nauplii stages. High densities of small rotifers were observed in April-May 1990 in stations 36, 31, 8 at shallow depths (3-4 m). Densities of large bodied Cladocera and Calanoida were low during the entire period (1989-1990) (Mavuti and Litterick, 1991).

We measured low densities of zooplankton during all periods (*table* 3) and the most abundant organisms were small. Low densities of total zooplankters and high relative abundance of small-bodied organisms also were recorded by Ndawula (1994).

Anoxia (*fig.* 4, *tables* 5, 6)

During March 1989 we measured dissolved oxygen (DO) levels less than 4.0 ppm (mg. l^{-1}) at stations 33, 32, 100 and 103 at 33-34; 30-35; 40 and 43-47 metres respectively. Results in *table* 6 indicated the presence of low oxygen conditions in the offshore stations, Rusinga channel and even in one shallow (6.5 m) station in Kavirondo Gulf. We recorded the DO isopleths of 1.0 mg/l between 18-48 m during 1990-1992 (offshore stations: n=23) (±SD 7) (*table* 5). We found that most of the deep water in Lake Victoria (below 34 m) is consistently anoxic (<1 mg/l) (*table* 5). During his survey in offshore stations between September 1960 and August 1961, Talling (1966) recorded the 4 mg/l DO isopleth at 40-50 m (one case of 38 m in October) during September-December 1960; below 50 m during January-March and August 1961; between 40-50 m during April-May 1961; and below 50 m during most of June and July 1961 (*table* 5).

Table 4. – Food composition of tilapias in Lake Victoria: % of fish specimens with indicated food items dominance (>30% of intestine content see text) are presented.

	Oreochromis niloticus	*Oreochromis variabilis*	*Tilapia zillii*
Benthos			
Insect fragment	1	2	2
Trichopteridae	8	22	20
Chironomidae	6	4	2
Oligochaetes	1	–	–
Nematodes	–	6	2
Spongillid spiculae	1	–	–
Ostracods	5	1	–
Caridina fragments	6	6	22
Bivalves	4	–	–
Fish scales	2	–	–
Plant debris	11	20	36
Sand and mud particles	13	12	2
Total	58	73	86
Plankton			
zooplankton fragments	2	–	–
Copepods	1	–	–
Moina	4	–	–
Chydorus and *Alona*	5	–	–
Microcystis	5	4	4
Unicell diatoms	7	4	4
Chlorophytes	4	3	2
Melosira	5	3	2
Ceratium	1	–	–
Filamentous cyanophytes	5	8	–
Detritus	3	5	2
Total	42	27	14

Maximal values in pH and temperature profiles (n=246) averaged 8.50 (±0.87 SD) and 26.15°C

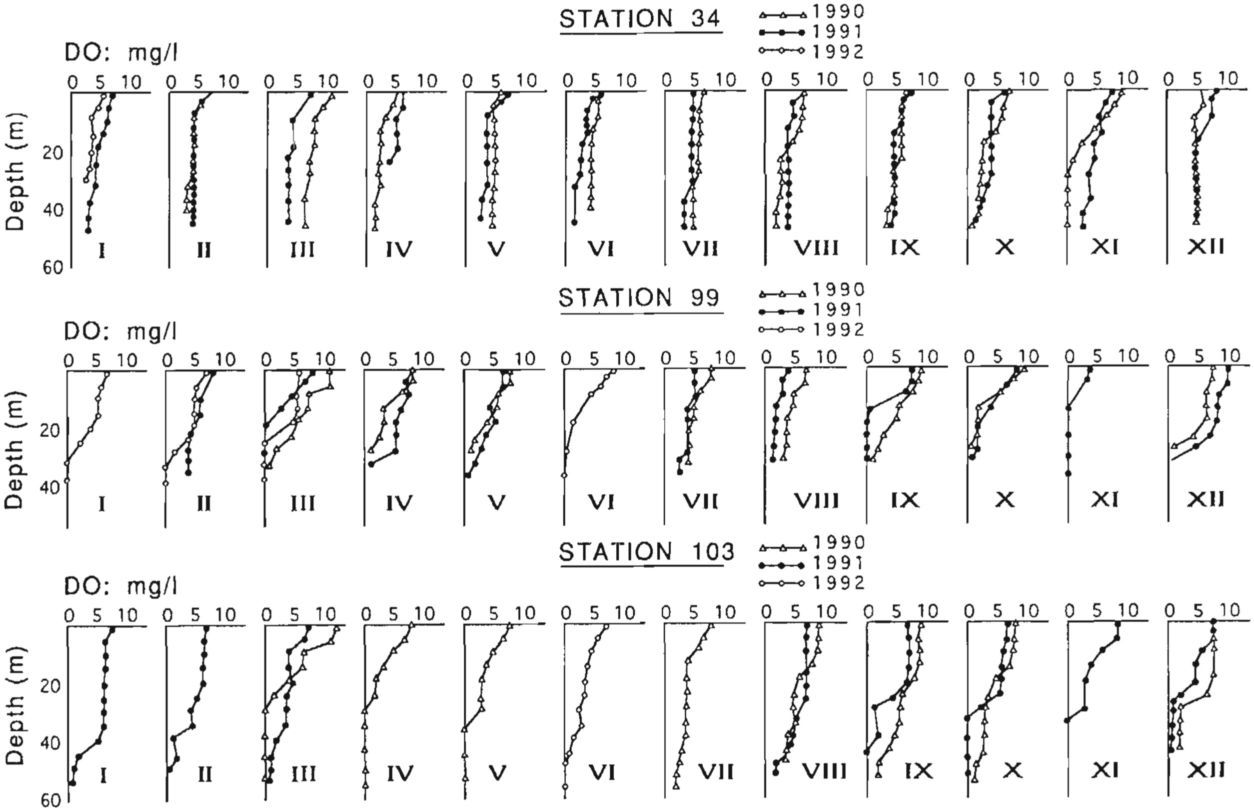

Figure 4. – Monthly profiles of oxygen content (DO) (mg/l) (Orthograde) during 1990 (Δ-Δ-Δ-Δ), 1991 (●-●-●-●) and 1992 (O-O-O-O) in stations 34 (Russinga, Channel), 99 and 103 (offshore).

(±2.83 SD) respectively; means of minimal values in these profiles were 7.35 (±0.71 SD) and 25.24°C (±2.77 SD) for pH and temperature respectively. These data (see *fig.* 4) represent a 12-month stable stratification in stations 99 and 103, where 30-50% of the water volume had an oxygen level below 4.0 mg/l. Only in July at station 103 was the hypolimnion less hypoxic (*fig.* 4). At station 34 (*fig.* 4) stratification was unstable due to internal seiches.

Nutrients

Results of the nutrient analyses are in *table* 7. High concentrations of total nitrogen (TN) in deep waters at stations 6, 17, 31, 34, 37 and 38 are indicated. Similar distribution of the total phosphorous (TP) concentrations were also observed at stations 6, 17, 31, 32, 38 and 103. This pattern of nutrient distribution was similar for ammonium-nitrogen at all stations except station 1.

Food composition of tilapias

Nile perch piscivory affected not only haplochromine diversity but also the abundance of Tilapiinae. The native tilapiine "ngege" (*Oreochromis esculentus*) was almost exterminated from the entire lake (Kaufman, 1992); it is currently very abundant in the nearby lake Kanyaboli, where Nile perch is not present (Kaufman and Ochumba, 1993). *Oreochromis variabilis* became extremely rare. We documented a change of tilapiine feeding habits as a result of habitat change after the invasion of Nile perch. The result of gut content analysis of three relatively common tilapiine cichlids are presented here (*table* 4).

Oreochromis niloticus was reported to feed on suspended matter (Okeyo, 1989). Our observations indicated that most of the food of this species was collected on the bottom or close to the sediment surface: Trichoptera, *Caridina*, mud, chirinomids, ostracods, bivalves, diatoms. It was also observed that some other components were ingested by the fish probably in deep or mid layers such as *Moina, Chydorus*, plant debris, *Microcystis, Melosira* and small chlorophytes.

The dominant components in the intestines of *Oreochromis variabilis* were Trichoptera, mud and plant debris. It is suggested that *O. variabilis* also collects most of its food near or in bottom sediments. Feeding habits of *Tilapia zillii* were similar to those of *O. variabilis*, with a predominance of Trichoptera,

Table 5. – Isopleths depths (mean = $\overline{X}$, SD, n) of dissolved oxygen (DO) concentration (mg/l) intrapolated from measured profiles during 1990-1992 in the offshore Kenyan part of Lake Victoria (stations 32, 33, 55, 99, 100, 103) and monthly values (mean = $\overline{X}$, SD, n) recalculated from Talling (1966; *fig.* 9) for the upper most depth of the isopleths as measured during 1960-1961 in the offshore zone. Relevant months for each isopleth are given.

DO	$\overline{X}$	SD	n	1990	1991	1992	$\overline{X}$	SD	n	1960	1961
1	34	7	23	3, 8-11	2-5, 9, 10, 12	1-7	54	4	6		1-6
2	28	9	23	3, 8-11	2-5, 9, 10, 12	1-7	52	4	8	9, 12	1-6
3	26	9	24	2, 3, 8-11	2-5, 9, 10, 12	1-7	50	3	10	9-12	1-6
4	23	7	23	2, 3, 8-11	2-5, 10, 12	1-7	45	6	11	9-12	1-6
5	19	8	23	2, 3, 8-11	2-5, 10, 12	1-7	42	8	12	9-12	1-8
6	15	7	22	2, 3, 8-11	2-5, 10, 12	1-7	34	7	12	9-12	1-8
7	9	5	22	2, 3, 8-11	2-5, 10, 12	1-7	7	6	6	9-12	1,8
8	5	5	17	3, 8-11	2-4, 10-12	1, 4-6					
9	4	5	12	8-11	2-4, 10, 12	6					
10	4	6	7	8-11		1					

Caridina and plant debris. *Microcystis* is a pelagic form but dead or senescent colonies are probably collected by the fish near the bottom.

DISCUSSION

Phytoplankton

The pattern of species composition during the entire period of the study was similar at all depths but phytoplankton abundance decreased in deep layers. Viable algae were recorded at 30 m depth, whereas at 40 m only empty frustules of diatoms and empty membranes of algae were found. Talling (1966) suggested that in the tropical belt annual patterns of phytoplankton distribution are sometimes controlled mostly by hydrological conditions. Phytoplankton distribution in the Kavirondo Gulf was probably affected by hydrological features (river inflows) and nutrient influx, whereas water circulation affected algal development in the offshore regions.

Phytoplankton in large lakes of the warm belt (Serruya and Pollingher, 1983) is characterized by the dominance of Chlorophyta and Cyanophyta and sometimes diatoms. During our study the phytoplankton was characterized by a high diversity and abundance of Cyanophyta, high diversity and low abundance of Chlorophyta and low diversity but relatively high abundance of diatoms. The Dinophyta, Cryptophyta and Euglenophyta (flagellates) were represented by a low number of species.

A heavy bloom of *Microcystis* sp. during February and August 1986 in the open waters of the Kenyan part of the lake was documented by Ochumba and Kibara (1989). In our samples *Microcystis* sp. were present but not very abundant.

Synedra cunningtonii was first described from near Bukoba and Entebbe by G.S. West (1907) and included by Bachmann (1933) in Lake Victoria records (gulfs and bays), but was not mentioned by Talling (1965, 1966, 1987) or by Akiyama *et al.* (1977) at Mwanza Gulf. Most algae reported by the last two authors were found in our samples. Lake Victoria phytoplankton is dominated at present by blue-greens whereas Talling (1966) recorded much higher relative and absolute abundances of diatoms.

The Secchi depths we measured during 1989-1991 ranged between 0.8 and 2.8 m, whilst Mugidde (1993) presented a range of 0.84-6.40 m in 1960-1961. Talling (1966) indicated the euphotic zone depth as 15 m in 1960-1961 and Hecky (1993) estimated the limit of the euphotic zone at 7.5 m in 1989-1990 (*table* 1). A comparative study of the distribution of dissolved oxygen (Hecky *et al.*, 1994) indicates high levels in upper layers with consequent oversaturation, due to denser phytoplankton biomass and more intensive photosynthetic activity, whereas Talling (1966) reported oxygen values below saturation at similar depths. Consequently, a higher algal biomass and photosynthetic activity in the epilimnion of Lake Victoria during the 1980s-1990s is indicated.

Talling (1987) comparatively analyzed the phytoplankton composition from earlier studies (Talling, 1965, 1966 and others) and suggested that the species composition had been stable over the previous eighty years. We recorded much higher algal densities per ml than the values presented by Talling (1957, 1965, 1966, 1987) and a clear change in relative abundance of taxa.

From the 1960s through the 1980s the phytoplankton assemblages shifted from diatom (Talling, 1966, 1987) to cyanophyte predominance, and primary productivity increased (*table* 1) (Ochumba *et al.*, 1992; Gophen *et al.*, 1963; Hecky, 1993; Mugidde, 1993). The major change in phytoplankton species composition during 1990-1991 was in relative abundance (more cyanophytes and less diatoms) and higher total densities. It is likely that nutritional value of cyanophytes and their detrital organic degraded products is lower than that of the dominant diatoms prior to the late 1980s for phytoplanktivores and detritivorous haplochromines. However, Goldschmidt *et al.* (1993) documented significant consumption of

Table 6. – Deoxygenated conditions (<4.0 mg/l-DO) in the Kenyan part (see map) of Lake Victoria: the upper depth (m), temperature (°C) (Feb., March, May 1990) and pH of the deoxygenated layer (DOL) are presented. Numbers in brackets are bottom depths (m).

Station	Date	Hour	DOL		Temp. (°C)	
Depth (m)			Depth (m)	pH	Surface	DOL
99 (40)	19.2	08:30	29	7.82	26.08	25.93
100 (39)	19.2	10:45	31	8.02	25.83	25.80
32 (40)	19.2	12:30	37	7.55	26.20	25.77
33 (37)	19.2	13:30	32	7.55	26.43	26.04
33-B (35)	19.2	14:15	33	7.45	26.85	25.97
34 (45)	20.2	09.00	40	7.51	26.09	26.02
34-B (52)	20.2	11:15	45	7.57	26.02	25.58
6 (47)	20.2	13:30	22	7.36	26.64	25.92
33-A (38)	18.3	15:20	18	6.91	26.87	25.12
33 (37)	19.3	13:30	19	6.97	26.95	25.13
55 (34)	19.3	10:00	26	6.91	25.74	24.85
99 (40)	20.3	15:00	10	6.97	27.50	25.13
100 (33)	20.3	12:30	21	7.03	26.58	24.96
103 (63)	21.3	10:45	19	7.00	26.81	24.78
99 (40)	21.3	13:45	26	6.96	27.41	24.78
32 (49)	21.3	16:00	22	7.08	26.71	24.87
3 (4)	13.5	14:10	3.5	7.09	27.06	24.14
5 (6.5)	14.5	08:25	5.5	7.07	26.64	25.04
33 (37)	15.5	12:00	30	7.21	26.48	25.61
32 (43.5)	16.5	10:42	25	7.31	25.81	25.51
99 (40)	16.5	12:40	20	7.28	27.27	25.51
100 (34)	16.5	13:35	22	7.38	27.24	25.73
103 (59)	17.5	10:45	20	7.30	26.15	25.19

cyanophytes prior to the Nile perch explosion. Hecky (1993) suggested enhancement of benthic invertebrates as a result of accumulation of organic particulate in the water and sedimentation to the bottom. He postulated that these invertebrates improved food resources for young perch and resulted in high recruitment. An obvious question is why native bottom-dwelling haplochromines were not also enhanced. Is it because they were preyed upon by adult Nile perch, or because of increasing anoxia in deep waters, or both? We assume that most of the deep water food resources are unavailable to young and adult perch during most of the year because of anoxia near the bottom.

Talling (1987) suggested a very high stability of the phytoplankton assemblages in Lake Victoria over 80 years of recorded data (1892-1972). He related this stability to the large lake dimensions and the low level of industrialization and urban developments in the catchment. Consequently, an important question is which effect was greater–Nile perch enhanced piscivory which started in the late 1970s, or the increase of P availability initiated earlier during the 1960s (Hecky, 1993). The increase of phytoplankton photosynthetic activity during the 1990s compared to the 1960s was presented by Mugidde (1993). The higher levels of chlorophyll in the 1990s compared to Talling's (1965, 1966, 1987) record were documented by Hecky (1993), Lehman and Branstrator (1993), and Mugidde (1993). On the other hand min-max values of algal biomass in offshore water given by Hecky (1993) (0.14-2.6 $\mathrm{mg}_{(ww)}$/l) are lower than those presented for total diatoms by Talling (1966; *fig.* 27) (2-6 $\mathrm{mg}_{(ww)}$/l).

Zooplankton

We suggest that before 1980 zooplankton predation (then by haplochromines) was less intensive than after the increase of *Rastrineobola*) (*figs.* 1, 2). Before 1980 the lower predation pressure by haplochromines enabled large zooplankters (herbivorous calanoids and cladocerans) to be more abundant than at present and, consequently, zooplankters grazed more intensively on algal matter. We postulate that after 1980 the zooplanktivorous *Rastrineobola argentea*, which is not efficiently eaten by Nile perch, and demographically enhanced rather than depressed (Wanink and Goudswaard, 1994) (*figs.* 1, 2), suppressed grazer zooplankton which resulted in phytoplankton enhancement. We observed higher densities of large-bodied zooplankters in deep layers, one possible indication of intensive predation pressure in the pelagial of Lake Victoria. It is likely that numerical densities of zooplankton in the pelagic zone changed little in the last 60 years, while community structure was highly modified (Worthington, 1931; Rzoska, 1956; Ndawula, 1994; Talling, 1966, 1987; Mavuti and Litterick, 1991). During 1931 (Worthington, 1931) and 1956 (Rzoska, 1956) the zooplankton community in the pelagic offshore zone of the lake was dominated

Table 7. – Nutrient concentrations (mg/l) in samples (depths, m) collected in March 1989 (TN/TP: Total nitrogen/total phosphorous).

Station	Depth (m)	Total N (mg/l)	NH_4 (mg/l)	NO_3 (mg/l)	Total P (mg/l)	SRP (mg/l)	TN/TP
1	0	0.89	0.016	0.04	0.130	0.015	6.8
1	2	0.62	0.033	0.07	0.113	0.028	5.5
6	1	1.37	0.070	0.02	0.074	0.009	18.5
6	20	1.12	0.112	0.02	0.062	0.004	18.1
6	39	2.96	0.367	<0.01	0.091	0.012	32.5
17	1	1.44	0.076	<0.01	0.070	0.027	20.5
17	2	2.83	0.224	0.06	0.095	0.048	29.8
31	1	1.08	0.062	<0.01	0.060	0.018	18.0
31	3	1.96	0.254	0.01	0.680	0.040	28.8
32	1	0.60	0.013	0.01	0.068	0.035	8.8
32	23	0.60	0.043	0.01	0.070	0.025	8.6
32	42	0.53	0.051	0.02	0.113	0.073	4.7
33	1	0.57	0.079	0.02	0.061	0.035	9.3
33	15	0.76	0.152	0.05	0.096	0.052	7.9
33	35	0.44	0.046	0.06	0.087	0.053	5.1
34	1	0.76	0.041	0.01	0.103	0.031	7.4
34	25	0.61	0.067	<0.01	0.083	0.030	7.3
34	40	0.90	0.128	<0.01	0.070	0.013	12.9
36	1	0.80	0.007	<0.01	0.052	0.018	15.3
36	11	0.67	0.073	0.01	0.052	0.031	12.9
37	1	0.94	0.124	0.02	0.050	0.021	18.8
37	5	2.24	0.131	0.002	0.088	0.038	25.5
37	6	0.64	0.023	0.01	0.045	0.019	14.2
38	1	0.82	0.012	0.06	0.068	0.020	12.1
38	9	0.60	0.065	<0.01	0.049	0.025	12.2
38	20	5.37	0.249	0.02	0.821	0.337	6.5
100	1	1.16	0.008	<0.01	0.089	0.008	13.0
100	20	0.90	0.055	0.02	0.085	0.013	10.6
100	40	0.84	0.021	0.03	0.090	0.012	9.3
103	23	0.47	0.041	0.02	0.072	0.050	6.5
103	30	0.42	0.057	0.07	0.083	0.055	5.1

by calanoid copepods (adults and copepodites) and cladocerans (90-55% by numbers), whereas their proportions were <5% in 1990 (Ndawula, 1994) and similarly were low during 1984-1987 (Mavuti and Litterick, 1992). *Table* 3 shows similar low densities Cladocera, whereas the high numbers of Cyclopoida and Calanoida are mostly contributed by nauplii and young copepodites. We suggest that during the period before the Nile perch, large-bodied zooplankters like Cladocera and adult copepods were more abundant in the pelagic zone than at present, after the increase of Nile perch. We attribute the decline of large zooplankters to intense predation by *Rastrineobola argentea,* which became more abundant during 1980-1992 (*figs.* 1, 2).

Anoxia

Comparison of our measurements with earlier data (Talling and Talling, 1965; Talling, 1966; Ochumba and Kibaara, 1989; Ochumba, 1987) suggested that during the last 20 years the volume of hypoxic waters in Lake Victoria has increased, and stratification is more long-lasting. During 1950s-1960s Newell (1960) and Talling (1966) measured the depths of 1.0 mg/l DO isopleths between 38 and 75 m at the offshore zone.

During this survey, Talling recorded DO levels below 2 mg/l during January-June 1961. Hypoxic waters with dissolved oxygen below 4 mg/l were never recorded shallower than 38 m in offshore stations by Talling (1966; *fig.* 9). The similarity between thermal structure of the Kenyan and the Ugandan offshore zones presented by Hecky *et al.* (1994) make our comparative analysis of our data and Talling's record relevant.

Final verification is still lacking that the thermal structure of Lake Victoria was significantly changed after the 1960s. Nevertheless, the changes of bathymetrical distribution of dissolved oxygen (Hecky *et al.,* 1994) are not necessarily correlated to thermal structure. Due to the tropical conditions intra-annual climatic fluctuations are minimal and therefore water thermal gradients are small. Nevertheless, deoxygenation and thermal structure changes are two independent processes. Densities of suspended particles (algae) increased during the 1980s as we documented, and their size is smaller (Talling, 1966) therefore it is possible that back-scattering of light increased during the 1980s and resulted in a shallower thermocline (Mazumder and Taylor, 1994). Independently deoxygenation was enhanced by increased organic matter degradation. Two other factors which might be relevant to long-term changes in thermocline depth (shallower) are wind and air temperature (Hambright *et al.*, 1994). However, unavailability of a long-term climatological record makes this analysis impossible.

There are preliminary indications that the thermal gradients between the epilimnion and hypolimnion measured during 1990-1992 are sharper than those measured by Talling (1966), and also that the thermocline is now more shallow (Kaufman, 1992; Gophen *et al.*, 1993; Hecky *et al.*, 1994). Further comparative analysis of our data is needed for verification of thermal changes. The significant relationships among temperature, DO and pH minima (Gophen *et al.*, 1993; Ochumba *et al.*, 1994) indicate the long-term existence of a low oxygen hypolimnion in Lake Victoria.

Nutrients

The high levels of nutrients in deep waters (see also Lehman and Branstrator, 1993) were probably partly enhanced by higher sedimentation of organic matter (senescent algae) and partly by longer duration of anoxic conditions in the hypolimnion. We suggest that daily upward movements of hypolimnetic nutrient-rich waters (internal seiches) transport nutrients to the epilimnion as well. This upward nutrient flux is probably efficient because of the relatively low thermal gradients, *i.e.* low Relative Thermal Resistance (RTR) values in the water column: 7.0-24.0 range of maxima in the metalimnion and the epilimnion, and 0.0-3.3 in the hypolimnion (see also Gophen *et al.*, 1993). The high nutrient concentrations, low pH and low DO in the hypolimnion, together with the long period of stratification, support the hypothesis of effects of degradation of sedimented organics on these factors as well as release of nutrients from the sediments. Consequently, nutrient flux was probably enhanced from the hypolimnion to the epilimnion, increasing availability for algal production in the euphotic zone. Therefore, we suggest that the ecosystem perturbations (decline of grazing capacity, enhancement of nutrient loads) also included the internal dynamics of nutrients, leading to increased algal activity in the epilimnion.

Food composition of tilapias

Our results show that three common tilapiine species are not presently planktivorous as was reported 30 years ago (reviewed by Okeyo, 1989) and they now feed mostly on benthic items. These modified food habits may have been precipitated by the Nile perch invasion, as tilapiines were displaced by the perch from open water to the shallow refuges. In the shallows, benthic food items are available and consumed by the tilapiines, resulting in modified feeding habits.

Limnological modifications

Tropical Lake Victoria, like some other African lakes, has very little seasonal fluctuation in physical factors such as temperature and water level changes. Unlike temperate lakes where seasonal and daily physico-chemical fluctuations are major factors in lake dynamics, biological factors are much more influential in tropical aquatic systems (Kilham and Kilham, 1990). Lake Victoria has undergone profound changes of the biota and bathymetrical distribution of dissolved oxygen. Comparison of our data with those of Hecky (1993) and records from the 1950s-1970s and 1980s (Akiyama *et al.*, 1977; Hecky *et al.*, 1994; Ochumba and Kibara, 1989; Talling, 1965, 1966, 1987) indicated increased eutrophication in Lake Victoria as evidenced by the following changes: higher algal production, enhanced oxygen depletion and fish kill, a shift from dominance of diatoms to blue-greens, and a longer annual stratification period (Ochumba, 1987; Kaufman, 1992; Hecky *et al.*, 1994; Ochumba *et al.*, 1994). There are recent indications of increased nutrient inputs and higher algal productivity that started during the 1920s (Hecky *et al.*, 1993). Thus, the changes in fish community structure (*i.e.* a top-down effect) may have enhanced earlier bottom-up effects (nutrient inputs). The change in phytoplankton community structure that we observed in 1989-1991 relative to Talling's (1966, 1987) records and long term (1892-1972) analysis can be attributed to changes in nutrient dynamics (Hecky, 1993): increased fluxes of P (actual ambient concentrations are not measurable because of a very high rate of intake by algae) and N, decline of silica and lowering of N/P ratio in the loads (rain and catchment) which probably suppressed diatoms and enhanced blue-greens. Increased algal production and the often observed phytoplankton blooms were stimulated by higher P supply, immediately taken up by alga, and caused intensification of algal silica consumption (Ochumba and Kibara, 1989; Hecky, 1993). This resulted in depletion of availability of silicon and a decline in diatoms (Hecky, 1993). The ambient SRP concentration in Lake Victoria did not change during 1960-1990 because of the high rate of algal uptake. Nevertheless, the fluxes of SRP to algal biomass and consequently to bottom sediments were enhanced. The sequence of algal succession which started during the 1920s was later accompanied by fish community structure modifications caused by the Nile perch. It is distinctly possible that the shift from diatoms to blue-greens negatively impacted indigenous suspension-feeding haplochromine and tilapiine fishes. Nevertheless, Goldschmidt *et al.* (1993) documented blue-green consumption by haplochromine fishes prior to the perch invasion. However, the paleodynamics of diatoms (Hecky, 1993) indicated a decline of *Melosira* sp. and an increase of *Nitzschia acicularis* (1960-present) and *Cyclostephanos* sp. (1920-present with peak in 1960). Moreover, *figure* 9 in Hecky (1993) does not represent a dramatic change of sedimentary N: before 1920's ca. 12 mg N/g(sed) and during 1920-present 14 mg N/g(sed)(+17%). The change of sedimentary P was more significant: sedimentary P before 1950 was ca. 1.3 mg P/g(sed) and during 1950-present 1.7 mg P/g(sed)(+31%). If diagenetic change is negligible, Hecky's data indicate a significant change in P fluxes after 1950. Sedimentary C changes were insignificant.

On the basis of the above observations, we suggest that from 1950 to the present there has been a coincidence of two independent events with overlapping effects on the ecosystem: (1) increase of P load, with a consequence of enhanced algal production, decline of the N/P ratio in lake water because of higher P concentration and intensification of denitrification in the hypolimnion (Hecky, 1993), increase of blue-greens and decline of silica with decline of diatoms; (2) Nile perch invasion and haplochromine decline, and as a consequence, suppression of suspension-feeding capacity by the fish community. Elsewhere (Kaufman, 1992; Kaufman and Ochumba, 1993) we have alluded to the possibility that enhanced algal production and concomitant oxygen depletion could itself have contributed to the demise of benthic haplochromines. In any event, the overall outcome is eutrophication through accumulated organic particulates and oxygen depletion. The thermal structure independently changed also as indicated by shorter turnover (ca. one month a year) and shallower depth of the thermocline (Gophen *et al.*, 1993; Ochumba *et al.*, 1994).

The food web structure

The two major modified ecological factors involved in the food-web dynamics of Lake Victoria from the 1950s to the 1990s changed energy flow patterns in the lake. In 1960-1961, deoxygenation to less than 1 mg/l DO lasted from January to June, but anoxia was not shallower than 54 m (covering a bottom area 2.5 times smaller than present) (Talling, 1966), and zero levels of DO were rarely recorded (February), and most (0-54 m) of the water column was occupied by dense population of pelagic, suspension-feeding haplochromines. Their grazing capacity, combined with that of herbivorous zooplankton, was sufficient to prevent accumulation of organics and algal blooms rarely occurred. During this period, densities of the prawn, *Caridina nilotica* were probably lower than at present (Goldschmidt *et al.*, 1993). Primary production was mostly channelled to fish and zooplankton grazing, and sedimented organics were utilised by the low density populations of *Caridina nilotica* and bottom fauna. From the beginning of the 1980s, after the upsurge in numbers of Nile perch, grazers were eliminated from the ecosystem (fishes by the perch and zooplankton by *Rastrineobola*) and, due to changes in nutrient dynamics, blue-greens became dominant and primary production increased. The greatest trophic radiation known in one water-body in the world faced catastrophe, and the food web structure was changed. As a result of these changes the split of the ecosystem between the two chains was strenghened: (1) the epilimnion (0-34 m) (*table* 6), with dense, small-sized phytoplankton assemblages dominated by blue-greens, low concentrations of large-bodied grazer zooplankton, high densities of Nile perch and *Rastrineobola argentea* and haplochromine biomass close to zero. In this epilimnion the primary production is now much greater than grazing capacity and excess organics flux to the hypolimnion. (2) The second chain is a low oxygen hypolimnion (34 m-bottom) (*table* 6) where populations of *Caridina* proliferated, probably due to the high tolerance of this prawn to low DO levels. During our cruise in December 1990, we used the Remote Operated Vehicle (ROV) (submersible equipped with video camera with onboard monitor) and videotaped high densities of live *Caridina* in the deoxygenated (<1.0 mg/l DO) hypolimnion, with numerous dead *Rastrineobola* on the bottom (Kaufman, 1992). Only a minor part of *Caridina* biomass is eaten by Nile perch at the hypo-epilimnion interface. The deoxygenated hypolimnion is a refugium for the prawns which feed on degraded organic matter (detritus) which falls as sediment into the hypolimnion. The hypolimnetic food chain components are: dead phytoplankton mass and fish (mostly *Rastrineobola argentea*), bacteria and *Caridina*. The nutrient supply to the hypolimnion is from suspensoids settling from the epilimnion and nutrients released from bottom sediments.

As a result of the destruction of the fish biodiversity and changes of nutrient dynamics, not only was the eutrophication process enhanced, but ecosystem instability is predicted. Relative to the known long-term stability of the lake ecosystem until the 1980s, extreme fluctuations are now to be expected as a new norm. Annual primary production in the euphotic layer (7.5 m depth) for the whole lake during the 1990s was calculated as: 1990: $1.4\text{-}4.4 \times 10^7$ tonnes of carbon (Hecky, 1993); 1992: $3.8\text{-}11.3 \times 10^7$ C (Lehman and Branstrator, 1993); 1992: $7.9\text{-}19.6 \times 10^7$ C (Mugidde, 1993). Talling's measurements indicated an annual fixation of carbon in the euphotic zone (15 m depth) of the whole lake of $1.5\text{-}1.9 \times 10^7$ t (Talling, 1965, 1966, 1987). Conversion of primary production O_2 values to carbon were done by $12/32 = 0.375$ factor. The overwhole range of 1990s annual values of carbon fixation is $1.4\text{-}19.6 \times 10^7$ t of C, (median of 1.5×10^7 t of C).

The present fishery, mostly of the piscivorous Nile perch and the zooplanktivorous *Rastrineobola argentea*, is about 50×10^3 t of carbon (according to 10% C of fish wet-weight) per year (ca. 0.05% of primary production). During the 1960s and early 1970s the annual fishery was about 2.5×10^3 t of carbon/y (0.01% of the photosynthetically produced carbon), i.e. higher fish biomass as grazer haplochromines were present in the water, and thus greater grazing capacity was maintained than is possible at present.

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