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Feeding Habits of Tilapias and the Limonology of Lake Victoria

Final Report: 1989-1991

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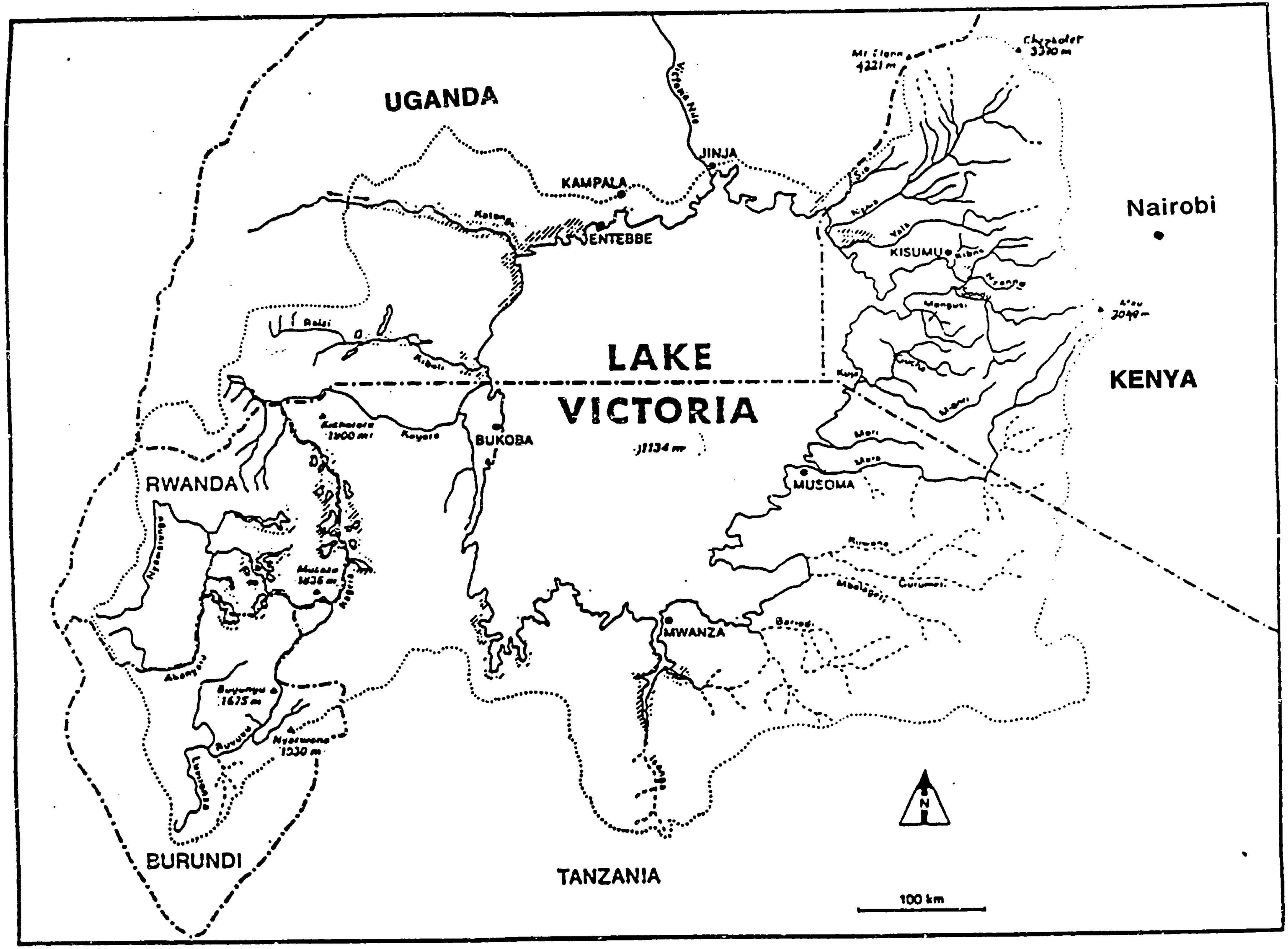
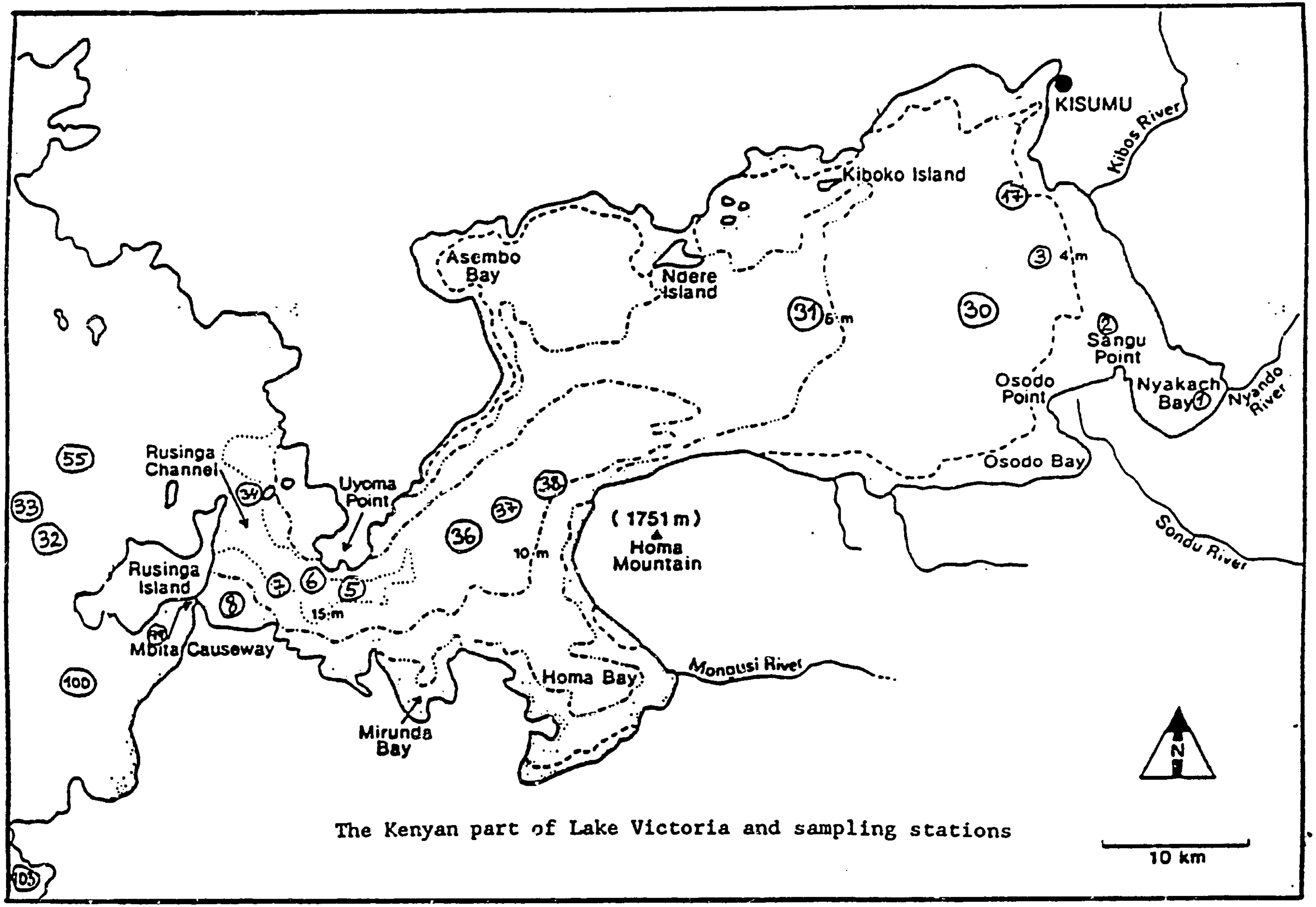
In one of our field trips to the lake we lost an outstanding scientist and a good friend, Prof. Peter Kilham. Peter died in Kisumu. so close to Lake Victoria. the lake he loved, studied, and contributed so much to understand its ecosystem. We dedicate this report to the memory of a friend and colleague, Peter Kilham.



Lake Victoria and its Drainage-Basine



The Kenyan part of Lake Victoria and sampling stations

INTRODUCTION

During the period of 1/7/1988 and 31/6/1989, the Israeli Principal Investigator, Prof. M. Gophen, has made two working visits to Kenya. The first, December 1988 and the second, March 1989. The second visit was cooperated with the NOAA-ROV team for the USA. Samples were collected by two methods: 1.) Transportation by car along the beaches where we hired boats from local fishermen as well as buying fish from them. 2.) During the second visit we participated in a cruise with the ICIPE R/V "Dragonfly" and collected samples at all stations in the Kisumu Bay and the deep water sites at offshore areas.

During the cruise in March 1989 we collected samples and the following parameters were analyzed: phytoplankton, zooplankton, nutrients (N and P forms), pH, DO, conductivity, secchi-disk, and fish (TL, SL, total weight, viscera weight, gut content).

In March 1989 we also conducted feeding experiments with several _Tilapia_ species in the Kisumu Laboratory and Mbita-Point ICIPE Institute.

Between December 1988 and March 1989 the local team of Kisumu Laboratory in Kenya sampled fish and on several occasions plankton samples were also taken. These type of activities were also carried out before December 1988, and after March 1989. The Israeli team (two PI's, Gophen and Pollingher and a technician) analyzed gut content, phytoplankton, zooplankton samples and samples from feeding experiments. The nutrient analyses were also carried out in the Kinneret Limnological Laboratory, Israel.

This report presents results from fish measurements and gut contents, phytoplankton and zooplankton counts, feeding experiments, nutrients and physical measurement, all collected between 1/7/1988 and 31/6/1989.

During the second half of 1989 and 1990 and the first half of 1991, Gophen visited Lake Victoria, Kenya five times: in two of his visits he accompanied the ROV team from Michigan and Boston and in the last trip R. Hecky from Canada joined and collected core in station 99. During the cruises with the ROV (Remote Operated Vehicle) we made observations in the anoxic hypolimnion and Haplochromine refuges in the shallows. Most of the project money for the Kenyan co-partners became available just at the end of 1990. Therefore the Kenyan team continued to maintain a monthly sampling cruise during 1991 and the beginning of 1992. At the end of 1992, the data of physical measurements from end of 1990, 1991, and beginning of 1992 was transferred to M. Gophen for evaluation and finalized the present report.

The PI's, M. Gophen, P. Ochumba and U. Pollingher presented results from Lake Victoria AID-CDR-project in several international meetings: "INTECOL" in Japan, "Ancient Lakes Speciation" in Belgium, "Aquaculture/Schisostomiasis" in The Philippines, "Fish removal" in Finland, "species changes in African Lakes" in UK, "SIL" in Spain, "Socio-economics aspects of Lake Victoria Fisheries" in Burundi, "Biodiversity, Fisheries and the Future of Lake Victoria" in Uganda, "Lake Conservation" in P. R. China. As an outcome of the research funded by US-AID-CDR in Lake Victoria 9 publications in international and national journals were published.

The final report is presented in five chapters: Part A- Fisheries overview and general characteristics of Lake Victoria ecological modifications as a result of the Nile perch (*Lates niloticus*) introduction; Part B- describe the ecological alterations in the Lake Victoria drainage basin and the fisheries, as analyzed for the project evaluations; Part C- deal with the phytoplankton and zooplankton samples analyzes, fish feeding: *Tilapias* experiments and *Tilapias* food sources as well as water chemistry and stratification regime. Part D- summarized the physical measurements of temperature, conductivity, DO, and pH taken during 1990-1991 and the beginning of 1992, and conclusive remarks on stratification, and the biota of the lake. We present a comprehensive abstract and one reference list for all 4 parts.

ABSTRACT

Lake Victoria is the second largest lake in the world: surface area - 68,800 km^2; volume - 2.8 x $10^{12}m^3$ and water residence time is 23.4 years. Most (85%) of the water input (1 x $10^{11}m^3$/year) is direct rainfall and the rest is river inflow. Water loss from the lake is mostly by evaporation. Temperature and light have only a limited influence on the development of the phytoplankton. Upwelling and mixing have an important role in nutrient supply. At the end of the 1950's and early 1960's, specimens of Nile perch were removed from lakes Albert and Turkana to Lake Victoria not without scientists concerns. Twenty years later, this became a major component (>50%) in catches. The Nile perch invaded throughout the entire lake and became dominant from early 1980's. Prior to the invasion of the Nile perch, the lake was densely populated by more than 400 endemic species of Haplochromine cichlids. As a consequence of Nile perch piscivory, the endemic haplochromids as well as 6 introduced and 2 native species of Tilapia were severely suppressed. Consequently, non-grazed algal matter accumulated and anoxia was enhanced. Following the alterations of fish species composition fisheries were changed as well: haplochromid catches declined, those of perch and Rastrineobola increased and total landings significantly increased.

The phytoplankton is presently characterized by a high abundance of coccoid cyanophytes accompanied by small filamentous forms (Lyngbia spp.) and diatoms (Nitzchia and Melosira spp.). The chlorophytes are represented by many species of Chlorococcales and Desmids. Few species of Dinophyta and Cryptophyta were observed. The zooplankton densities are

relatively low and the body sizes of the organisms are small. Five species of copepods (Cyclopoids and Calanoids) were found. The different life stages of copepods were in greater numbers in deep layers, except for nauplii which were also abundant at 1 m, during daylight hours. Similar distribution was represented by six species of Cladocera. Rotifera (about 10 species), were found mainly in the upper layers. In feeding experiments we observed predation of zooplankton by Tilapia nilcticus, Tilapia zillii and Tilapia variabilis. In contrast, these species when sampled in the lake, have a gut content comprising mainly of bottom components.

Lake Victoria, has undergone successive dramatic changes since the 1920's; intensive non-selective fisheries; extreme changes in the drainage basin of vegetation, industrialization, agricultural development, dams, etc; introduction and invasion of exotic fish species that led to the destruction of the native and endemic components followed by a progressive build-up of physico-chemical changes in the lake environment. Recent studies of Lake Victoria have identified substantial increases in chlorophyll concentration and primary productivity as well as decreases in silica compared to values, measured 30 years ago. Present sulfate concentrations (0.1 mg/1) are lower than the lowest values reported from other large lakes in the world. There has been a shift in the phytoplankton community towards dominance of blue-greens. The zooplankton densities are relatively low. Anoxic waters have recently been found at shallower depths than previously reported suggesting significant increase of oxygen demand in the seasonally formed hypolimnion. Algal blooms have also been enhanced in Lake Victoria. Fishery management in Lake

Victoria has led to a shift in the fishery from a multispecies (about 400 haplochromids) to only two major exotic species Lates niloticus and Orechromis niloticus and the native Rastrineobola argentea.

Lake Victoria presently exhibit traditional symptoms of eutrophication including decreased water transparency, blue green blooms enhancement, elevated phosphorous concentrations and hypolimnetic deoxygenation. Changes in the phytoplanktons community altered available food sources to primary consumers but these grazers were considerable suppressed by higher trophic levels. Lake Victoria fish species are threatened by the worsening conditions in the lake itself and from the rivers in the catchment area. It is suggested that urban, agricultural and industrial pollution climate change and the introduction of predatory Nile perch and competitive Tilapiine species are the major factors for the deterioration of Lake Victoria's ecosystem. Oreochromis esculentus is almost extinct and many more haplochromid species are endangered. Current fisheries legislation and operations aimed at reduction of soil erosion and sedimentation in inflowing rivers in the catchment area are insufficient for significant improvement of the present deterioration of water quality. Localized manual harvest of papyrus, shoreline dredging and sandmining did not sufficiently improve lake conditions.

6A

Part A: Fisheries Overview and Limnological aspects of the Ecological Modifications

INTRODUCTION

Lake Victoria, the second largest lake in the world, and a source livelihood for over thirty million people in Kenya, Uganda and Tanzania is in a state of ecological transition. In the past thirty years, the Lake Victoria ecosystem has undergone one of the most profound ecological disruptions ever observed (Ochumba et al., 1992). The severity of the disturbance is the result of several inter-related forces, including the introduction of alien species, overfishing and increased nutrient inputs to the lake. The most decisive impacts was attributable to the introduction of Nile perch (Lates niloticus) and Nile tilapia (Oreochromis niloticus). Nile perch consumed most of the native fishes, eliminating them from the ecosystem and bringing most of them to commercial extinction (Barel et al., 1985; Ogari and Dadzie, 1988 and Ogutu-Ohwayo, 1990). The Nile tilapia outcompeted other tilapiine species, changed their feeding from phytoplankton to benthic organisms. These actions slightly altered the water quality and food chain connections in the lake.

There is evidence that limnological processes of the lake has also changed over the period of the transformation of the fishery. Current studies have identified substantial increases in chlorophyll concentration and primary production (Talling, 1987; Ochumba and Kibaara, 1989). Silica concentrations in the lake have dropped by an order of magnitude (Hecky and Bugenyi, 1992). Present sulfate concentrations are lower than the lowest values ever reported from other large lakes of the world. There has been a shift in the phytoplankton community towards dominance of blue greens. The zooplankton densities are relatively low and the body sizes of the organisms are small. Anoxic water, have recently been found at shallower depths (Ochumba, 1990) than previously reported in Lake Victoria suggesting significant increase of the oxygen demand in the seasonally formed hypolimnion. Periodic fish kills and algal blooms further raises concern about the environment of Lake Victoria. These discoveries have major implications for fisheries management, biodiversity, conservation and human health.

Historical Overview of Impacts on the Lake Victoria Fish Assemblages (Figures 1-9)

The first major impact on the Lake Victoria ecosystem came with the advent of modern gillnets in the 1920's (Graham, 1929). Indiscriminate fishing practices (Fryer and Iles, 1972) combined with a poor choice of mesh size led to the rapid decimination of tilapia food species *Oreochromis esculentus* and the potamodromous carp *Labeo victorianus* (Garrod, 1961). Four alien tilapiine species were introduced in the 1950's to replace the native food species. Between 1954 and 1961, an attempt was made to augment the limited success of the tilapiine introductions by bringing in Nile perch (*Lates niloticus*) (Stoneman and Rogers, 1970). Nile perch can reach nearly 2 meters in length and 300 kilograms in weight, and in Lake Victoria they grow faster than anywhere else in their present range (Lightvoet and Mkumbo, 1990). At first, Nile perch constituted less than 2% of the fisheries landing, and was cursed by the native fishermen because it destroyed their nets. An oily fish, it stubbornly resisted sundrying, the standard processing methods. Due to lack of refrigeration, it had to be smoked or deep-fried and both required large quantities of wood, which accelerated deforestation in the Victorian catchment basin.

Graham (1929) originally speculated that the introduction of a large predator could convert the enormous biomass of haplochromine cichlids into a more palatable and marketable form. The hypothesis proved sound. A massive eruption of the Nile perch fishery occurred in the lake 1977 in Uganda, 1980 in Kenya and 1987 in Tanzania (Figs. 3, 8) (CIFA, 1990). This was concurrent with 10,000 fold reduction in the abundance of haplochromine (Witte et al., 1992), and the abrupt disappearance of at least half of the cichlid species from the lake (Figs. 2, 6). Fishermen could not longer afford to spurn the perch, and with new government strategies to finance ships, refrigerated transport and Nile perch processing plants, a lucrative new fishery was born (Reynolds and Grebovall, 1988). Today Nile perch is thought of as a savior, (Fig. 5) and is heavily exploited by trawlers, longliners, beachseiners and gillneters. Along with the upsurge in Nile perch came lesser increases in the fisheries for the introduced tilapia Oreochromis niloticus, (Figs. 4, 7) and the native Cyprinid Rastrineobola argentea (Figs. 1, 9) (Ogutu-Ohwayo, 1990a). The latter is the target of a light-fishery that nightly decks the lake with streams of canoes bearing kerosene lamps creating a remarkable illusion known as "The City on the Lake."

<u>Nile perch effects on haplochromines</u>

Prior to the introduction of the Nile perch, haplochromine fishes were the economic basis for fishery as well as the dominant protein resource for human consumption. The ecological adaptation of the haplochromine fishes was demonstrated by the existence of many trophic groups: piscivores, insectivores, molluscivores, phytoplankton feeders, paedophages, benthic crustacean feeders and macrophyte feeders (Greenwood, 1974; Barel et al., 1977; Witte and Oijen, 1990). Trawl surveys and landings during the 1970's in Lake Victoria (Kudhongania and Cordone, 1974; Benda, 1981; Muller and Benda, 1981) indicated large stocks of haplochromines and several endemic fishes. Trawl fishing surveys and landing statistics in the 1980's and 1990's (Okemwa, 1984; Asila and Ogari, 1988; Cifa, 1990 and Rabuor, 1990) indicated that the endemic cyprinids, catfishes, lungfishes and mormyrids were too scarce to form a viable fishery. Consequently, it was concluded that both endemic species, haplochromines and the tilapias in Lake Victoria were massively extincted (Balon and Bruton, 1986; Ribbink, 1987; Kaufman, 1991 and Witte et al., 1992). The decline of the haplochromine not only resulted in a reduction of the commercial catch, but also disrupted the food chain trophodynamics in the lake ecosystem. These fishes played a major role in phytoplankton and detritus grazing and when they were suppressed, algal material gradually increased (Ochumba and Kibaara, 1989) and accumulated in all depths but mostly in deep layers. The decomposed algal cells reduced oxygen in deep waters.

Owing largely to the work of Fish (1957) and Talling (1965, 1966) Lake Victoria's limnology were better understood than its fishery biology during the time before the Nile perch introduction. Lake Victoria' shallow depth (<100 m) and young age (ca 10^6 years total, but nearly totally dryed only 14,000 years ago) Kendall (1969) set it apart from the much deeper, older lakes in the eastern African branch of the Rift Valley. During the 1960's Lake Victoria lacked a permanent hypolimnion. Instead, the lake underwent two cycles of stratification and mixing that corresponded to the long and short rainy seasons. In recent years, increasing international attention has been focused on the lake as the fishery has been undergoing a radical transformation because of the success of introduced Nile perch (Lates niloticus) and the Nile tilapia (Oreochromis niloticus) (Coulter et al., 1986 and Ogutu-Ohwayo, 1990a).

There is evidence that the nutrient chemistry of the lake also changed over the period of the transformation of the fishery (Hecky and Bugenyi, 1992). A comparison of Talling (1966) stations' in nearshore Uganda waters between 1961 and 1988 show no change in total phosphorous (Hecky and Bugenyi, 1992) a ten fold increase in chlorophyll concentration. Large bluegreen algae are abundant in the open lake (Ochumba and Kibaara, 1989). Frequent localized fish kills have been recorded in nearshore shallow waters in association with temporary anoxic conditions (Ochumba, 1987, 1989). The evidence for increased algal biomasses in Lake Victoria is worrisome as this eutrophication could lead to increased oxygen demand in the lakes deep waters and decrease the hypolimnetic volume habitable by fish during seasonal stratification.

Our study in Lake Victoria, Kenya was designed to test the hypothesis that anoxia is persistent throughout the year, to examine the annual mixing and determine the eutrophic status of the lake since the introduction of nile perch. In the 1950's, when stratification formed during the long and short rainy seasons, the oxycline was found at about 50m depth, beneath which oxygen levels dropped occasionally to as low as 1mg/L. Fish life flourished in the lake's deeper waters at all times of the year. In the 1980's and 1990's the situation for the June-August mixing seemed worse than that of the 1950's. Severe deoxygenation at shallow depths, (Ochumba, 1989) indicated that large volume of Lake Victoria waters is incapable of sustaining aerobic life. A major factor is the elimination of Cichlids species that formerly helped safeguard anoxic conditions within the lake by cropping phytoplankton. Therefore, the Nile perch and commercial fishing activity have deciminated the algal grazing fish species which resulted in a significant increase in organic detritus into the hypolominion. Increased microbial processing results in oxygen depletion in the hypolimnion (Kilham and Kilham, 1990a). Lake Victoria Kenya was studied during 1989-1992. Limnology and fisheries data available in the literature before and after the Nile perch introduction were selected for this study, from Fish (1957), Newell (1960), Talling (1966), Kitaka (1971), Akiyama et al. (1977), Melack (1979), LBDA (1984), Ochumba and Kibaara (1989), Hecky and Bugenyi (1992), and Calamari et al. (1992).

Description of the study area

Lake Victoria is the worlds second largest freshwater body by area (68,800 Km^2 shared between Kenya, Uganda and Tanzania; max. depth 79 m, residence time 23.4 years), altitude 1,134 ASL, location 0°20'N - 3°0'S; 31° 39'W - 34° 53'E, maximum length 400 km and maximum breadth 240 km. The shoreline is 3,440 km long and is indented with shallow bays, sandy, muddy and rocky beaches. There are number of large islands whose shoreline are as varied as those of the mainland. The catchment area is 263,000 km^2 and the drainage basin is covered by grassland savanna, agricultural crops, urban centers and forested mountains of Rwanda and Burundi. The Kagera and Nzoia are the main inflowing rivers and the outflow is the River Nile. The lake is seasonally stratified (Fish, 1957; Talling, 1966) and wind is the driven force that determines the annual thermal structure cycle and water column mixing (Newell, 1960 and Talling, 1969). The long water residence time increases vulnerability to long term changes caused by environmental modification in the catchment area. Rainfall onto lake surface accounts for about 85% of the water input, and evaporation for over 80% of the output (Rzoska, 1957).

MATERIALS AND METHODS

A Hydrolab surveyor II connected to an SVR 2 display unit and a 4041-Circulator assembly was used to measure monthly (1990-1992) temperature, pH, dissolved oxygen, conductivity, and depth at stations 32, 33, 34, 99, 100, 103 (see map in Part C). These parameters were used to determine the annual stratification and anoxic depths. Water transparency was estimated with 20 cm diameter black and white secchi disc. Samples for chemical analysis were collected in polythene bottles using a wildco sampler and stored at 4°C in a cooler box and analyzed within 3 days. All water samples were filtered through fibre filters. Chemical determinations were made according to the methods of the America Public Health Association, ALPHA (1985) using a Pye Unicam SP 600 spectrophotometer. Chlorophyll-a concentration was measured according to the methods of Volleweider (1974) and Melack (1979).

We conducted systematic visual reconnaissance fisheries survey of Lake Victoria water column and benthos with a Phantom 300 remotely operated vehicle (ROV) and Impulse 2800 Sonar system. Fishing trails were done by trawling with KMFRI RV UTAFITI. Meteorological data was collected onshore near station 34 at Mbita Point.

RESULTS

The results of pH, temperature, conductivity and DO at stations 32, 33, 34, 99, 100 and 103 are presented on Figures 10-15. It appears that, coincident with the Nile perch explosion, came a violent change in the physical conditions of Lake Victoria. Our results show that the lake is stratified for the entire year. Seasonality is still apparent, but mixing is restricted to periods during June, July and August when the oxycline, though persistent, will at least sink to about 50 meters. The region between 50 m and 20 m is subjected to year round severe deoxygenation. During the study, extensive areas of Lake Victoria at the bottom were covered by anoxic waters which moved onshore and into the gulfs and bays freely as internal water mass motions driven by winds, currents and seiches. These events were associated with extensive fish kills.

Conductivity, secchi depths, and pH had distinctively marked patterns at various sampling stations. There was a decrease in conductivity from the shallow station 36 to the deep open lake stations (100, 103). The measured secchi depth and pH values were lower than previous studies. Results of our study compared to others (Table 1) show that Lake Victoria exhibits signs of eutrophication, including decreased transparency, biomass of blue green algae, elevated nutrients concentrations and hypolimnetic oxygen depletion. Substantial increases in chlorophyll (x10) and primary productivity (x3) and substantial decrease in silica concentrations (x10) were observed. Sulfate concentrations are x100 lower than the lowest concentrations measured in the large lakes in the world. There has been a shift in the phytoplankton community towards blue green species, fewer green algae and diatoms. The zooplankton community is presently dominated by small bodied species of copepods with low densities of cladocera.

Remotely operated vehicles (ROVs) reconnaissance dives in the open lake revealed extensive areas littered with dead fishes and invertebrates. The results confirmed the presence of severe oxygen depletion in the hypolimnion, as well as oxycline that was shallower than before. The volume of Lake Victoria may be incapable of sustaining aerobic life. Systematic data from the portable fish finder indicated that Nile perch and bigger fish jammed up into Rusinga channel (station 34) the gulf (station 36) and bays. During the short mixing periods, the Nile perch migrate back into the open lake. We observed the presence of dense populations of active shrimp *Caridina nilotica* below the oxycline. This may suggest that the bottom waters of Lake Victoria may be almost permanently deoxygenated and therefore out of bounds for a commercial fishery.

DISCUSSION

The main activity of people in the Lake Victoria catchment area is agriculture. Consequently, great amounts of silt and sediments from erosion of the cultivated areas, together with industrial and urban wastes are washed into rivers and ultimately reach the lake. These activities can be traced as far back as 1920s when large forested areas were cleared for tea, coffee and sugar plantations. As the whole region lacks a unified agency for watershed management for Lake Victoria, increased soil loads, tree logging and other activities remain unchecked, (Calamari et al., 1992). Since conditions in the catchments area favor high water discharge, pollution has no direct impact on the aquatic communities of the rivers and eventually settle in the lake. High water flow and the length of the rivers make pollutants travel long distances. In the absence of precise data on loads, the degree to which pollutants might be harmful cannot be accurately assessed. Records of environmental changes in the catchment area suggest a series of abrupt and severe changes in the aquatic of Lake Victoria during the 1980's

The above explanation is not the only explanation for the astonishing turn of events on Lake Victoria. A major factor is the elimination of Cichlids species that formerly helped to safeguard element conditions within the lake by cropping phytoplankton. The introduction of the Nile perch (Lates niloticus) eliminated the major part of haplochromine populations (Witte et al., 1992) resulting in the decline of grazing pressure on algae. Algal matter is now incompletely removed, accumulating in the lake and enhancing anoxia in the open lake. Comparison of historical limnological observations with modern condition indicates that the present situation is quite different in structure and function from what it was in the 1950's and 1960's (Hecky and Bugenyi, 1992). All these changes can be attributed to increased algal growth compared to 30 years ago. However dramatic changes in the 1960's were coincident with both the introduction of Nile perch and exotic tilapiines and with record high water levels on Lake Victoria (Welcomme, 1964, 1970). The increased nutrients may indicate widespread basin disturbance, probably related to increasing land use, is causing eutrophication of Lake Victoria. But as nutrient cycles in tropical lakes are controlled by organisms in a much greater extent than temperate lakes (Kilham and Kilham, 1990b) thereby reducing the impact of watershed.

Recent changes in climate may have altered water column structure and caused mixing patterns to favor development of blue green algae and the loss of oxygen in the bottom waters of Lake Victoria (Kling, 1992). For Lake Victoria, the rainy seasons, floods, stratification, upwelling and rising lake levels may have direct effects on organisms and nutrients cycling (Melack, 1979). The coexistence of the two classical ecoforces known in limnology as "top down" and "bottom up" processes in regulating the structural dynamics of large lakes is probably relevant to Lake Victoria. The hypothesis of "top-down" direction presently suggested as higher impact. Predation by Nile perch altered the food web, destroying the detritivore and benthic insectivore fish assemblages, and thus terminating recycling from benthos to the water column (Witte et al., 1992).

CONCLUSION

Lake Victoria has undergone dramatic alteration in recent years through a combination of eutrophication, species introductions and climate change. The effects of the introduced Nile perch alone are astounding and further changes are likely. However, exploitation of industrialized commercial fishery and international marketing and distribution network (Reynolds and

Grebovall, 1988). The open question now is to what extent is Nile perch fishery sustainable under the altered conditions in the lake? This will depend on the availability of the Nile perch forage as a predator and the way the forage species and the man induced changes in the environment are managed. Major food web changes in Lake Victoria are likely to continue. The population of Nile perch is heavily dependent on cannibalism at the moment (Ogari and Dadzie, 1988) and crash of the fishery has been predicted (Beadle, 1981; Ogutu-Ohwayo, 1990). The interaction of trophic structure with water quality has been hypothesized to have led to a decrease in water phytoplankton abundance through a trophic cascade effects in some large lakes (Scavia et al., 1986; Lehman, 1988). Only further research will resolve the cause of the increase in algal biomass in Lake Victoria.

Urban, agricultural, agro-based industries, climate change and the introduction of Nile perch and competitive tilapiine species are the major factors for the deterioration of Lake Victoria's ecosystem. Oreochromis esculentus, O. variabilis and over 200 haplochromine species are commercially extinct and many more are endangered. Current fisheries legislation and operations aimed at reduction of soil erosion and sedimentation in rivers and the catchment area are insufficient to improve the lake's water quality. It is probably impossible to completely eliminate the Nile perch from Lake Victoria (Marten, 1979 a,b), but it is urgently required to reduce algal matter in the water content. It has been found that large bodied cichlids are less preyed by Nile perch (Ogari, 1985 and Ogutu-Ohwayo, 1985, 1990b). Therefore we propose to develop techniques of rearing phytoplanktivorous and detritivorous large bodied cichlids in protected bays or half-open lagoons and release them into the entire lake when they are enough not to be preyed upon by Nile perch.

Figure Legends:

Figs 1-9: Fisheries statistics (annual landing- metric tones) in Kenyan part of Lake Victoria during 1968-1991: 1) Rastrineobola; 2) Haplochromine; 3) Lates niloticus; 4) Tilapias; 5) Total; 6) Haplochromine vs. total; 7) Tilapias vs. total; 8) Lates niloticus vs. total; 9) Rastrineobola vs. total.

Figs 10-15: Conductivity, pH, DO, and temperature profiles, measured monthly in stations 32,33, 34, 99, 100 and 103 during 1990-1992.

Table 1. Comparative limnological data from various authors on Lake Victoria (ranges are given).

Year	1966	1977	1979	1984	1989	1990
Phosphate phosphorus (PO_4-P) ($\mu g/l$)	7.0-120	0.1-122		0.2-75	4.0-37.0	0.1-19
Nitrate nitrogen (NO_3-N) ($\mu g/l$)	10.0-112	0.5-122	0.16-0.18	21-237	0.1-513	1.0-30
Sulphate sulphur (SO_4-S) (mg/l)	0.4-4.0			0.1-5.0		
Silicate silica (SiO_2-Si) (mg/l)	4.0-8.0	0.2-3.0	2.0-7.9	0.1-7.6		0.06-0.72
Sechi disc transparency (m)	1.0-3.9	1.2-2.0		0.35-2.4	0.2-2.1	
Primary productivity mg(O_2/m^3)	100-130		400-600		180-600	100-1400
Chlorophyll concentrations ($\mu g/l$)	0.5-22.3	2.1-8.5		1.8-23.5	8.0-120	35.8-115.2
Algal dominance	diatoms	diatoms	diatoms	cyanophytes	cyanophytes	cyanophytes
Zooplankton dominance		copepods		Thermocyclops		

Sources: 1966 - Talling, 1966; 1977 - Akiyama et al. 1977; 1979 - Melack, 1979; 1984 - LBDA, 1984; 1989 - Ochumba and Kibara, 1989; 1990 - Hecky and Mungoma, 1990.

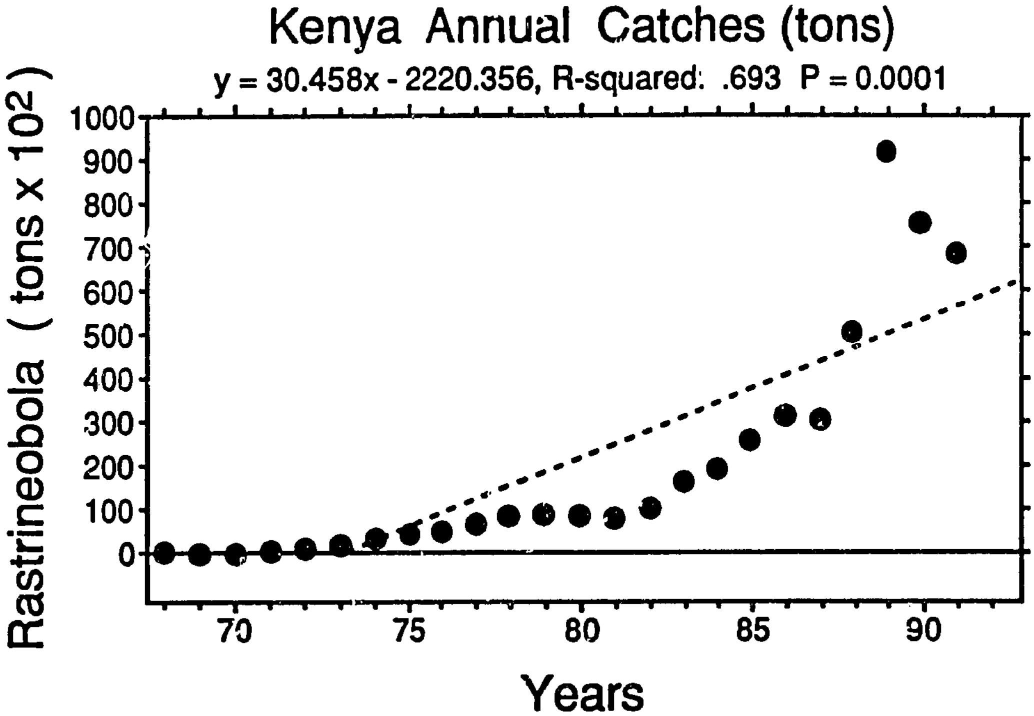


Fig. 1: Annual catches (tones) of Rastrineobola in Lake Victoria, Kenya, during 1968-1991.

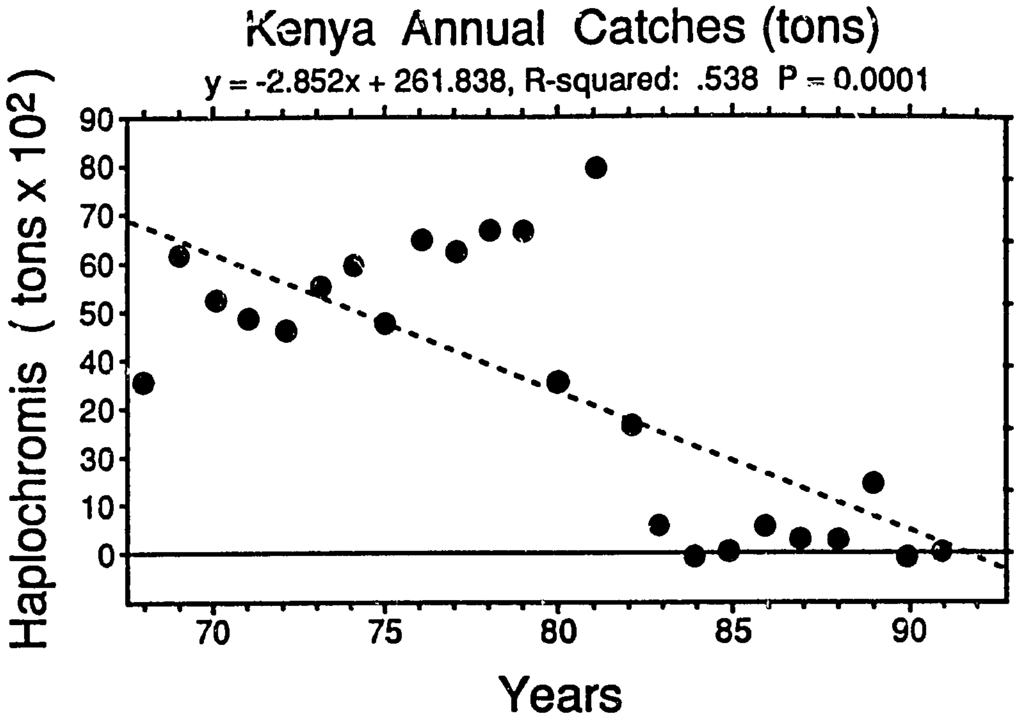


Fig. 2: Annual catches (tones) of Haplochromis in Lake Victoria, Kenya, during 1968-1991.

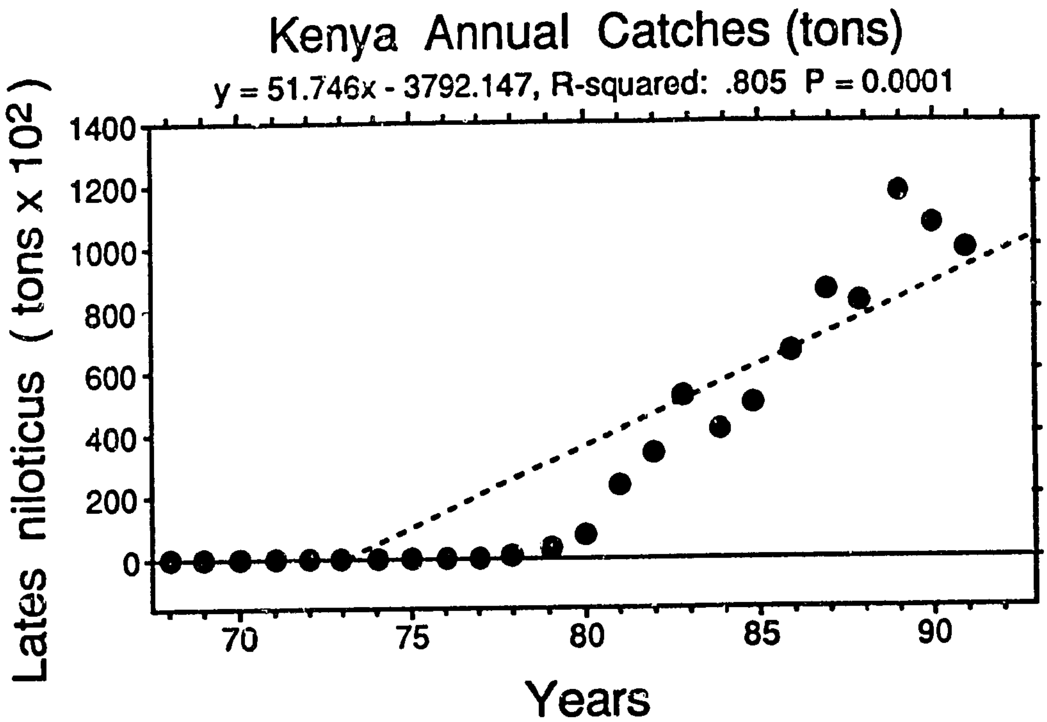


Fig. 3: Annual catches (tones) of Nile Perch (*Lates niloticus*) in Lake Victoria, Kenya, during 1968-1991.

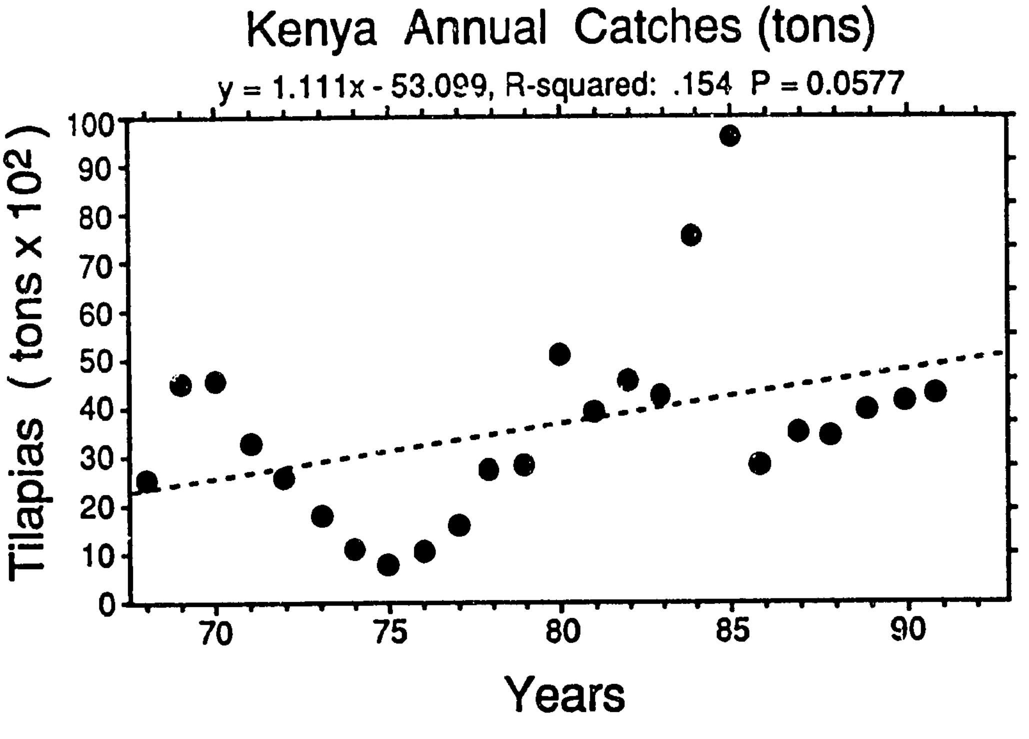


Fig. 4: Annual catches (tones) of Tilapias in Lake Victoria, Kenya, during 1968-1991.

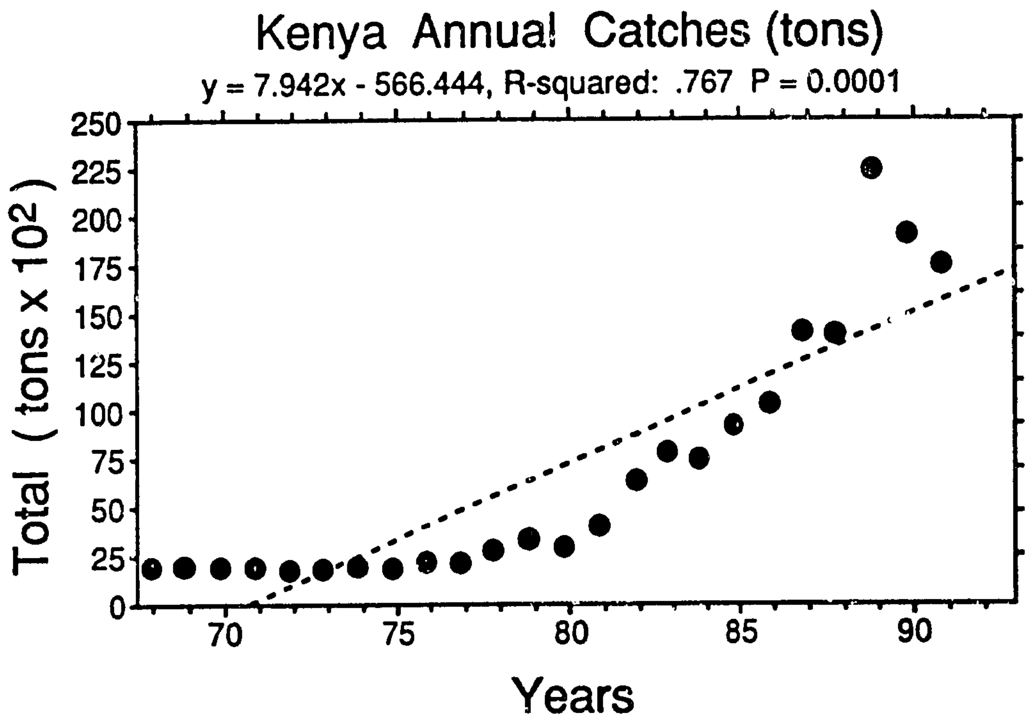


Fig. 5: Total annual catches (in thousands tones) in Lake Victoria, Kenya, during 1968-1991.

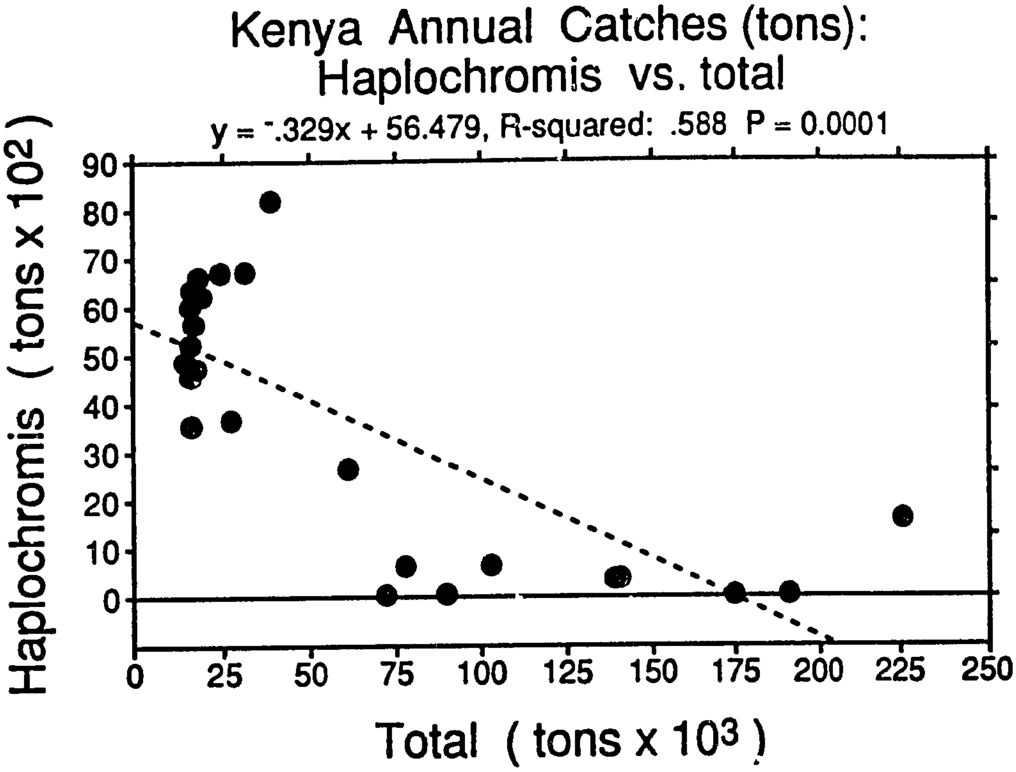


Fig. 6: Annual catches (tones) of Haplochromis vs. Total, in Lake Victoria, Kenya, during 1968-1991.

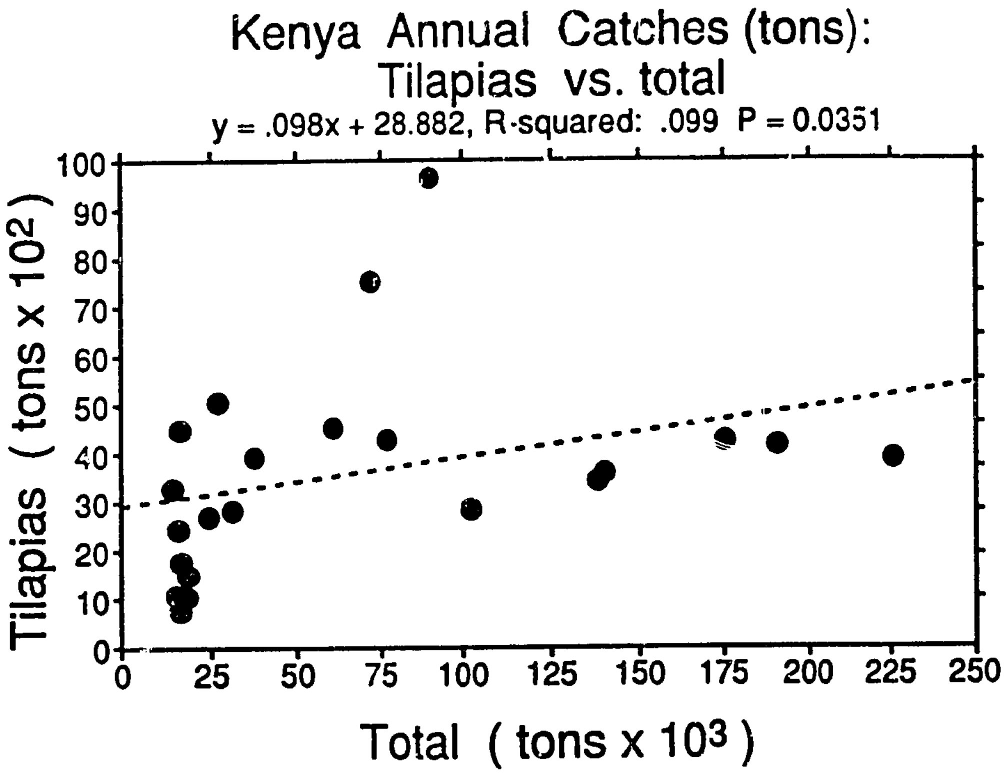


Fig. 7: Annual catches (tones) of Tilapias vs. Total, in Lake Victoria, Kenya, during 1968-1991.

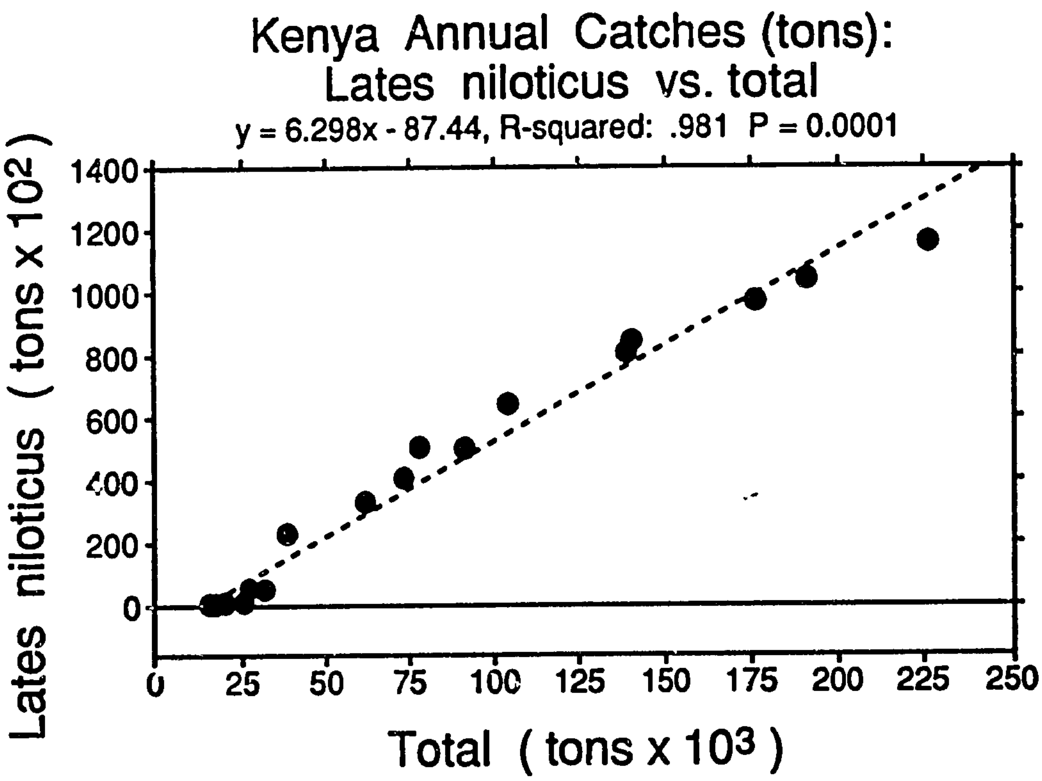


Fig. 8: Annual catches (tones) of Nile Perch (*Lates niloticus*) vs. Total, in Lake Victoria, Kenya, during 1968-1991.

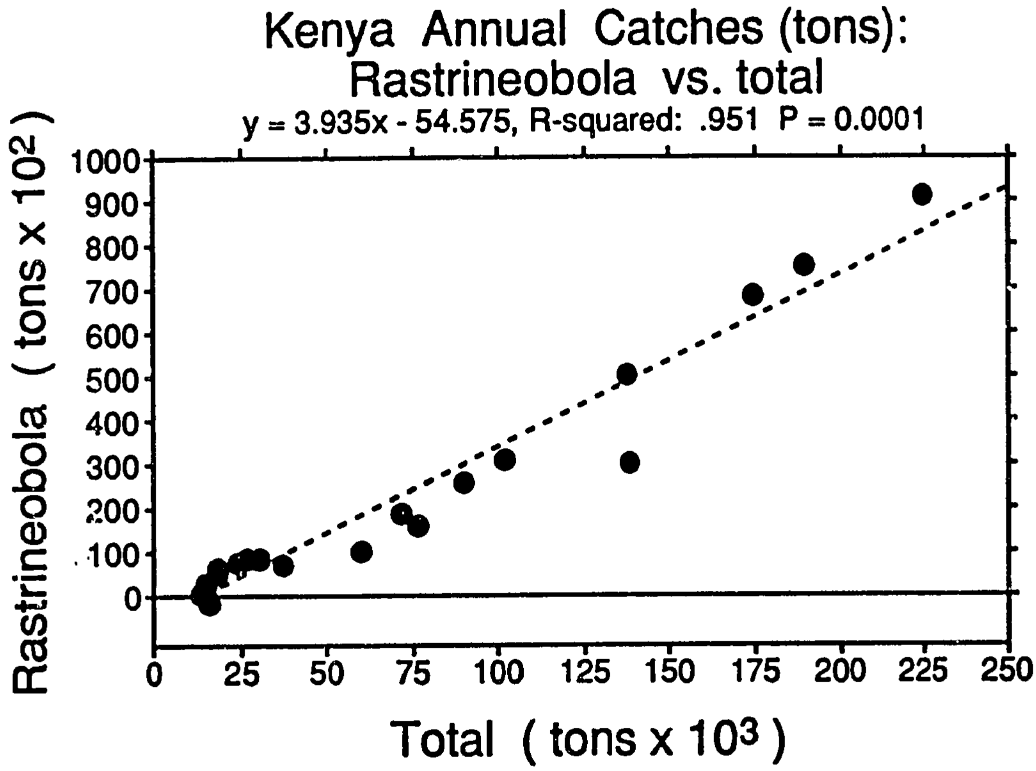


Fig. 9: Annual catches (tones) of Rastrineobola vs. Total, in Lake Victoria, Kenya, during 1968-1991.

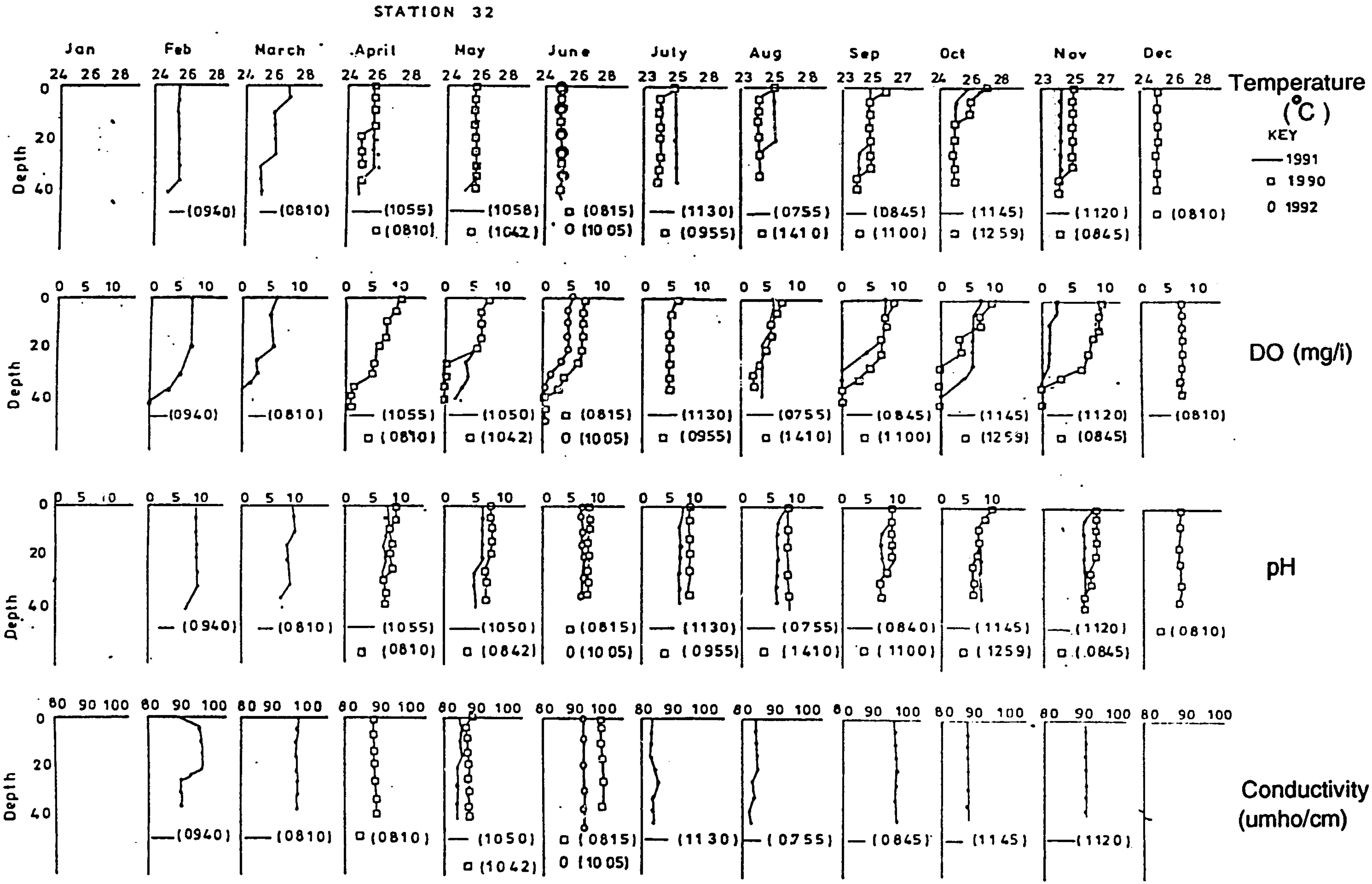


Fig. 10: Temperature, DO, pH, and Conductivity profiles, measured monthly at station 32 during 1990-1992.

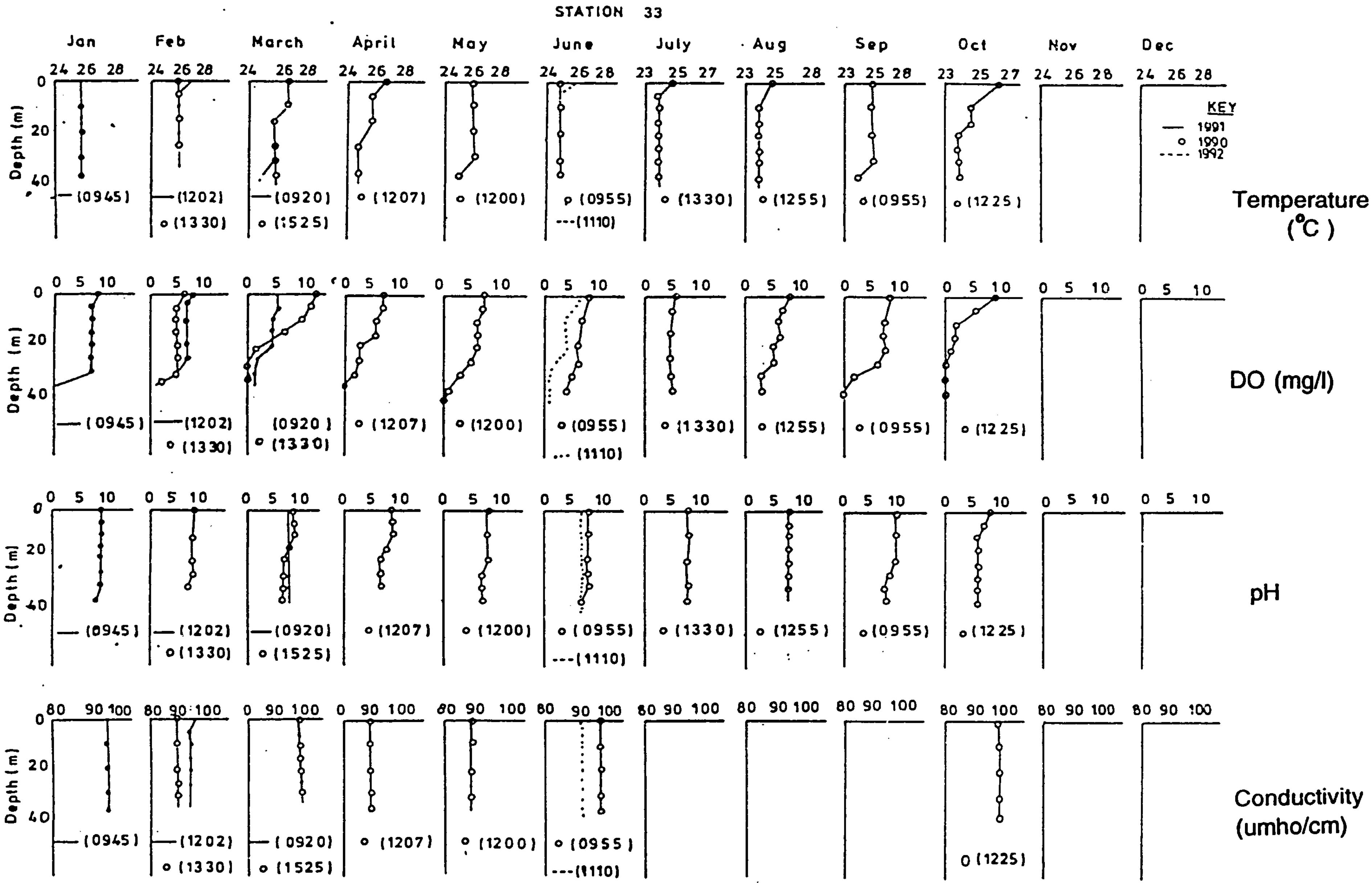


Fig. 11: Temperature, DO, pH, and Conductivity profiles, measured monthly at station 33 during 1990-1992.

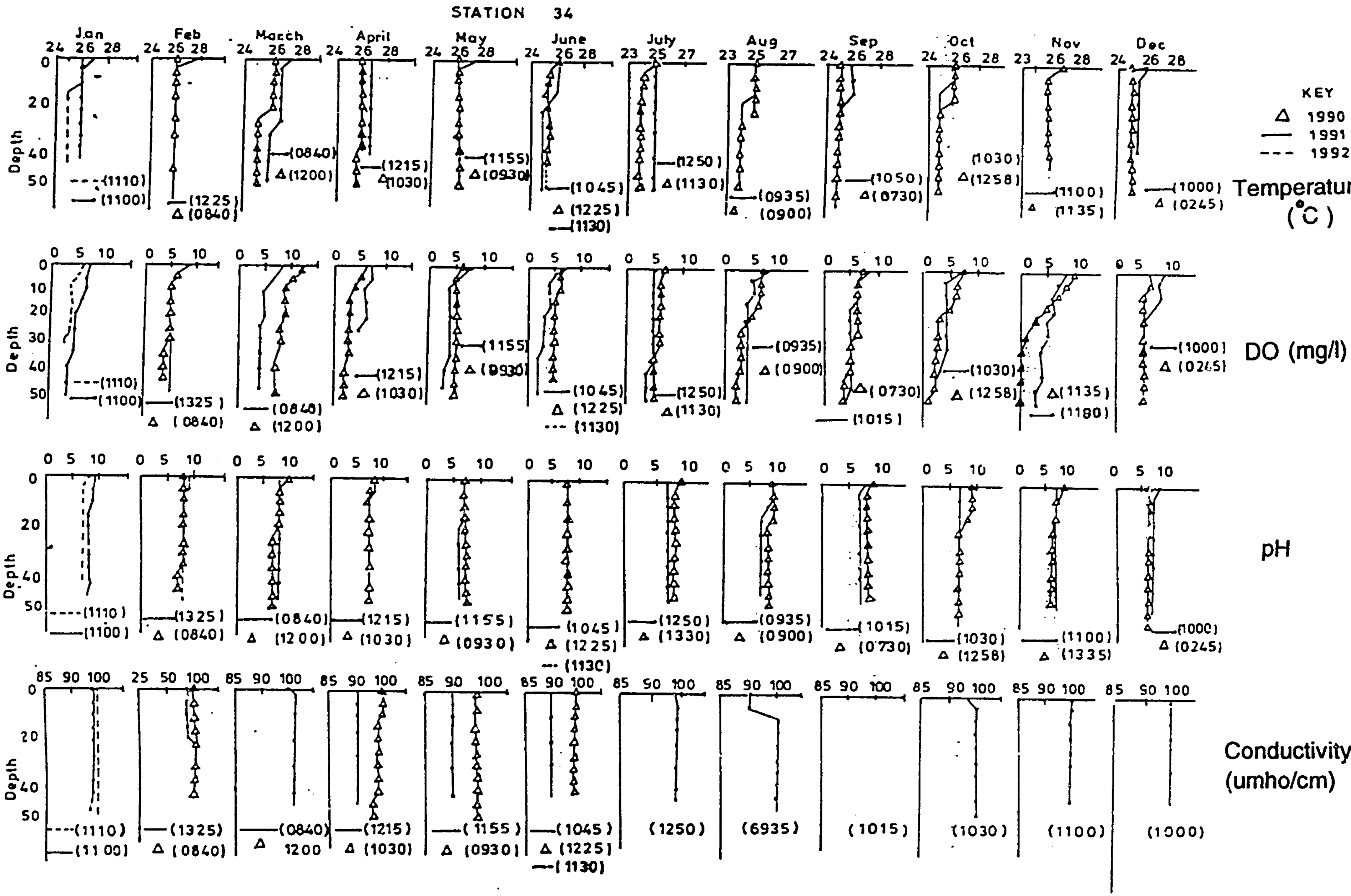


Fig. 12: Temperature, DO, pH, and Conductivity profiles, measured monthly at station 34 during 1990-1992.

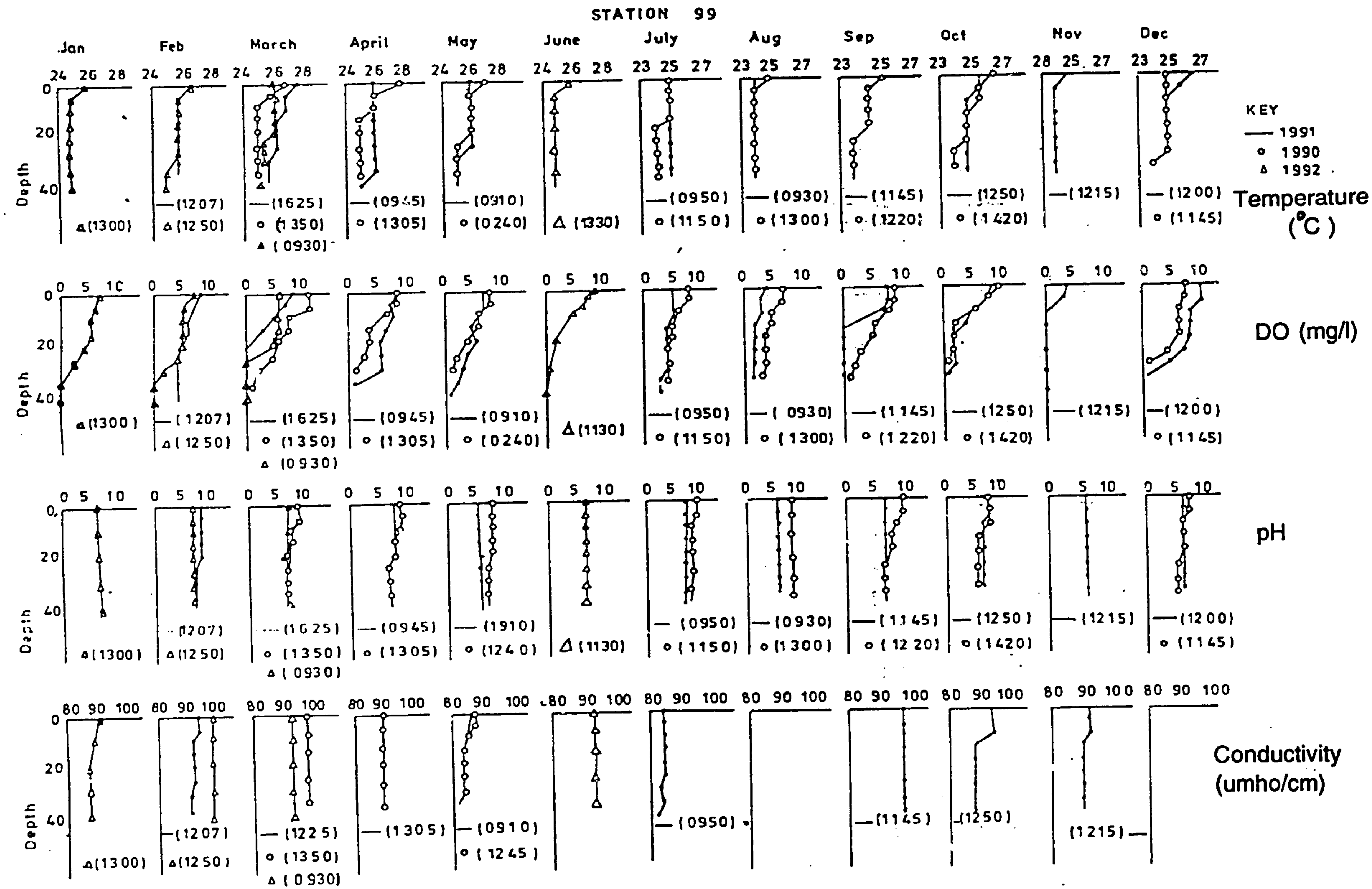


Fig. 13: Temperature, Do, pH, and Conductivity profiles measured monthly at station 99 during 1990-1992.

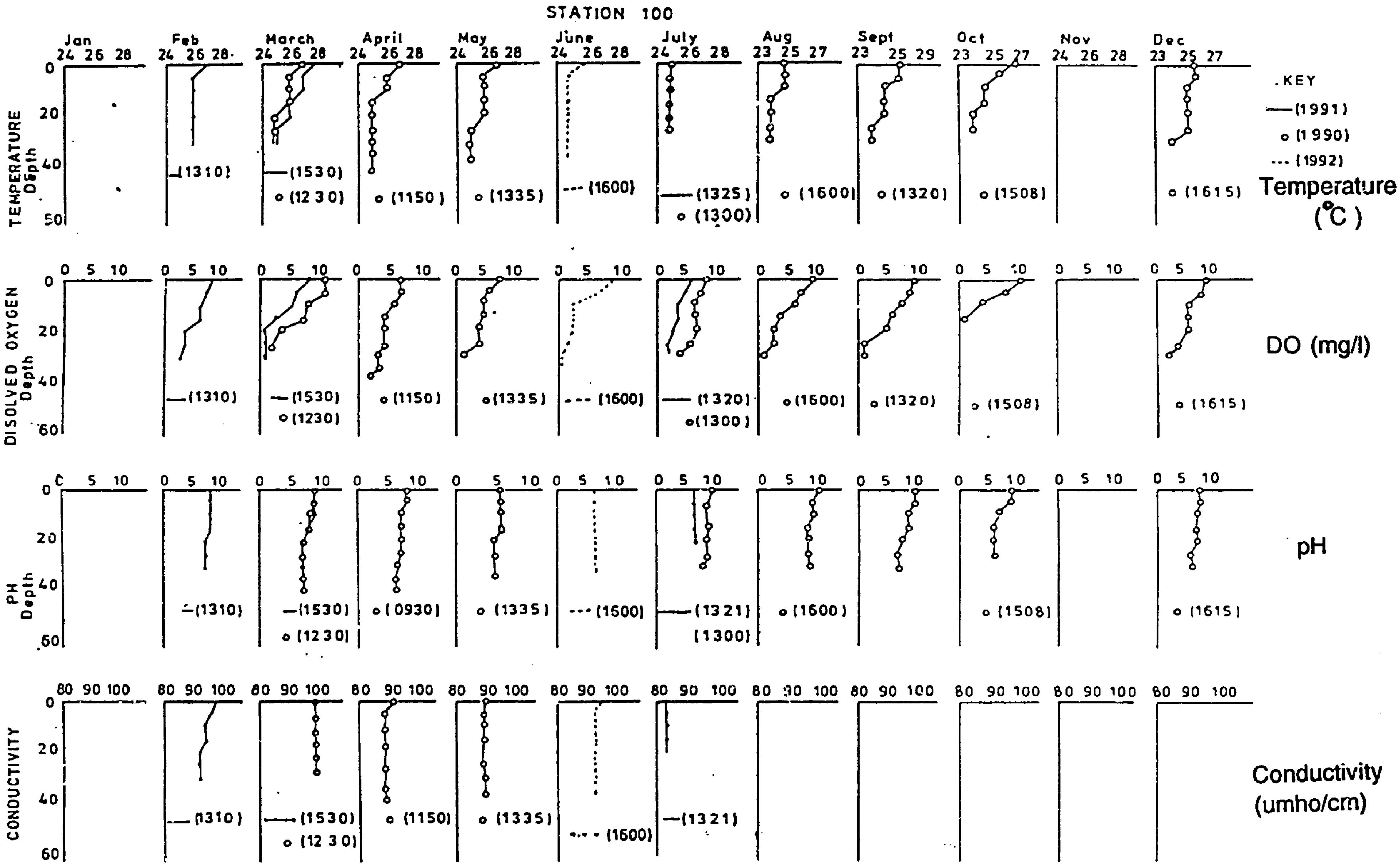
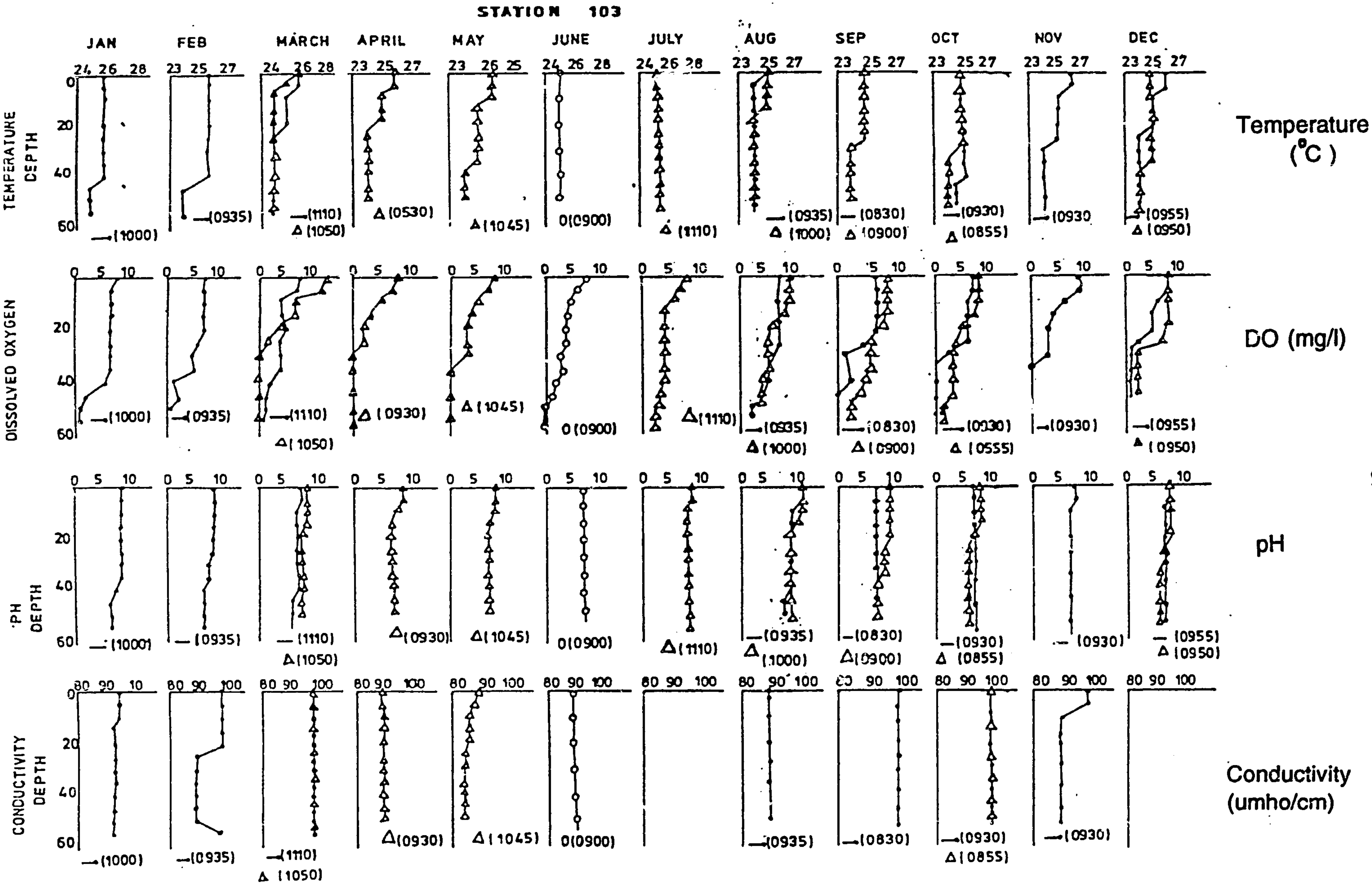


Fig. 14: Temperature, Do, pH, and Conductivity profiles measured monthly at station 100 during 1990-1992.



KEY
— 1991
Δ 1990
0 1992

Fig. 15: Temperature, Do, pH, and Conductivity profiles measured monthly at station 103 during 1990-1992.

Part B: Ecological Alterations in the Drainage-Basin and Fisheries

CHANGES OF FISH COMMUNITY AND FISHERIES

The nearshore fisheries dramatically alterated in terms of species composition and reductions of fish stocks since 1920. At the beginning of this century fishing effort was determined by subsistence requirements using traditional gears (Acere, 1988) which were replaced by introduction of cotton, nylon and multifilament gillnets. Lake Victoria fisheries as presented by Graham (1929), Fryer and Iles (1972) described Oreochromis esculentus and O. variabilis, over 250 species of haplochromine species, mormyrids, catfishes and cyprinids as major contributors to commercial landings. The introduction of the gillnets resulted in a drop in the catch per unit effort but initiated an overfishing conditions (Acere, 1988). It was accompanied by introduction of 6 species of exotic tilapias, Tilapia zillii, Oreochromis niloticus, O. leucostictus and O. mossambicus. The objective of these introductions was to increase fish production. Nevertheless since then the fishery was highly fluctuated and unstable values of catch per unit effort were recorded (Garrod, 1961).

Prior to the introduction of the Nile perch (early 1960's) haplochromine fishes were the economic basis for fishery as well as the dominant protein resource for human consumption. Detritivores and planktivores fishes were major prey species for the piscivore Nile perch (Fryer, 1973; Ogari and Dadzie, 1988). In 1976 only 0.5% of the commerical catch in the Kenyan waters of Lake Victoria was Nile perch, by 1983 it came up to 67.7%. Haplochromine in the catches varied between 21.6-36.8% during 1968-1979 and 0.8% in 1985 (Table 1) (Ogutu-Ohwayo, 1985). The landings of other native near-shore genera like Tilapia, Protopterus and Clarias declined as well (Okemwa, 1981). The present drastic reductions of non-predatory commercial fishes (Table 1) predictively will be accompanied by a decline of Nile perch populations and fishery (Ssentongo and Welcomme, 1985) due to its cannibalistic behaviour (Barel et al., 1985; Ogari, 1985).

Trawl surveys during the 1970's in Lake Victoria (Kudhongania and Cordone, 1974; Benda, 1981; Muller and Benda, 1981) indicated large stocks of haplochromines and several endemic fishes in nearshore and offshore waters (Table 2). Trawl fishing during the 1980's (Asila and Ogari, 1988; Okemwa, 1984) indicated that endemic fishes, including haplochromines, tilapiines, anadromous cyprinids, catfishes, lung-fishes and mormyrids were too scarce to support a significant fishery (Table 2). Consequently, it was concluded that both haplochromines and tilapiines in Lake Victoria were massively extincted (Balon and Bruton, 1986; Ribbink, 1987; Les Kaufman, personal communication). The decline of haplochromine and tilapine fishes resulted in not only a reduction of the commercial catch but also a disruption of the trophic dynamics in the lake ecosystem. These fishes were consumers of the dominant and/or bloom forming algae and detritus and their high feeding capacity prevented water quality deterioration. Their present absence is partly responsible for algal blooms (Ochumba and Kibaara, 1989), detritus accumulation in deep layers and consequently followed by enhancement of anoxia.

The stocking of exotic species in Lake Victoria increased the total catch (Welcomme, 1966; Fryer, 1973) with negative impacts on the lake' ecology. The increase of stocked species populations and catches caused a decline of haplochromine and tilapiine catfish landings (Table 1) with whom sesveral of the exotic species compete for food resources. We know of no previous comprehensive thorough study of the impacts of exotic fish introductions on the ecosystem of Lake Victoria (Fryer, 1973). Environmental changes caused by introduction Effects of exotic species were observed in several lakes after the occurence of irreversible changes in the food web as reported from Laurentian Great Lakes (Smith, 1968; 1972), various Scandinavian lakes (Svardson, 1976), Lake Tahoe (Morgan et al. 1978) and Lake Kinneret (Gophen et al., 1983).

CAHNGES IN THE CATCHMENT AREA

Changes in the Lake Victoria catchment (Bugenyi and Balirwa, 1989; Kendal, 1969) were construction of drainage systems, vegetation removal, soil erosion, increase livestock, recrational and industrial developments (Table 3). The most severe threat is the vegetation removal by tree cut (Hanking, 1987) for agricultural land development, charcoal and firewood production. The Kenyan part of the catchment area is populated by 42% of the country's population and is drained by several rivers. Pollutants and wastes from urban centres, industries and agricultural farmlands (Table 3 and Fig. 2)) (Ochumba, 1984) are inflowing (Allabaster, 1981) into Lake Victoria via these rivers and direct run off.

Natural conditions in the catchment provide a high river discharges therefore the pollutant impacts on the aquatic communities in the rivers and the lake itself is effectively prevented (LBDA, 1984). The high discharge and lengths of river routes cause the pollutants to be carried long distances before the lake inlets. The degree to which these pollutants might be harmful cannot be adequately assessed because of the absence of long term water quality data record. There are several isolated parts of Lake Victoria where pollution impacts are significant and fish kills as well as algal blooms were recorded (Ochumba and Kibaara, 1989; Ochumba, 1990). Chabeda (1982) pointed out that loads of drained pollutants from wheat fields contain higher levels of nutrients compared to sugar areas. River studies (LBDA, 1984) indicated a general decrease of water quality from the upper catchment areas to downstream sections. The average annual nutrient input from the catchment of the Kenyan part is 20 $kg/km^2/yr$ for total phosphorus and 400 $kg/km^2/yr$ for total nitrogen.

The present Kenyan legislations of water management are administered by several governmental institutions (Moore and Christy, 1978) with relatively low level of coordination: 1) The Ministry of Water Development control water use permits and pollution prevention; 2) Ministry of Health is responsible for traditional nuisance abatement, water supply protection and pesticide control; 3) The Ministry of Agriculture is responsible for soil erosion control, provision for food and chemical and toxic substances utilization; 4) The Chief's Authority coordinate the local administrations to issue instructions for prevention of streams pollution and refforestation programmes; 5) The Ministry of Environment and Natural Resources is responsible for watershed management. Presently efforts are underway focusing on pollution control, provisions achieving the statutory basis for environmental impact assessment.

The influence of modifications in the catchment area on fish stocks in Lake Victoria is difficult to estimate. Nevetheless, these effects are apparently significant (Marten, 1979; Benda, 1979; Barel et al., 1985). Early studies show that the potamodromous fish species were more abundant in the rivers but presently their densities are thoroughly reduced. Ancient commercial fisheries of Lake Victoria were based on migratory species that moored upstream to spawn during the rainy season when rivers were flooded (Whitehead, 1958; 1959; and Corbet, 1961). The abundance of these fishes was recently decreased and destruction of their fishing was observed (Whitehead, 1958; Balirwa and Begenyi, 1980). Construction of dams, unrestricted dumping of industrial and agricultural wastes and other pollutants in the catchment area, reduced flows and increased sediments accumulation accompanied by deforestation, and draining of marshes and swamps enhanced fishery decline. Soil erosion and increased concentration of suspended matter reduced algal photosynthesis and consequently fish productivity (Meadows, 1980). The stocks of riverine fish populations are at their lowest levels since the early 1960's (Rabuor, 1989). Consequently fishing potential significantly declined accompanied by a direct negative impact on fishermens' families that rely on fisheries for their livelihood from Lake Victoria. There is an urgent need for effective operations aimed at conservation of the native fish communities, accompanied by stocking operations of endemic species (Evans et al., 1988).

EUTROPHIC STATUS OF LAKE VICTORIA

Studies on the water quality of Lake Victoria reveal many uncertainties (Ochumba, 1987). The lake is acting as a sink for most of the imported contaminants by inflowing waters which accumulate in the ecosystem by increasing concentrations in the lake water, in the sediments and in the biota, especially fish. About 85% of inflowing waters into Lake Victoria evaporates (Talling, 1966). Few comprehensive studies of water quality were carried out thirty years ago focusing on inorganic substances but not on organic matter and heavy metal contamination. Chemical composition of lakes and rivers in Africa are predominantly controlled by atmospheric conditions (Kilham, 1990). The studies of changes in Lake Victoria's trophic status are scarce and fishery biology research mostly in bays was better developed. Fish kill cases stimulated the direct attention to the possible enhancement of eutrophication in Lake Victoria.

Recent comparative studies on the limnology of Lake Victoria (Table 4) emphasised eutrophication processes (Akiyama et al., 1977; Hecky and Mngoma, 1990; Ochumba and Kibaara, 1989). We identified substantial increases in chlorophyll (x3-10) and primary productivity (x2-3) and substantial decreases in silica concentrations (x5-10). Sulfate concentrations are x10 lower than the lowest concentrations measured in large lakes in the world (0.1 mg/l). There has been a shift in the phytoplankton community towards nitrogen fixing blue-green species, fewer green algae and the diatomid Stephanodiscus (Kitaka, 1971). The zooplankton community is presently dominated by small bodied species of copepods and claocerans with low densities (Gophen et al., 1990).

Table 4 represents anoxic cases measured in Lake Victoria during 1985-1987 (see also Fish, 1957). In Kenya, anoxic waters have recently been found at shallower depths than before (Table 5 and 6) suggesting an increase of oxygen demand in the hypolimnion. An eutrophication process whose causes need to be determined is now indicating. The decimation of the haplochromine fishes and endemic tilapias following the introduction of Nile perch may have profoundly altered the trophic status of the lake.

CONCLUSIONS

Lake Victoria presently exhibit tradional symptoms of eutrophication including decreased water transparency, blue-green blooms enhancement, elevated nutrient concentrations and hypolimnetic deoxygenation. Changes in the phytoplankton community altered availabilities of food sources to primary consumers but these grazers were considerably suppressed by higher trophic levels. Fish introductions modified the phytoplankton, zooplankton and fish assemblages in Lake Victoria that had the most intensive impact on water quality. Lake Victoria fish species are threatened by the worsening conditions in the lake itself and from the rivers in the catchment area. It is suggested that urban, agricultural and industrial pollution and the introduction of predatory Nile perch and competitive Tilapiine species are the major factors for the deterioration of Lake Victoria's ecosystem. Oreochromis esculentus is almost extinct and many more haplochromid species are endangered. Current fisheries legislation and operations aimed at reduction of soil erosion and sedimentation in inflowing rivers in the catchment area are insufficient for significant improvement of the present deterioration of water quality. Localised manual harvest of papyrus, shoreline dredging and sandmining did not sufficiently improved lake conditions.

It is recommended to intensify pressure on algal and detrital matter by stocking the lake with large bodied cichlids. These grazers are less vulnerable to Nile perch predation and can probably reduce algal and detrital densities. Further and long term monitoring of the lake and its tributary rivers is required for adminsitrative agencies for decision making with regard to protecting the Lake Victoria resource.

Figure Legends

Fig. 1. Lake Victoria and its catchment area.

- International boundries
- Catchment area
- River
- Seasonal river
- Lake
- Swamps
- Mountain summit
- City

Fig. 2. Kenyan part of Lake Victoria and its catchment area and pollutant sources.

- (P) - Paper mills
- (B) - Breweries distilleries
- (C) - Coffee processing
- (S) - Sugar refineries
- (Si) - Sisal factories

Table 1. Catch composition (%) of major fish species and total landings (tons x 10^3) in the Kenyan part of Lake Victoria (Getabu, 1987; FAO fish. Rep. 388, 1987).

Year	Tilapiine	Clarias	<u>Haplochromis</u> spp.	Bargus	<u>R. argentea</u>	Protopterus	<u>L. niloticus</u>	Total (tons x 10^3)
1968	14.8	10.6	22.8	7.0	4.5	17.2	0.0	16
1969	26.6	7.6	36.8	5.5	2.9	9.3	0.1	17
1970	27.5	9.7	32.7	6.7	3.2	11.0	0.2	16
1971	21.1	12.5	32.0	7.1	5.1	12.8	0.3	15
1972	14.8	17.0	29.0	5.4	7.8	12.7	0.2	16
1973	10.1	15.7	33.2	8.6	10.5	13.0	0.9	17
1974	5.6	12.9	35.0	6.4	21.8	8.6	0.5	17
1975	3.9	15.6	27.9	8.4	27.4	1.1	0.1	17
1976	5.4	13.0	34.1	5.5	30.3	5.0	0.5	19
1977	7.4	9.1	32.4	6.0	34.7	4.0	1.1	19
1978	10.9	7.2	27.8	5.9	36.5	2.6	4.5	24
1979	9.0	10.0	21.6	5.8	30.5	1.5	14.0	31
1980	18.6	4.5	13.5	2.4	35.1	1.4	16.0	27
1981	10.2	2.6	2.1	1.1	20.4	0.5	59.7	46
1982	7.3	3.4	4.2	4.2	17.1	0.4	54.4	61
1983	5.5	2.7	0.8	3.1	21.3	0.3	67.7	77
1984	10.4	1.1	0.0	0.1	27.1	0.1	57.5	72
1985	10.7	0.6	0.0	0.1	29.2	0.2	56.5	90
1986	2.7	0.3	0.6	0.1	30.5	0.2	63.5	103
1987	2.8	0.6	0.3	0.0	24.5	0.1	69.1	
1988	2.4	0.6	0.3	0.0	36.5	0.1	59.3	
1989	2.3	1.4	1.5	0.1	38.5	0.1	54.3	

Table 2. Bottom trawl catches (kg/ha) of dominant fish species (1969-1990) (Asila and Ogari 1987).

Species	1969-1970 (19 hauls)	1975 (69 hauls)	1977 (167 hauls)	1982-1983 (54 hauls)	1989-1990 (41 hauls)
Bagrus docmac	11.7	12.5	1.8	0.9	0.01
Clarias gariepinus	3.3	2.6	0.7	0.9	0.10
Haplochromis spp.	35.8	32.7	28.7	-	0.54
Labeo victorianus	0.1	0.1	0.1	0.1	0.10
Lates niloticus	0	0.8	2.8	29.0	68.90
Protopterus aethiopicus	3.7	10.7	0.3	-	0.01
Schilbe mystus	0.03	0.20	0.01	0	0.10
Synodontis spp.	2.10	0.20	0.50	0.04	0.10
Oreochromis variabilis	0.03	0.11	0.3	-	-
Oreochromis niloticus	0.01	0.20	0.70	1.40	0.83

(-) not recorded

(0) catch densities less than 0.01 kg/ha.

Table 3. Pollution sources in Ugandan part of Lake Victoria catchment. The major human activities in and around cities and consequent pollutant production are indicated (Bugenyi and Balirwa, 1989).

Masaka (commercial town)	Kampala (commercial and industrial city)	Jinja (mainly industrial town)	Other towns (mainly industrial)	Rural area (agricultural)
Domestic sewage	Domestical sewage	Domestic sewage	Domestic sewage	Faecal pollution: bacteria, viral and parasitic diseases.
Coffee processing	Textiles	Textiles	Testiles	
Others	Soap factories Oil mills	Soap factories Oil mills	Sisal Beer and soft drinks	Pesticides: insectides, weedcides, herbicides, molluscides
	Breweries	Breweries	Dairy products	
	Dairy products	Paper and packaging	Others	Soil erosion: water siltation.
	Coffee	Steel rolling mills		
	Others	Starch and other flour mills		Irrigation - water vectored diseases: bilharzia, malaria, onchocerciasis, etc.
		Tannery		
		Pharmaceuticals		Deforestation and overgrazing resulted in soil erosion and water siltation.
		Others		Farm: sugar, coffee, tea, intensive farms which use pesticides and fertilizers.

Table 4. Comparative limnological data from various authors on Lake Victoria (ranges are given)

	1966	1977	1979	1984	1989	1990
Phosphate phosphorus (PO_4-P) μg/l	7.0-120	0.1-122		0.2-75	4.0-37.0	0.1-19
Nitrate nitrogen (NO_3-N) μg/l	10.0-112	0.5-122	0.16-0.18	21 -237	0.1-513	1.0-30
Sulphate sulphur (SO_4-S) mg/l	0.4-4.0			0.1-5.0		
Silicate silica (SiO_2-Si) mg/l	4.0-8.0	0.2-3.0	2.0-7.9	0.1-7.6		0.06-0.72
Sechi disc transparency m	1.0-3.9	1.2-2.0		0.35-2.4	0.2-2.1	
Primary productivity mg O/m^3	100-130		400-600		180-600	100-1400
Chlorophyll concentrations μg/l	0.5-22.3	2.1-8.5		1.8-23.5	8.0-120	35.8-115.2
Algal dominance	diatoms	diatoms	diatoms	cyanophytes	cyanophytes	cyanophytes
Zooplankton dominance		copepods		Thermocyclops		

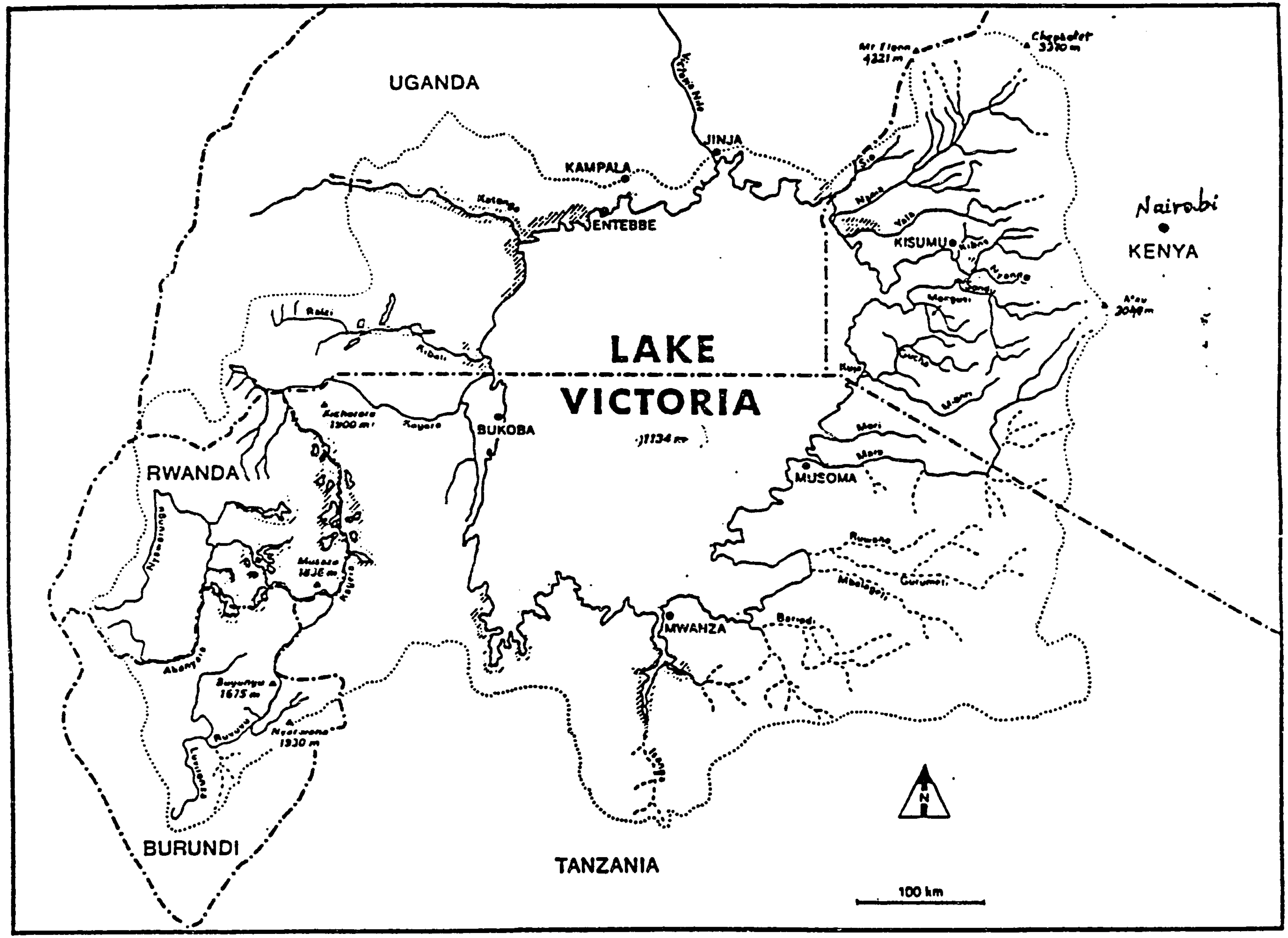
Sources: 1966 - Talling, 1966; 1977 - Akiyama et al. 1977; 1979 - Melack, 1979; 1984 - LBDA, 1984; 1989 - Ochumba and Kibara, 1989; 1990 - Hecky and Mungoma, 1990.

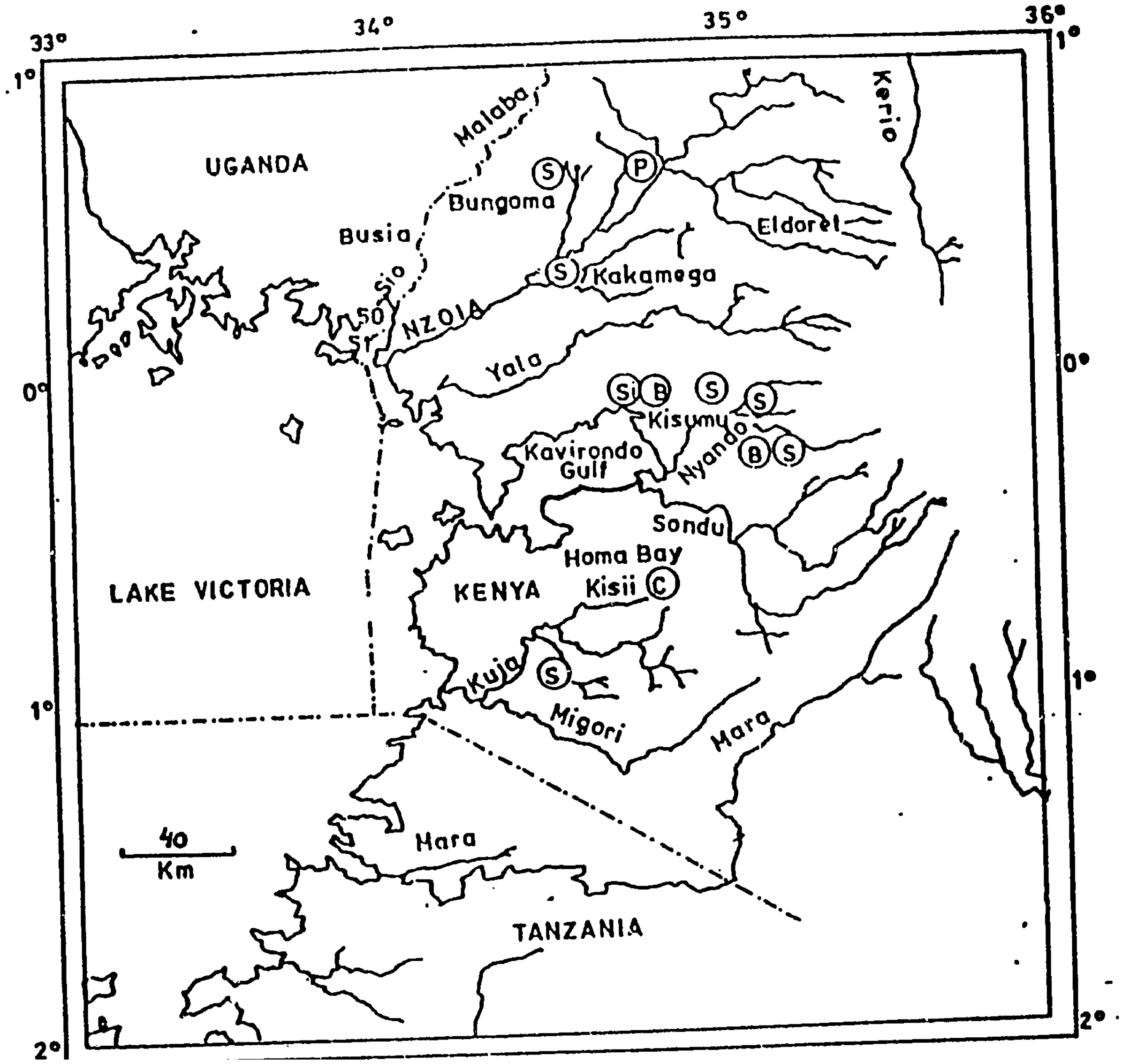
Table 5. Anoxic cases (0-4 mg O_2/1) recorded in Kenyan part of Lake Victoria during November, 1985; May, 1986; August, 1986; and March, 1987.

Upper depths of anoxic water (m)	Total depth of stations (m)	Number of anoxic cases recorded
4.5	5	2
9.0	10	2
9.5	10	1
10-25	25	1
7.0	10	2
5-10	11	4
20-25	25	2
5-9	10	2
5-6	7	2
10-12	12	2
10-20	25	3
8-25	30	3

Table 6. Dissolved oxygen concentrations (ppm) in bottom waters at open lake stations in the Kenyan part of Lake Victoria in chronological order.

Month/Year	Location	Depth Sampled (m)	Total Depth (m)	DO (ppm)	Reference
Jan. 1961	Deep north sta.	57-60	60	1-6	Talling, 1966
Feb.-May 1954	Deep north sta.	750	-	0	Fish, 1957
Feb. 1958	Lake transect	45-65	45-65	0.2-22	Newell, 1960
Feb. 1961	Deep north sta.	57-60	60	0-4	Talling, 1966
Feb. 1969	N-S lake transect	55-60	60	0	Kitaka, 1971
Mar. 1961	Deep north sta	57-60	60	1-6	Talling, 1966
Mar. 1968	N-S lake transect	55-60	55-60	0	Kitaka, 1971
Mar. 1989	Station 32	30-44	44	0.8-03	NURP, 1989
Mar. 1989	Station 33	33-34	34	0.7-0.02	NURP, 1989
Mar. 1989	Station 100	40	40	3	NURP, 1989
Mar. 1989	Station 103	43-47	47	0.1	NURP, 1989
Apr. 1961	Deep north sta.	55-60	60	1	Talling, 1966
May. 1961	Deep north sta.	57-60	60	1-2	Talling, 1966
May. 1986	Station 32	30	30	5	Ochumba & Kibaara 1989
Jun. 1961	Deep Sta.	55-60	60	1-6	Talling, 1966
Jun.-May. 1984	Station 32	30	32	1-6	Ochumba, 1984
Jun.-Aug. 1984	Station 33	40	41	0-7	Ochumba, 1984


UGANDA
KAMPALA
JINJA
ENTEBBE
KISUMU
Nairobi
KENYA
LAKE
VICTORIA
BUKOBA
RWANDA
MUSOMA
MWAHZA
BURUNDI
TANZANIA
100 km


33°
34°
35°
36°
1°
0°
1°
2°
UGANDA
Malaba
Bungoma
Busia
Sio
50
Sr
NZOIA
Kakamega
Eldoret
Kerio
Yala
Kisumu
Kavirondo
Gulf
Nyando
Sondu
Homa Bay
Kisii
LAKE VICTORIA
KENYA
Kuja
Migori
Mara
40
Km
TANZANIA

Part C: Phytoplankton, Zooplankton and Tilapias Feeding Habits in Lake Victoria

Background

General Limnology (Table 1).

Limnological features and utilization of Lake Victoria is presented in Table 1. Lake Victoria is important for the economy of three countries: Tanzawa, Kenya and Uganda. Major contribution of water and consequently nutrients by rainfall in Lake Victoria is clearly indicated. Furthermore, the high percentage of water loss by evaporation (85% of total inflow) and the low quality of outflow (15% in Lake Victoria is emphasizing the importance of internal processes like algal matter and nutrient recycling and mineralisation. In Lake Victoria, the energy loss by internal processes are significant for the maintenance of limnological stabilisation of the ecosystem. Such a structure make any significant change in the food web very pronounced towards system destabilisation.

Phytoplankton

The study of the phytoplankton from Lake Victoria started in 1898, by short-time expeditions collecting only net samples, thus, the studies until the sixties were limited to algal taxonomy and did not give information about seasonal variation of abundance, succession etc. More data became available since 1950. A chronological list of the taxonomic studies are given by Talling (1987). Talling (1965; 1966) was the first who studied a full year cycle of the composition, abundance, population dynamics and vertical distribution of the phytoplankton in relation to physical and chemical environment in the northern offshore zone of the lake (Talling 1966; 1987). Akiyama et al. (1977) studied changes in the phytoplankton population and nutrients in Mwanza Gulf from April 1973 to May 1975. The available data on the phytoplankton in the Kenyan part of Lake Victoria is little (Ochumba and Kibara 1989; Melack 1979).

Zooplankton

In the 1920's and 1930's numerous samples have been collected from lakes in East Africa by several European scientific expeditions (reviewed by Mavuti 1983). Green (1967; 1971; 1976) and Burgis (1969; 1971) studied the ecology, distribution and production of zooplankton communities in five lakes in western Uganda. Burgis (1971), Mavuti (1983) and Rzoska (1956; 1957; 1976) reviewed research on zooplankton of Lake Victoria since 1888 and produced a list of the main zooplankton species sampled till then.

Very little information about the distribution, seasonal changes and production of zooplankton is available (Worthington 1931; Rzoska 1957; Green 1971; Akiyama et al. 1977; Ochieng 1981; Goldmschmidt et al. 1989). The copepoda were found as dominant zooplankters in Lake Victoria (Rzoska 1976; Akiyama et al. 1977; Burgis et al. 1988).

Seasonal fluctuations of zooplankton in the Mwanza Gulf were studied by Akiyama et al. (1977): copepods biomass increased from May to August and decreased in September 1973 whilst Cladocera were more abundant in the rainy season (February-July) than in the dry season (September-December).

Akiyama et al. (1977) measured Copepoda densities of 100 to 400 individuals l^{-1} and cladoceran concentrations of 10 individuals l^{-1} in June-July and up to 30 in November-December. Bosmina longirostris, Moina dubia, Ceriodaphnia cornuta, Alona sp., Diaphanosoma sp., Chydorus sphaericus and Daphnia sp. dominated the population. Rotifera, (30 individuals per litre) was mainly represented by Brachionus angularis var. bidens, B. falcatus, B. forficula, B. diversicornis, B. quadridentatus, Keretalla, Tetramastix, Filinia, Conochiloides and Asplanchna spp.

The number of individuals is much lower in open water. Green (1971) found 1.4 Cladocera individuals per litre (mean value) at a deeper station

(27 m depth). The general picture described by Akiyama et al. (1977) is in good agreement (dominance of copepods) with Rzoska (1957).

Feeding habits of cichlids and Lates niloticus

The overwhelming success of the cichlid haplochromids in Lake Victoria is the major feature of fish feeding habits adaptation in Lake Victoria (Serruya and Pollingher 1986). The adaptive radiation of fish feeding specialisation is very wide among haplochromids (HEST 1988). The other cichlids in the lake including two endemics (Tilapia esculentus and T. variabilis) and 6 introduced species (1951-1953) (Tilapia zillii, Orechromis niloticus, O. leucostictius, Tilapia rendalii, T. mossambicus and O. aureus) were described as phytoplanktivorous (reviewed by Okeyo 1989).

The predatory feeding of Lates niloticus in Lake Victoria was very widely described (Barrel et al. 1985; Ogari 1984; 1990; Arunga 1981; Ogari and Dadzie 1988; Marten 1979; Okemwa 1983 and others).

Among haplochromid communities 14 different feeding types were described (HEST 1988): detritivores, zooplanktivores, insectivores, molluscivores (pharyngeal crushers and oral shellers), algal grazers (epilithic and epiphytic), phytoplanktivores, obligatory piscivores, facultative piscivores, suckers and/or scrapers of eggs and aquatic macro-animals (Paedophages), scale eaters, prawn eaters and crab predators. In data presented by HEST (1988) which is one of the most comprehensive description of the ecological features of haplochromids in Lake Victoria it is clearly shown that detritivores and phytoplanktivores together were the most important group in Lake Victoria. They were the most abundant populations and contributed together the highest number of endemic species. Before the invasion of the Nile Perch detritivore haplochromids were one of the main groups in converting primary produced algal matter into fish biomass.

Physical and Chemical Measurements

Turnover and upwelling processes in Lake Victoria waters has been recognised as an important factor in nutrient cycling (Worthington and

Beadle 1932; Newell 1960; Talling 1966; Kitaka 1971; Ochumba and Kibara 1989). We measured profiles of temperature, pH and dissolved oxygen (DO) to allocate anoxic cold layers. The effect of south-south-east wind driven forces on downward movement of anoxic layers in northern parts of the lake were described by Fish (1957) and Newell (1960). The organic rich sediments entirely aerobic, were described by Hesse 1957, 1958; Mothersill et al. 1980; and others. The expansion (horizontally and bathimetrically) of unoxic waters, rich in nutrients, as well as its effect on fish kill were described by Ochumba (1985; 1987). Kilham and Kilham (1990) suggested that elemental cycles in tropical lakes are controlled by biological factors whereas in temperate lakes nutrient cycles are dominated by physical processes for a large part of the year.

Materials and Methods

Phytoplankton and Zooplankton

Samples for zooplankton and phytoplankton analysis were collected during 1988-1990 in Kavirondo Gulf and open water stations in the Kenyan part of Lake Victoria (Fig. 1). Zooplankton analysis were carried out by sieving 1-3 litre samples through net (100 u mesh size) and counting all organisms in the sample. Samples were filtered on board or in the Kisumu Laboratory, preserved in 10% formaline and later, counted in the Kinneret Limnological Laboratory. Phytoplankton samples were analysed by using Utermohl's sedimentation method and 10 ml were examined under an inverted microscope. Samples of 125-400 ml volume were collected and preserved on board with Lugol.

Fish samples.

Fish for gut content analysis and body measurements were collected from fishermen catches and immediately measured, dissected and the viscera was preserved in 10% formalin. The following measurements were taken: Total and Standard lengths (TL, SL), total weight, viscera (stomach intestines and related fatty tissues) weight. We measured mostly Tilapias and few haplochromids and small perches. Index of satiation (IOS) was calculated for each measured fish by the formula:

$$\frac{\text{Viscera weight}}{\text{Body weight}} \times 100 = \text{IOS}$$

Fish Feeding Experiments

Living specimens of T. leucostictus, T. variabilis, T. zillii, T. niloticus and haplochromids were collected from beach seine catches and immediately transferred into aquaria (60-70 L volume) for acclimatization of 10-24 hours. The water in the aquaria were filtered (63 u mesh size nets). In each experiment there was also one fishless aquaria as a control. Freshly collected live zooplankton were added in similar aliquots to fish, and fishless aquaria. Water samples were taken from the tanks at initial (zero) time and 3-5 times with intervals of 30 mins. to 1 hr. The samples were taken by plastic pipe closed with a rubber cup randomly placed on the bottom of the aquaria. Samples were taken both from the control container and aquaria with fish to estimate zooplankton mortality. All samples were filtered on 63 u mesh size net and zooplankton organisms were counted. After substraction of zooplankton mortality, removal of zooplankton by fish was calculated. Six experiments were carried out. Tanks were slightly aerated. Experimental conditions are given in Table 2.

Physical and Chemical Samples:

The following physical measurements were taken simultaneously by Hydrolab system: temperature, dissolved oxygen (DO), pH, conductivity, redox potential, depth and salinity. In this paper we present only DO, depth, temperature and pH. Chemical samples were collected the same as for phytoplankton and zooplankton by 5 litre sampler. Samples were put on ice, and later frozen, and taken in dry ice (CO_2) to be analysed in the Kinneret Limnological Laboratory.

Results and Discussion

1. Phytoplankton.

The results, given as number of organisms per ml, of phytoplankton densities are given in Tables 3-5. The Kenyan part of Lake Victoria was divided into 3 regions: Winam (Kavirondo, Nyanza) Gulf (station no. 1, 2, 3, 17, 30, 31, 36, 37, 38), Rusinga Channel (station no. 5, 6, 7, 8, 34) and offshore region (station no. 32, 33, 55, 99, 100, 103).

Kavirondo Gulf (Table 3).

During June and December 1989 and January-February 1990 the coccoid coenbial cyanophytes dominated by filamentous forms (Lyngbya circumcreta and Anabaena flos-aquae were present but not in high numbers. The chlorophyta were not abundant but presented a relatively high diversity. The Cryptophyta appeared during the whole period of sampling, the dinoflagellates were recorded in June, January and February.

At shallow station 2 in May 1989 all the taxonomic groups were recorded and the green algae presented a high diversity and density. In May 1990 the composition of the phytoplankton was completely different: a heavy water bloom of Anabaena flos-aquae developed; coenobia of Microcystis and filaments of Melosira were rare, other algae were not recorded.

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

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 spp. chlorophytes, cryptophytes, dinoflagellates and euglenoids were recorded. In February 1990 the high quantity of coenobial cyanophytes (composed of very small cells) accompanied by filamentous forms were recorded at stations 17 and 31. At stations 36 and 38 the coenobial cyanophytes wee common, but the diatom Synedra cunningtonii dominated. At those two stations the diversity and abundance of the green algae were lower than at stations 17 and 31.

In April and May 1990 the phytoplankton was studied on net samples. During this period Melosira spp. dominated (at stations 17, 30, 31, 37) except in station 36 where S. cunningtonii was the dominant alga and in April and May it was accompanied by Melosira spp. The coccoid coenobial cyanophytes and Anabaena flos-aquae were common at all stations, as well as the green algae and the cryptophytes.

Rusinga Channel (stations 6, 7, 8, 34; February-March-April-May (1990) (Table 4):

The filamentous cyanophytes dominated and were accompanied by S. cunningtonii at stations 7, 8, 34, whereas at station 6 Synedra cunningtonii was more abundant than the filamentous cyanophytes. Coccoid cyanophytes and cryptophytes were recorded; all other taxonomic groups were nearly absent. The same situation was recorded in March. In April-May S. cunningtonii dominated at all stations and was accompanied by filamentous and coccoid cyanophytes, which became more abundant. The green algae appeared but were represented by a low number of species.

The offshore zone stations 32, 33, 55, 99, 100, 103 (Table 5).

In March 1989 at the three sampled stations (99, 100 and 103) Lyngbya circumereta dominated. It was accompanied by Nitzschia acicularis; coccoid coenobial cyanophytes were present; the green algae appeared sporadically. The filamentous cyanophytes dominated also in February 1990, but the recorded diatom was Synedra cunningtonii, chlorophytes were not recorded. A month later (20 March) the filamentous cyanophytes continued to dominate, S. cunningtonii became more abundant, a few chlorophytes, dinoflagellates and cryptophytes appeared. In April-May S. cunningtonii increased and dominated together with the filamentous cyanophytes (Lyngbya spp., Cylindrospermopsis). The coccoid cyanophytes were present. The other taxonomic groups were represented by a few species which appeared in low number (Oocystis solitario, Scenedesmus quadricauda, Glenodinium pulvioulus).

The phytoplankton composition was similar at all depths but the abundance decrease in deep layers. Viable algae are still 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 is mostly controlled by hydrological or by hydrographic conditions. Phytoplankton distribution in Kavirondo Gulf was probably affected by hydrological features (rivers, inflows) and the water column physico-chemical structure whilst water circulation dominantly affected algae community structure in the offshore regions. In Rusinga Channel a seasonal stratification cycle is apparent. Since sampling was not carried out on a monthly basis, it was not possible to detect seasonal variability but some inshore-offshore differentations in the species composition were detected.

Phytoplankton in large lakes of the warm belt is characterised by the dominance of chlorophyta and cyanophyta and in some cases also diatoms (Pollingher 1990).

During the period we studied the phytoplankton it was characterised by a high diversity and high abundance of cyanophyta, a high diversity and low abundance of chlorophyta and a relatively 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 spp. developed between February and August 1986 in the open waters of the Kenyan part of the lake (Ochumba and Kibaara 1989). Microcystis spp. were present in our samples but not very abundant.

It is worth noting that S. cunningtonii was described for the first time by G.S. West (1907) on samples taken in Kavirondo Gulf. Bachmann (1933) included it in the list of the plankton recorded in Lake Victoria, in gulfs and bays. S. cunningtonii was note mentioned by Talling (1965; 1966; 1987) and Akyama et al. (1977). The majority of the algae cited by the last two authors were recorded in our samples.

Talling (1987) comparing the earlier with later accounts (Talling 1965; 1966) of the phytoplankton composition suggests that the species diversity has been stable over the past eighty years.

In recent years, periodic massive fish kills occurred in the Kenyan part of Lake Victoria. It was correlated with the deterioration of the lake's water quality and as a consequence the development of algal blooms (Ochumba 1987). The ventual changes in the algal composition may be revealed only on a study based at least on monthly samplings during a full year cycle.

2. Anoxia

Results of the measurements of temperature, pH, dissolved oxygen (DO, ppm) are presented in Table 6. In this table we presented temperature data only from the upper boundary of anoxic waters and surface water. During 1989 we observed anoxic waters in March, at stations 33, 32, 100 and 103 at 33-34; 40 and 43-47 meters respectively. Results in Table 6 indicated the presence of anoxic waters in the offshore stations, Rusinga and Kisengera channels and even in one shallow (6.5 m) station in Kavirondo Gulf. When looking at data from Talling (1966), Ochumba and Kibara (1989), Ochumba (1984; 1985; 1987; 1990) comparatively with our results it is suggested that during recent 20 years the volume of anoxic deep waters in Lake Victoria is increasing.

3. Chemistry

Results of the nutrient analysis are presented in Table 7. The higher concentrations of TN in deep waters at stations 7, 17, 31, 34, 37, 38 compared to shallow layers are indicated. Similar distribution of the TP concentrations were also observed at stations 6, 17, 31, 32, 38 and 103. This pattern of nutrient distribution is clearly similar for ammonium at all stations except station 1. The daily upward movements of anoxic waters with high concentrations of nutrients are suggestively a factor of nutrient transportation from deep to shallow waters in Lake Victoria. This nutrient supply to shallow layers is probably possible because of the very small thermal gradient from upper and warm to lower and colder and anoxic waters (see Table 6) (Ochumba 1989).

4. Zooplankton

The following species of zooplankton were identified in the samples collected during 1989-1990.

1. Copepoda
   a. Cyclopoida
      Thermocyclops neglectus
      Thermocyclops hyalinus
      Mesocyclops leuckarti

2. Cladocera
   a) Sididae
      Diaphanosoma excisum
   b) Daphnidae
      Ceriodaphnia rigaudi

Microcyclops minutus

b. Calanoida

Thermodiaptomus neumanii

3) Rotifera

a) Brachionidae

Brachionus caudatus

Brachionus calyciflorus

Keratella tropica

Polyarthra remata

b) Flosculariacae

Filinia longispina

c) Asplanchnida

Asplanchna brightwelli

Others: Collotheca sp., Trichocerca sp., Ascomorpha sp.

Daphnia longispina

c) Moinidae

Moina macrourus

d) Bosminidae

Bosmina longirostris

e) Chydoridae

Chydorus sphaericus

All the samples in 1989 were collected in March and the distribution of zooplankton during this month is as follows:

Cyclopidae - In stations 6, 34, 36 and 100, relatively high densities were observed in deep layers at 6, 11, 20-25 and 39-40 m. Nauplii and copepodites were found also at 1 m depth in high densities.

Cladocera - Most of the organisms were found in deep layers 11-40 m. Moina and Bosmina were also abundant at 1 m.

Rotifera - The highest densities of rotifers were observed mostly at shallow depths 1-11 m (except 39 m, st. 34).

Calanoida - The high densities in deep layers (6-40 m) also characterised the vertical distribution of calanoids. Low densities of all life cycle stages swere observed at 1 m depth.

The low numbers of rotifers is probably due to the fact that the samples were sieved through 100 u mesh sized net and the organisms are smaller.

During 1990 high densities of cyclopoids were observed. The highest densities of cyclopoids were measured in stations 36, 31, 100, 32, 5, 33, and 30 at the following depths: 4 m, 0 m, 3 m, 3 m and 4 m respectively. i.e. in upper layers. These high values are mostly due to nauplii stages. High values of Rotifera were observed during April-May 1990 in station 36, 31, 8 and at shallow depths (3-4 m). It should be noted that very low densities of Cladocera and Calanoida were observed during both periods (1989 and 1990). It is in agreement with values which were presented by Mavuti (1990).

5. Fish: A) body size measurements

Number of specimens of each species that were measured (TL, SL, viscera weight and total weight) are as follows:

Tilapia variabilis (69 specimens)

Tilapia zillii (22 specimens)

Tilapia niloticus (33 specimens)

Tilapia esculentus (13 specimens)

Nile perch (Lates niloticus) (14 specimens) (fingerlings)

Tilapia leucostictus (13 specimens)

SL of all specimens varied between 10-50 cm.

TL varied between 10-55 cm.

Total weights varied between 100-600 g

Viscera weight varied between 0.2-22.0 g

Index of satiation (IOS) was calculated for all specimens individually.

Results of IOS are given in Table 10.

IOS of T. variabilis and T. niloticus were highest and T. esculentus and T. leucostictus were lower. The small Nile perch that were analysed had also relatively low IOS values.

Linear regressions of the relations between TL, SL, total weight viscera weight and IOS indicated the following: TL-SL relations gave high values of r^2: 0.93-0.99. Relations between TL and total weight gave r^2 values which varied between 0.4-0.9 (except 0.1 for T. zillii). All other values of r^2 for the linear relations of TL with viscera weight and IOS were below 0.1.

The satiation conditions of T. niloticus and T. variabilis were found to be better than the other tilapias and small Nile perch which were analysed. We suggest that these two fishes have fairly good feeding conditions compared to other species.

5B. Feeding experiments

zooplankton densities in all samples (in duplicates) were counted and compared with control tanks (without fish) to calculate mortality rates of zooplankton. Then, % removal of zooplankters by fish were calculated.

It was indicated that significant zooplankton removal by fish was as follows (f - female; m - male):

Exp. No.	Fish species	Zooplankters removal
1	T. niloticus	Nauplii; small rotifers
1	T. illii	Nauplius; adult m and f of cyclopoids Large and small rotifers
2	T. variabilis	Nauplii; small rotifers
2	T. leucostictus	Nauplii; small rotifers
3	T. variabilis	Adult f of cyclopoids
4	T. niloticus	Nauplius; cyclopoid copepodites; adult m of cyclopoids
4	Haplochromids	Nauplius; adult m of cyclopoids; small rotifers
5	T. Variabilis	Nauplii and cyclopoid copepodites

Most of the removed zooplankters were small organisms. It is suggested that these food items are collected by filter feeding mechanism. T. zillii, T. variabilis, T. niloticus and the haplochromids also captured cyclopoid copepodites and adult males (mostly) and very little adult females and large rotifers (T. zillii). Consequently it can be suggested that these tilapias feed more by utilising filter mechanics than visual particulate attack, under conditions of suspended particles availabilities.

In the experiments presented here there were not any other food sources like bottom fauna, phytoplankton or macro invertebrates.

5C. Gut content analysis

One hundred and fifty fishes were analysed: 70 - T. niloticus; 46 - T. variabilis; 24 - T. zillii; 3 - T. leucostictus; 3 - Haplochromids and 4 - fingerlings of L. niliticus.

The analysed fishes were randomly taken from samples for body measurements. All gut contents were analysed under both dissecting microscope (M-5 Wild) and optic microscope (Dialux 20) and quantitatively classified. The food components were classified by biomass estimation into 5 levels: 1) 5-15%; 2) 15-30%; 3) 30-50%; 4) 50-70% and 70-90%. Results presented in Table 11 include all classes were food items comprised between 30-90%. It should be considered that in many cases more than one (1-5) food components was found to be present in high quantities in one fish. e.g. total number of cases in Table 11 could be higher than the number of analysed fishes.

The following conclusions can be indicated:

T. niloticus:

This fish was reported in publications during 1950-1960 by several authors as a filter feeder (Okeyo 1989). Our observations indicated that most of the food of this fish is collected on the bottom or close to the sediment surface: Trichoptera, Caridina, mud, chyronomids, ostracods, bivalves, diatoms. It is also suggested that some other components, not typical to the bottom layers are also ingested by the fish in deep or mid layers: Moina, Chrydorus, plant debris, Microcystis, Melosira and small chlorophytes.

T. variabilis:

The dominant components in the food of this fish are Trichoptara, mud and plant debris. It is suggested that T. variabilis also collect food mostly near or in the bottom sediments.

T. zillii

Feeding habits of T. zillii are similar to those of T. variabilis with dominance of Trichoptera, Caridina and plant debris.

Low numbers of specimens of haplochromids, T. leucostictus and fingerlings of L. niloticus were analysed. These analyses indicated dominance of bottom components in their food: Trichoptera, detritus, mud, Melosira, Microcystis, chironomids, fish scales, plant debris, insect fragments and Caridina.

It should be considered that Microcystis is a pelagic form but dead or moribund sedimented colonies are probably collected by the fish near the bottom.

Conclusions

The tropical Lake Victoria, as other African lakes, represent very low seasonal fluctuations of physical factors like temperature and water level changes. Not like temperate lakes where physico-chemical fluctuations during the year or temporarily are major driven forces in lake dynamics the biological features are much more effective in tropical aquatic systems (Kilham and Kilham 1990). We suggest that fundamental modifications of the biological structure in Lake Victoria caused significant change in energy flow channels in the Lake Victoria ecosystem.

These modifications initiated direct and indirect effects on the ecosystem structure.

Our results show that Tilapia species in Lake Victoria are not pure planktivorous as was reported 30 years ago (Okeyo 1989); and they feed mostly on benthic sources. The modified food sources was probably enhanced by the Nile perch invasion. Tilapia were pushed from open water by the predator Lates to shallow water. In these shallow waters Tilapia and probably Haplochromids found refuge and therefore they have to utilise available food in their new niche. This food is mostly bottom fauna and flora. The ability of these Tilapia to utilise planktonic food recources when they are not suppressed by Lates were presented by the feeding experiments. In these experimental conditions they utilised zooplankton efficiently.

The invasion of the Nile perch eliminated major part of haplochromid populations resulted in decline of grazing pressure on alga. Algal matter is now incompletely removed. This is also emphasised by the fact that a big part of algae species are unflavored food for zooplankton. Zooplankton biomass is therefore relative to other temperate lake low and its grazing pressure on phytoplankton is less effective. Prior to the Nile perch invasion algal matter and consequent detritial substances were efficiently consumed by haplochromids. This matter is now accumulated in the lake ehancing anoxia in deep waters. Tilapia also change their diet. As was reported before the Nile perch introduction Tilapia in Lake Victoria were phytoplanktivores. Presently as our data represent those Tilapia are mostly benthic feeders.

So far, inspite of the very high level of physical stabilisation of the Lake Victoria ecosystem - the biological modification caused by the Nile perch introduction resulted in an ecological "earthquake" for the lake: chlorophyll content is increasing gradually anoxia in deep waters is enhanced a great scientific loss of endemic species of haplocromid fishes occurred and the overall outcome is an unstable ecosystem.

Future Perspectives

It would be probably impossible to completely eliminate Lates niloticus from Lake Victoria. But, it is urgently required to reduce algal matter content in the water. It was found that large bodied Tilapia niloticus are less preyed by Nile perch (Ogari 1990). Therefore we proposed to develop techniques of rearing phytoplanktivorous large bodied Tilapia in protected bays or half-open lagoons and release them into the entire lake when they are large enough not to be preyed by Nile perch (see also Marten 1979).

Figure Legends

Fig. 1. The Kenyan part of Lake Victoria and sampling stations (numbers in circles).

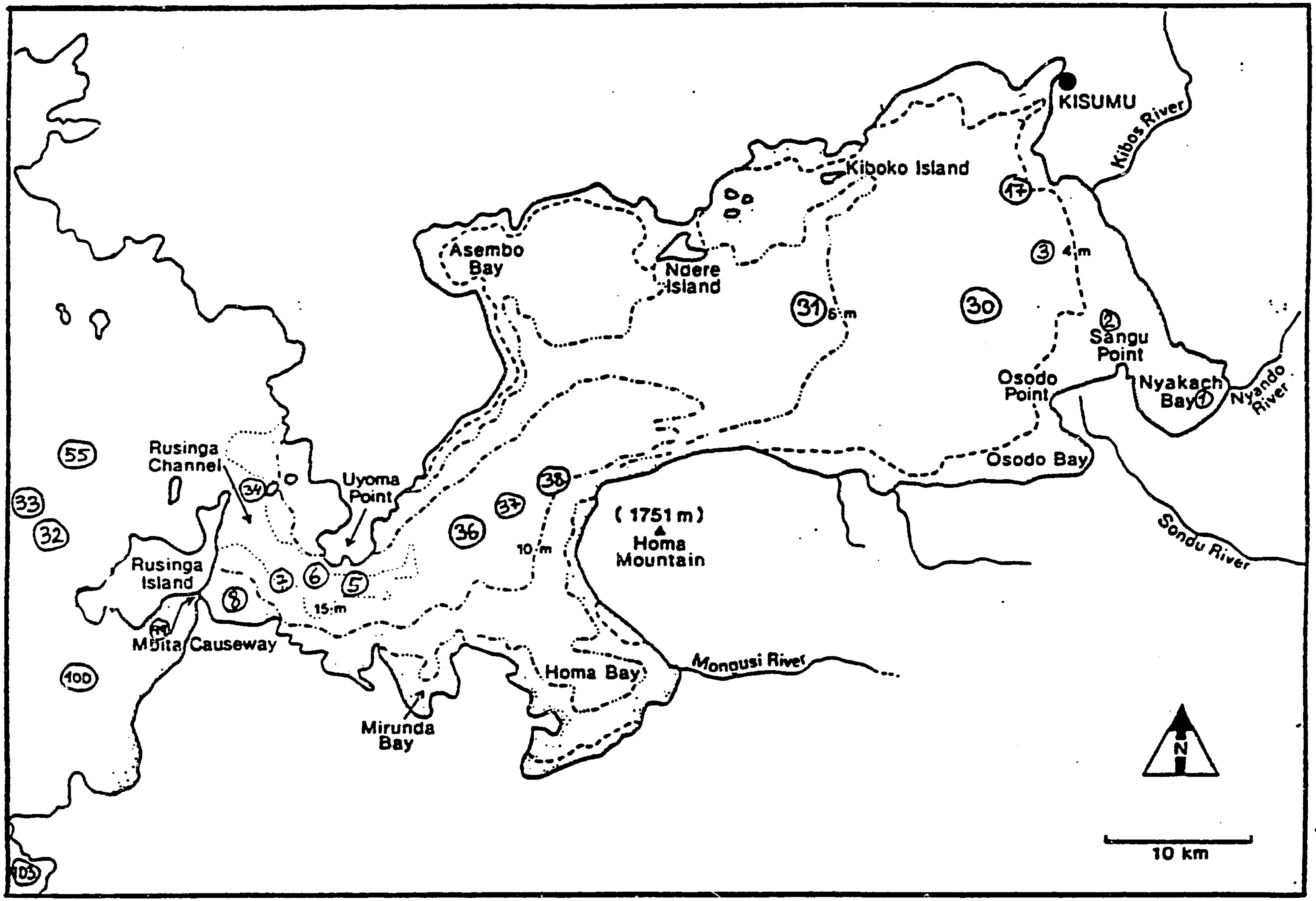

KISUMU
Kibos River
Kiboko Island
17
3
4 m
Asembo Bay
Ndere Island
31
6 m
30
2
Sangu Point
Osodo Point
Nyakach Bay
1
Nyando River
Osodo Bay
Rusinga Channel
34
Uyoma Point
55
33
32
38
37
36
(1751 m)
Homa Mountain
10 m
Sondu River
Rusinga Island
7
6
5
8
15 m
Mbita Causeway
100
Homa Bay
Monousi River
Mirunda Bay
N
10 km
103

Table 1. Limnological features and the utilization measures of Lake Victoria (HEST 1988; Ochumba, personal communication; FAO, Fish Rep. 1987; Reynolds and Greboval 1988; Serruya and Pollingher 1983; KMFRI 1981).

	Lake Victoria
Catchment area	$193 \times 10^3 km^2$
Lake surface	$70000\ km^2$
Lake volume	$2760 \times 10^9 m^3$
Water inflow	$118 \times 10^9 m^3$
Shoreline	3440 km
Water outflow	$18.4 \times 10^9 m^3$ (15%)*
Direct rainfall	$100 \times 10^9 m^3$ (85%)*
Evaporation	$100 \times 10^9 m^3$ (85%)*
Residence time	23. 4 years
Rivers inflow	$18 \times 10^9 m^3$ (15%)*
Catchment/volume	0.07
Shoreline/surface	0.05
Fishery:	
Annual landings	70 kg/ha
Lake area utilized	~60% of inshore
Number of fishermen	41800
Number of boats	10500
Utilization priorities	I) Fisheries
	II) Transportation

* = % of total inflow.

Table 2. Conditions of fish feeding experiments: TZ - T. zillii; TN - T. niloticus; TV - T. variabilis; TL - T. leucostictus; HAP - Haplochromids.

Exp. No.	Species	Fish size TL (cm)	Sampling time Intervals (mins)
1	TZ	20; 12;	0, 40, 40, 60
1	TN	13; 12.6; 14; 12.3	
2	TV	11.4; 12.7; 11.7	0, 30, 45, 60
2	TL	8.1; 10.2; 14.0; 8.1	
3	TV	15.9; 17.3; 11.8; 22.3	0, 30, 30, 60, 60, 105
4	TN	14.8; 21.6; 22.3; 20.7	0, 30, 30, 60, 60
4	HAP	10.4; 11.8; 6.8; 5.4; 7.1; 6.3; 6.2; 6.0; 5.5; 5.4	
5	TV	14.6; 12.2; 10.4; 11.8; 12.5; 9.8; 10.2; 9.5; 9.9	0, 30, 30, 60, 60
6	TV	22.7; 14.8; 11.8; 22.6; 22.3	0, 30, 30, 60

Table 3. Algal densities in Kavirondo Gulf (1989-90). Given species are only those with densities above 200/ml. K = near Kisumu.

Species	Station	Date	Density (No/ml)	Depth (m)
<u>Aphanocapsa</u> spp.	K	12.6.89	1225	0
<u>Merismopedia</u> spp.			300	
<u>Lyngbya</u> spp.			265	
<u>Melosira nyassensis</u> vav. <u>victoria</u>			1385	
<u>Cryptomonas</u> spp.			430	
<u>Aphanocapsa delicatissima</u>	K	26.6.89	3480	0
<u>Microcystis</u> spp.			470	
<u>Merismopedia punctata</u>			1010	
<u>Anabaena flos-aqua</u>			1025	
<u>Lyngbya</u> spp.			805	
<u>Chlamydomonas</u>			250	
<u>Cryptomonas</u> spp.			320	
<u>Aphanocapsa</u> spp.	K	12.12.89	1775	0
<u>Merismopedia</u> spp.			210	
<u>Chroccoccus</u> spp.			840	
<u>Anabaena</u> spp.			305	
<u>Scenedesmus</u> spp.			220	

Table 3 continued.

Species	Station	Date	Density (No/ml)	Depth (m)
Aphanocapsa spp.	K	12.12.90	1740	0
Microcystis spp.			1150	
Merismopedia spp.			325	
Chroococcus spp.			915	
Anabaena spp.			480	
Lyngbya spp.			420	
Synedra cunningtonii	38	21.2.90	3275	5
Lyngbya circumcreta			3850	10
" "			1788	5
" "			3037	10
Scenedesmus spp.			263	10
Merismopedia spp.	31	21.2.90	780	1
"			516	7
Microcystis spp.			830	1
"			558	7
Chroococcus spp.			225	1
"			308	7
Lyngbya spp.			4040	1
"			2424	7
Lyngbya bipunctata			2210	1
" "			533	7
Melosira granulata var angustissima			600	1

Table 3 continued

Species	Station	Date	Density (No/ml)	Depth (m)
Scenedesmus spp.			345	1
"			258	7
Rhodomonas sp.			335	1
Coenobial cyanophytes	17	18.2.90	Very high	1.5
Merismopedia spp.			395	
Microcystis spp.			355	
Cylindrophermopsis			465	
Lyngbia spp.			1590	
Synedra cunningtonii			220	
Navicula rynchocephala			340	

Table 4. Algal densities in Rusinga Channel (1990). Given species are only represented by densities higher than 200/ml.

Species	Station	Date	Density No/ml	Depth (m)
Filamentous cyanophytes	7	19.2.90	very high	2
Synedra cunningtonii			4780	
Cylindrosphermopsis			4120	
Lyngbya spp.			16990	
Lyngbya circumcreta			1500	
Lyngbya bipunctata			3050	
Cryptomonas spp.			400	
Hormogonales	8	18.2.90	very high	3
Lyngbya spp.			9940	
Lyngbya bipunctata			2880	
Lyngbya circumcreta			3180	
Cylindrosphermopsis			3180	
Aphanocapsa spp.			1610	
Microcystis spp.			600	
Chroococcus spp.			410	
Synedra cunningtonii			3740	
Rhodomonas spp.			470	
Lyngbya spp.	34	20.2.90	10025	5
"			7415	20
Lyngbya bipunctata			3525	5
" "			3065	20
Lyngbya circumcreta			1015	5
" "			940	20
Cylindrosphermopsis			590	20
Synedra cunningtonii			2400	5
" "			3600	20

Table 5. Algal densities in offshore stations (1990). Only species with densities higher than 200/ml are given. 'High' represent >1000/ml.

Species	Station	Date	Density (No/ml)	Depth (m)
Lyngbya spp.	32	19.2.90	10629	5
Lyngbya circumcreta			2116	
Lyngbya bipunctata			3932	
Cylindrosphermopsis sp.			2724	
Synedra cunningtonii			1958	
Filamentous cyanophytes (*Lyngbya bipunctata* and *Lyngbya circumcreta*)	99 & 100	20.2.90	high	1.5 & 25
Filamentous cyanophytes (*Lyngbya* spp.)	103	20.2.90	high	0, 1, 5 & 16
Cylindrosphermopsis sp.			high	
Synedra cunningtonii			high	
Filamentous cyanophytes (*Lyngbya* spp.)	55	19.2.90	high	0, 1, 5, & 20
Cylindrosphermopsis			high	
Synedra cunningtonii			high	

Table 6. The presence of anoxic waters (<4.0 ppm-DO) in Kenyan part of Lake Victoria. The upper boundary is given in m - from surface. The temperature of upper part of anoxic layer and surface are given as well as pH at the anoxic upper limit. Numbers in brackets are bottom depths.

Station bottom depth (m)	Date	Hour	Anoxia depth (m)	pH	Surface temp. (°C)	Anoxic temp. (°C)
Kisengera Bay	20.3.90	15:00	10	6.97	27.5	25.13
100 (33)	20.3.90	12:30	21	7.03	26.58	24.96
33 (37)	19.3.90	13:30	19	6.97	26.95	25.13
55 (34)	19.3.90	10:00	26	6.91	25.74	24.85
33-A (38)	18.3.90	15:20	18	6.91	26.87	25.12
103 (63)	21.3.90	10:45	19	7.00	26.81	24.78
99 (46)	21.3.90	13:45	26	6.96	27.41	24.78
32 (49)	21.3.90	16:00	22	7.08	26.71	24.87
99 (30)	19.2.90		29	7.82	26.08	25.93
100 (39)	19.2.90	10:45	31	8.02	25.83	25.80
32 (40)	19.2.90	12:30	37	7.55	26.20	25.77
33 (37)	19.2.90	13:30	32	7.55	26.43	26.04
N-W 33-B (35)	19.2.90	14:15	33	7.45	26.85	25.97
34 (45)	20.2.90	09:00	40	7.51	26.09	26.02
N 34-B (52)	20.2.90	11:15	45	7.57	26.02	25.58
6 (47)	20.2.90	13:30	22	7.36	26.64	25.92
3 (4)	13.5.90	14:10	3.5	7.09	27.06	24.14
5 (6.5)	14.5.90	08:25	5.5	7.07	26.64	25.04
33 (37)	15.5.90	12:00	30	7.21	26.48	25.61
32 (43.5)	16.5.90	10:42	25	7.31	25.81	25.51
Kisengera channel						
(40)	16.5.90	12:40	20	7.28	27.27	25.51
100 (34)	16.5.90	13:35	22	7.38	27.24	25.73
103 (59)	17.5.90	10:45	20	7.30	26.15	25.19

Table 7. Nutrient compositions (mg/l) (Total N. N-NH_4, N-NO_3, total P, Ortho-P, and the ratios between TN/TP) in samples collected in the Kenyan part of Lake Victoria during March 1989.

Station	Depth (m)	Total N (ppm)	NH_4 (ppm)	NO_3 (ppm)	Total P (ppm)	Ortho-P (ppm)	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	0.068	0.040	28.8
32	1	0.6	0.013	0.01	0.068	0.035	8.8
32	23	0.6	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	0.9	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	-	18.8
37	5	2.24	0.131	0.02	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	0.6	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

Table 8. zooplankton densities (No/l) in samples collected during March 1989. Copepoda include all life cycle stages.

Date	Station	Depth (m)	Copepoda No./l Calanoida	Copepoda No./l Cyclopoida	Cladocera No./l	Rotifera No./l
23.3.89	6	1	1	53	1	1
23.3.89	6	20	4	66	4	0
23.3.89	6	39	4	46	3	0
25.3.89	8	1	1	13	1	0
25.5.89	8	7	15	88	0	0
20.3.89	17	1	2	83	0	9
20.3.89	17	2	5	13	0	8
20.3.89	31	1	0	3	0	1
20.3.89	31	3	1	6	0	1
24.3.89	32	20	0	2	0	0
20.3.89	33	5	2	81	1	1
23.3.89	34	1	6	10	2	0
23.3.89	34	25	10	17	4	0
23.3.89	34	40	12	71	5	1
21.3.89	36	1	1	39	1	1
21.3.89	36	6	5	86	2	2
21.3.89	36	11	14	20	10	0
20.3.89	37	1	1	7	0	1
21.3.89	38	1	17	15	7	15
21.3.89	38	9	1	64	4	2
25.3.89	99	17	9	84	1	0
24.3.89	100	1	5	6	1	2
24.3.89	100	20	12	55	2	0
24.3.89	100	40	2	23	2	0

Table 9. Zooplankton densities (no/l) in samples collected during

Month	Station	Depth (m)	Copepoda Calanoida	Copepoda Cyclopoida	Cladocera	Rotifera
April	36	0	0	60	0	56
May	36	4	46	27	14	36
May	36	2	0	54	0	0
April	31	0	0	17	0	42
May	31	5	0	14	0	0
April	31	4	18	27	20	11
April	29	0	0	4	6	0
April	100	0	0	48	0	0
May	100	5	0	10	0	0
April	100	4	0	30	0	0
April	100	3	0	10	0	0
May	100	10	0	18	0	0
April	6	0	0	13	0	28
May	6	8	0	13	14	14
May	2	0	0	30	8	0
May	3	0	0	13	0	0
May	37	0	0	1	0	0
May	37	5	14	15	10	14
May	32	0	56	33	14	0
May	32	5	0	18	0	0
May	5	5	14	46	0	42
April	5	3	0	15	0	28
May	103	5	0	14	0	0
May	103	20	0	4	0	0
May	8	1	0	1	0	14
May	8	5	0	8	0	0
May	8	3	0	54	28	27
April	33	3	0	10	0	14
May	7	2	0	7	0	0
May	7	4	0	3	0	28
May	34	8	0	11	14	0
May	34	10	0	6	0	0
April	30	4	11	36	25	0

Table 10. Ranges of index of satiation (IOS) (see text): TV = *T. variabilis*; TZ = *T. zillii*; TN = *T. niloticus*; TE = *T. esculentus* NP = Nile perch; TL = *T. leucostictus*.

Date	Species	IOS range
4.1.1989	TV	0.2 - 1.1
4.1.1989	TZ	0.2 - 0.8
6.1.1989	TN	0.3 - 1.3
6.1.1989	TV	0.2 - 0.6
6.1.1989	TZ	0.9 - 1.2
19.1.1989	TV	0.5 - 2.1
19.1.1989	TZ	0.5 - 1.6
19.1.1989	TN	0.5 - 4.3
3.2.1989	TV	0.5 - 1.0
21.2.1989	TV	0.3 - 1.3
21.2.1989	TN	0.3 - 1.1
28.2.1989	TN	0.6 - 2.8
28.2.1989	TV	1.0 - 2.8
11.3.1989	TZ	1.0 - 1.1
11.3.1989	TN	0.3 - 1.1
11.3.1989	TV	0.71-0.74
12.3.1989	TV	0.3 - 0.5
12.3.1989	TZ	1.1 - 1.7
12.3.1989	TE	0.40-0.44
12.3.1989	TZ	0.4 - 3.4
12.3.1989	TV	0.6 - 1.6
12.3.1989	TL	0.4 - 0.6
12.3.1989	NP	0.8 - 2.8
12.3.1989	TV	1.1 - 6.1
12.3.1989	TE	0.9 - 2.3

Table 11. Food composition of T. niloticus (TN), T. variabilis (TV), and T. zillii (TZ). Numbers are cases of dominance (30-90%), and % are given.

	TN		TV		TZ	
	%	No.	%	No.	%	No.
Insect fragments	0.8	3	1.9	2	1.9	1
Trichoptera	8.0	31	22.1	23	20.8	11
Caridina	6.5	25	6.7	7	22.6	12
Sand grains	1.0	4	0.9	1	-	-
Mud	12.4	48	11.5	12	1.9	1
Chyronomids	5.7	22	3.8	4	1.9	1
Nematodes	-	-	5.8	6	1.9	1
Ostracods	5.4	21	0.9	1	-	-
Zooplankton fragments	2.1	8	-	-	-	-
Copepods	1.3	5	-	-	-	-
Bivalves	4.1	16	-	-	-	-
Moina	3.6	14	-	-	-	-
Chydorus	4.4	17	-	-	-	-
Fish scales	1.6	6	-	-	-	-
Spongilid spiculae	0.6	2	-	-	-	-
Simocephalus	-	-	-	-	-	-
Oligochaeta	0.6	2	-	-	-	-
Alona	0.3	1	-	-	-	-
Plant detris	10.6	41	20.2	21	35.8	19
Microcystis	4.9	19	3.89	4	3.8	2
Diatoms	7.4	28	3.89	4	3.8	2
Chlorophytes	3.6	14	2.9	3	1.9	1
Melosira	5.5	21	2.9	3	1.9	1
Detritus	3.2	12	4.9	5	1.9	1
Lyngbia	2.8	11	5.8	6	-	-
Anabaena	1.3	5	1.9	2	-	-
Ceratium	1.0	4	-	-	-	-
Filamentous chlorophyte	1.3	5	-	-	-	-
Total	100	386	100	104	100	53

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Part D: Summary of the Present Conditions of Physico-Chemical Structure and the Biota

Materials and Methods

During 1990-91 monthly (II, III, VIII-XII in 1990 and II-XI in 1991) 246 profile measurements of pH, DO, and Temperature were taken by Hydrolab System at 15 stations in 4 regions of the Kenyan part of Lake Victoria: 1) shallow (3-10 m depth) stations in Wynam Gulf, 2) deep (30-56 m) and 3) shallow (4-10 m) parts of Rusinga Channel (30-56 m) and in open-deep (30-66 m) waters. Measurements were carried out during day time between 0900 a.m. and 1700 p.m. Phytoplankton and zooplankton samples were collected during 1989-90 in Wynam Gulf, Rusinga Channel and offshore at 3 depths in each station: 1) 0 m or 1 m; 2) 7-10 m; and 3) 16-25 m (offshore zone). Fish were sampled from fishermen offshore catches and their viscera (intestine and stomach) was removed and weighed and the gut content was gently squeezed out and suspended by Vortex and analyzed (counted) in two steps: 1) under binocular for large items (small clams, insect cases and fragments, Caridina fragments, etc.) and b) under Flouvert Microscope for small organisms (algae, zooplankton, plant debris, etc.). The relative abundance (%) was calculated.

Results and Discussion

Averages of maximal and minimal values and gradients of pH and temperature are presented in Table 1. Profile gradients are the differences between maximal and minimal values measured for each parameter in each profile. Linear regressions between 1) maximal values of temperature and pH, 2) minimal values of temperature and pH, and 3) gradients of pH and temperature, were significant for the 2nd and 3rd groups: $r = 0.341$ ($p = 0.0001$) and $r = 0.463$ ($p = 0.0001$) respectively (DF = 245). These relations reflect a normal decline of temperature, and pH and DO depletion in the thermocline. In profiles with anoxia, a close association was indicated between minimal temperature, pH values of 7.70-7.00 and DO concentrations of < 4.0 ppm. The averages of pH gradients in profiles without anoxia varied between 0.54 (±0.31; n = 28), 0.36 (± 0.29; n = 14), 0.38 (± 0.24; n = 28) and 0.66 (± 0.50; n = 4) in the Wynam Gulf stations, shallow (4-11 m) stations and deep (30-56 m) stations of Rusinga Channel and offshore stations, respectively. The pH in profiles with anoxia varied between 9.60 and 6.65. Nevertheless, in anoxic profiles in offshore region and Rusinga Channel the averages of pH gradients varied between 1.75 (± 0.71; n = 63) and 1.63 (± 0.4; n = 74) respectively. The average depths (and ranges) of the stations in 4 lake regions, the depths of anoxic waters (i.e. depths of < 4.0 ppm DO layer) and secchi depths are presented in Table 2. Secchi depths measured during 1950-1960's by Talling (1966) varied between 1.0 and 3.9 m whilst our measurements (155) were 0.8-2.8 m.

We suggest that the disappearance of anoxic waters from the deeper (>30 m) part of Rusinga Channel was driven by internal seiche movements (Gophen et al. in preparation) which also injected anoxic waters to the shallows (< 10 m) as measured in two profiles. Nonanoxic profiles in Rusinga Channel (30-56 m depth) were observed during 7 months (II-IV, VII-IX and XI) and in offshore region in two months (II-III). We suggest that the 4 nonanoxic profiles (from surface to bottom) in the offshore region is also a result of internal seiche movements. Before the Nile perch invasion (Newel 1960; Talling 1957; Kitaka 1972) the upper depths of anoxic waters were measured between 45 and 75 m. Whereas, we found it at an average depth of 22-23 m (± 7-15) (Table 1). We suggest that major part of the deep waters (>23 m) of Lake Victoria, is consistently anoxic. This must be verified by an international efforts of the entire lake study. Moreover, we observed a 24 hour existence of anoxia in August and October in Rusinga Channel, the marginal zone of thermocline movements.

<u>Phytoplankton</u>

The phytoplankton in Lake Victoria is presently characterized by the high abundance of Cyanophyta. A high diversity but low abundance of Chlorophyta and diatoms was indicated. In Wynam Gulf species diversities and densities of algae were high whilst the offshore region was dominated by filamentous and coccoid cyanophytes accompanied by diatoms. Few chlorophytes were also recorded in the open water stations. Densities ranged between 300-10000 cells/ml. This range is higher than data presented by Talling (1987).

Zooplankton

Five, 6 and 10 species of Copepoda, Cladocera and Rotifera were respectively recorded. Copepod nauplii were abundant between 1-20 m depths. Whilst other copepod stages and cladocerans between 10-20 m. Rotifers were found mostly in the upper 5 m layer. Densities of Copepods varied between 1-46/l and 2-60/l for calanoids and cyclopoids respectively. Rotifers concentrations range was 0-56/l and Cladocera densities were very low.

Tilapias Food Composition

Total number of analyzed fish was 140: 70- T. niloticus; 46- T. variabilis; 24- T. zillii. Major part of the food of T. niloticus consisted of bottom fauna or deep water organisms (Trichoptera, Caridina, Chironomids, Ostracods, Clams, Moina, Chydorus, plant debris, Microcystis, Melosira, Pennales diatoms and small chlorophytes and mud particles. The gut contents of T. variabilis were dominated by Trichoptera, mud particles and large (> 50 μ) plant debris probably collected on the bottom.
The food composition of T zillii was similar to T. variabilis predominating by Trichoptera, Caridina and plant debris. Tilapias were indicated as pelagic planktivores in Lake Victoria before the Nile perch invasion (Okeyo 1989) and now, they are probably, more benthophagous feeders.

We compared our data with records from the 1960-1970's and 1980's (Talling 1966; Akiyama 1977; Melack 1979; LBDA 1984; Ochumba and Kibara 1989; Hecky and Mungoma 1991; and Goldschmidt et al 1990). It was indicated that secchi depths became shallower, algal concentrations were enhanced, zooplankton densities slightly declined, phytoplankton assemblages shifted from diatoms to cyanophytes dominance and primary productivity increased. HEST (1988) described feeding habits of haplochromid species in Lake Victoria as about 60% plankton-detritivorous. We suggest that the decline of these haplochromine species by Nile perch piscivory enhanced eutrophication in Lake Victoria.

Table 1: Averages (X), and SD's, of the maximal and minimal and gradients (the averaged differences between max. and min. values in each profile) of temperature (°C) and pH (n = 246).

		X	SD
Maximal Value:	pH	8.50	0.87
	Tem.	26.15	2.83
Minimal Value:	pH	7.35	0.71
	Tem.	25.24	2.77
Gradient:	pH	1.16	0.78
	Tem.	2.89	2.68

Table 2: Averages and ranges of station depths (m), secchi depths (m) and upper depths (m) of anoxic layer (<4.0 ppm DO) in 4 lake regions: Rusinga Channel (deep and shallow), Wynam Gulf, offshore (SD) (1990-1991).

Region	Depth	Ranges	Secchi*	Anoxia
Rusinga Channel-deep	47 (5)	30-56	2.0 (0.3)	22 (15)
Rusinga Channel-shallow	8 (2)	4-11	1.5 (0.2)	No
Wynam Gulf	8 (4)	3-15	1.4 (0.3)	No
Offshore	40 (8)	28-66	2.1 (0.3)	23 (7)

* Average of all (155) measurements: 1.8 m (± 0.4 SD) (0.80 m Min.-2.8 m Max.)

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