# LAKE VICTORIA WETLANDS AND THE ECOLOGY OF THE NILE TILAPIA, *OREOCHROMIS NILOTICUS* LINNÉ

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DISSERTATION
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*by*
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*To my parents, my family, brothers and sisters; to my teachers and my friends*

*Punctuated Equilibrium Comes of Age*

Stephen Jay Gould
Nature, 1993

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# Abstract

An ecological study of wetlands was undertaken in northern Lake Victoria (East Africa) between 1993 and 1996 with a major aim of characterising shallow vegetation-dominated interface habitats, and evaluating their importance for fish, in particular, for the stocked and socio-economically important *Oreochromis niloticus* LINNÉ (the Nile tilapia). From field and laboratory experiments, five major habitat types could be defined by the type of the dominant emergent macrophyte at the shore from the more than 40 identified plant species along a 110 km shoreline. These were: *Cyperus papyrus* L. (papyrus), *Phragmites mauritianus* Kunth (reeds), *Typha domingensis* Pers. (bulrush), *Vossia cuspidata* (Roxb.) (hippo grass), and the alien floating *Eichhornia crassipes* (Martius) Solms-Laubach (water hyacinth). From digital data, considerable long term changes in the shoreline wetland landscape of the lake were discerned and appeared to be primarily associated with increasing human activity (e.g., agriculture, biomass harvests) which had resulted into a 5 % reduction of wetland cover. Inspite of the absence of a well developed euhydrophyte community (e.g., *Potamogeton* and *Ceratophyllum*), and increasing infestations with *E. crassipes* mats, the width of the littoral zone was established by secchi transparency as being about 50 - 70 m away from the shallow (less than 1 m deep) vegetation fringe sloping to between 2 and 4 m in depth at its outer fringe. Hydrological influences associated with seasonal changes (the alternation of rainy with dry periods) explained most of the observed variation in abiotic (e.g., Si, tot.-P, soluble reactive-P, $NO_3$-N, pH, temperature) and biotic (phytoplankton, macrofauna, fish) factors, but there was also significant ($p <$ 0.05) variation due to vegetation, distance from the shore out towards open water and interaction effects between these factors. At least 30 species of fish were identified from the shallower (2.5 m) vegetated habitats in contrast to 10 species from the deeper (4 - 8 m) open water habitats. There were other significant ($p <$ 0.05) spatial and temporal differences in habitat use by fish. Species diversity was dominated by haplochromine species but three stocked species (the Nile perch, *Lates niloticus* L., *O. niloticus* and *Tilapia zilli*) contributed at least 90% of the estimated numerical and biomass densities of which, the Nile tilapia was the most important component making up 45 - 65 % of the biomass of all fish. Season was a major factor in size-related abundance patterns but generally, most of the Nile tilapia biomass was associated with *Phragmites-Vossia-Typha*-dominated habitats which were also important for small (<15.0 cm) and juvenile fish. The shallow vegetated habitats were found to be ecologically important for the Nile tilapia for sheltering and feeding, and, it was also found that Lake Victoria Nile tilapia were significantly more fecund (with 3723 ± 147 eggs.female[-1]) and had a higher condition index than populations of the species in Lake Kyoga (also stocked) and Lake Albert (a native habitat). It was inferred that these differences could be a result of a better nutritional base in Lake Victoria where the species was shown to be omnivorous (with detrital and animal foods as major dietary items) contrary to the previously believed herbivorous (phytoplankton) habits. Successional patterns associated with water hyacinth and the strong hydrological influences on shallow vegetated habitats imply that basin disturbances could therefore be a major threat to water quality and the fisheries.

# Chapter 1

## Introduction

Lake Victoria in East Africa covers an open water surface of about 68,500 km$^2$ making it the second largest lake in the world. Major determinants of its morphometry, hydrological balance and geographical features (Table 1) include a 3,440 km long shoreline characterised by a variety of vegetated littoral habitats frequently referred to as swamps. The plant communities of these swamps are closely linked to the ecology of the lake (Beadle, 1981), particularly that of the littoral zone.

Table 1.    Morphometry, hydrological balance and geographical features of Lake Victoria

| Characteristic | measure | |
|---|---|---|
| Position:  Latitude | 0° 20'  - | 3° 00' S |
| Longitude | 31° 39'  - | 34° 53' E |
| Altitude (m above sea level) | 1134 | |
| Catchment area (km$^2$) | 184,000 | |
| Lake basin area (km$^2$) | 68,500 | |
| Lake area as % catchment | 37 | |
| Shore line (km) | 3,440 | |
| Max. length (km) | 400 | |
| Max. width (km) | 240 | |
| Mean width (km) | 172 | |
| Max. depth (m) | 84 | |
| Mean depth (m) | 40 | |
| Volume (km$^3$) | 2,760 | |
| Inflow (km$^3$.yr$^{-1}$) | 20 | |
| Outflow (km$^3$.yr$^{-1}$) | 20 | |
| Precipitation (km$^3$.yr$^{-1}$) | 114 | |
| Annual lake level fluctuations (m) | 0.4  - | 1.5 |
| Max. rise in lake level (m) | 2.4 | |
| Flushing time (years) | 138 | |
| Residence time (years) | 21 | |

Sources: (Crul, 1995; Scheren, 1995; Hecky & Bugenyi, 1992)

Among the more common wetland plant communities at the shore are those dominated by the emergent species: *Cyperus papyrus* L. (papyrus), *Vossia cuspidata* (Roxb.) (hippo grass), *Typha domingensis* Pers. (bulrush) and *Phragmites mauritianus* Kunth (reeds). Their areal extent is large but not exactly known. These wetlands have undergone considerable hydrological and geographical changes; initially following a rise in lake level in 1960/62 (Welcomme, 1965), and, over the last decades, an increase in the human population in the catchment. Reclamation of the remaining swamps could lead to a reduced buffering capacity resulting in a

further eutrophication of the lake (Crul, 1995). The relatively recent (1989) appearance but rapid spread of the exotic floating aquatic weed, *Eichhornia crassipes* Mart. Solms-Laubach (water hyacinth) in the lake (Twongo, 1991) especially along the shores seems to have become a permanent structural part of the lake's shoreline ecology.

In general, large stretches of the Lake Victoria shoreline lack a characteristic and well developed underwater flora (e.g., of *Ceratophyllum* and *Potamogeton*) at the shallow interface between the shoreline and open water. In addition to the eutrophication (Hecky, 1993), extensive water hyacinth mats may suppress development of natural euhydrophytes in general. Therefore, it is difficult to define the lakeward extent of the littoral zone solely in terms of these plants, even though they are often used (Odum, 1971) to classify such areas. Interface habitats can be classified according to their dominant structural features at the lake shore. These may be macrophytes, rocky or sandy areas.

This study mainly concerns aquatic habitats backing on emergent macrophyte dominated shorelines. Other structural elements in these shallow habitats include nutrients, plankton, macrofauna, bottom sediments and fish. The relative qualitative and quantitative importance of the structural elements is strongly influenced by physical factors (temperature, oxygen, pH, conductivity, depth, slope and fetch) as well as space (distance from the shore) and time (diurnal and seasonal) scales. By use of secchi transparency, it is possible to define the width of the littoral zone off the respective dominant macrophytes at the shore, and to study the ecology of shallow aquatic ecosystems. For Lake Victoria, this is a new approach as most studies on this lake have been based either within the swamps (e.g., Carter, 1955; Lind & Visser, 1962) or further away from the edges i.e., from the sub-littoral zone out into the open water (the majority of studies). In the latter, habitats have frequently been referred to as inshore, offshore, open water, etc without much indication of the defining structural elements.

## Overview of the research problem

Specific concern for the health of the Lake Victoria ecosystem is directly related to human impacts on fisheries, wetland buffers and water quality. As a result of these, fish species changes, wetland degradation, water quality changes (eutrophication) and invasion by the exotic water hyacinth, *E. crassipes*, currently threaten Lake Victoria's littoral zone. These impacts probably account for part of the ecological changes in Lake Victoria as a whole about which much has been reported. However, in comparison to the open lake, much less is known about the ecology of the shoreline wetland belt in spite of its assumed ecological and biodiversity importance. This lack of detailed knowledge adds to uncertainties caused by the rapid human population expansion (including urbanisation), leading to more pressure on wetland and aquatic resources, and thus fuelling further ecological changes in the whole Lake Victoria ecosystem but especially in the littoral zone. In addition, the previously important endemic fish species (e.g., *Oreochromis esculentus* Graham, *O. variabilis* Boulenger) in the littoral zone and the

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high fish species diversity there, have been replaced by stocked species, especially *O. niloticus* Linné (the Nile tilapia) which now dominate the socio-economically important fisheries. Because of the rapid and relatively recent changes in the lake ecosystem, many of which are due to external factors, and are more quickly manifested in the littoral zone, there is a need to establish to what extent the associated wetland dominated habitats are playing a significant role in the ecology of the lake, in order to sustain multiple uses of the aquatic resources.

Fish as an important socio-economic tool could be used to improve aquatic resources' management and conservation strategies, for instance for wetlands. Therefore, the main interest of the present study was to identify and characterise major shoreline wetlands in Lake Victoria's littoral zone in relation to the ecology of the commercially important fish, the Nile tilapia (*O. niloticus*).

Based on literature and general assumptions, it appeared reasonable to assume that wetlands, especially macrophyte dominated interface habitats, are important in the ecology of fish. The main goal of the study was thus to identify and characterise shoreline vegetation dominated habitats in Lake Victoria, and to show which of the structural elements in these habitats were important in the ecology of the Nile tilapia.

As these habitats are assumed to be important fishery areas, it was also expected that there would be significant differences in fish populations between areas adjacent to the lake edges and those further away towards open water habitats of the lake. To prove whether or not this is the case, two null hypotheses for the study had to be formulated thus:

(1) There are no significant structural differences among or within shoreline vegetation dominated habitats, (2) there are no significant effects of the habitats on the ecology of fish.

To establish influence or non-influence of wetland type, the experimental design was based on *in situ* structural features of the littoral zone rather than on hypothetical populations as in controlled experiments. Hence, the sites sampled were selected with the aim of maximising the range of littoral vegetated habitat types which were considered to be representative of the large scale shoreline landscape. *C. papyrus* is the most dominant fringing community type at the shore and was therefore more represented in the sampling regime. *E. crassipes* which is a new wetland feature of the shoreline, was included in this study, and was considered to be a form of modification of the natural wetland landscape.

## Study approach and structure of the thesis

The study was planned as an integrated ecological investigation. The Jinja area of Lake Victoria was selected as the base for the studies because of the logistical and laboratory facilities it could provide for lake sampling. Since it was assumed that these wetlands have undergone considerable areal geographical changes, the area

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was first examined for evidence of cover change which could be ascribed to human activity. Therefore, an initial survey of the major wetland vegetation types in the Jinja area was undertaken to evaluate whether the area indeed represented the larger scale landscape of the lake's shoreline. For each habitat type, replicate sites were identified and within each site, two zones were categorised: the first being nearest to the vegetation fringe and another representing areas perpendicular to but further away from the fringe vegetation towards open water. In addition, an evaluation of climatic data indicated that four seasons could be recognised. These seasons together with the periods to which they approximately corresponded (in parentheses) were: the main dry season (15 December to 15 March), the main rainy season (16 March to end of June), the short dry but cool season (July to 15 September) and the short rainy season (16 September to end of November). Therefore, sampling of most sites was carried out in specific seasons, usually during the middle of each season. However, there was unexpected rain (February, 1996) during a normally dry period. Subsequently, apart from characterising habitats of assumed importance for fish populations, exploratory data analyses were aimed at detecting possible influences and relationships which could lead to further hypothesis testing. For a number of experiments comprising of this study, interrelated hypotheses were generated and they form part of this study.

As this is a pioneering study in the region, a lot of background information is given in **Chapter 2** with regard to the lake shore wetland habitats and fisheries of Lake Victoria in general. In order to highlight the importance of the littoral zone for fish, some emphasis is given to the littoral zone as a mosaic of interface habitats, distinct from both the interior of the swamps, and, areas further away from the shoreline towards open water. Although there seems to be substantial information on the biology and ecology of the Nile tilapia in East African lakes, the literature does not provide much quantitative data on the species in wetland habitats of these lakes, especially those of Lake Victoria about which there is even less information. This chapter therefore also provides an assessment of what is known about the Nile tilapia in the lake, since its stocking there in the 1950's.

In **Chapter 3**, the study area is described and results of preliminary investigations on wetland distribution in the area are given. Apart from an inventory of plant communities for the area, temporal changes (between 1950/60 and 1992) in the wetland landscape are evaluated from topographic and satellite images. The chapter also characterizes study sites according to dominant macrophytes at the shore. The investigated habitats were associated with *C. papyrus*, *V. cuspidata*, *T. domingensis*, *P. mauritianus* and *E. crassipes* as the dominant macrophytes, and are regarded as habitat types. Analyses of significant differences in structural aspects are therefore based on differences in comparable factors among these habitats. It is shown that most components of structure (e.g., sediment types and their composition, nutrients, pH, oxygen, etc), including the biotic (e.g., macrophyte biomass, phytoplankton and macrofauna) significantly vary among habitats. Seasonal (hydrological) and horizontal (distance from the edge off each dominated macrophyte habitat) effects appear to be equally important, and are

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emphasised in relation to landscape changes. This chapter lays the basis for fish studies.

**Chapter 4** deals with fish populations of the shallow habitats after reviewing fish species and other trophic changes in the lake. The overemphasis on sub-littoral habitats in past fish studies meant that complimentary data on macrophyte-dominated habitats lagged behind as these habitats became degraded. However, like in many other parts of the lake, fish community structure here is dominated by the stocked species, especially *O. niloticus*, but the habitats still contain many other endemic species. This chapter therefore provides data on fish species composition and relative abundance in shallow macrophyte-dominated habitats in comparison to areas further away from the shores. In addition, the chapter findings are compared with what has been observed in other parts of the lake. The increasing influence of *Eichhornia crassipes* infestations is also evaluated in relation to its association with other macrophytes. As a result it is possible to distinguish between two major types of papyrus dominated habitats.

Nile tilapia of all sizes have been caught in different seasons from various habitats, ranging from shallow to the deep open areas of the lake. The hypothesis that abundance and size structure in *O. niloticus* vary independently of wetland habitat type, season and distance from the shore is tested in **Chapter 5**. In terms of biomass, *O. niloticus* is the most dominant fish species in macrophyte-dominated habitats of the littoral zone, and in general, the biomass decreases with distance from the shore. This chapter discusses significant patterns explaining size and biomass dependency on, and, differences among the investigated habitats. Seasonal patterns seem to be associated with reproduction, and this aspect is explored further in **Chapter 6** which also compares the species life history in Lake Victoria with data from Lakes Kyoga and Albert. Physico-chemical differences (e.g., conductivity, alkalinity, pH) among lakes and biotic factors (e.g., predation, food) which could account for variations in maturation and fecundity are discussed.

**Chapter 7** is a detailed examination of the feeding and trophic characteristics of the Nile tilapia. One of the most investigated aspects of the species' ecology in various lakes is its feeding, and the species has been described as a primary consumer feeding mainly on phytoplankton. Analyses of its diurnal activity and feeding patterns, and examination of stomach contents, indicate an omnivorous diet including insects as main prey items. The association between ingested phytoplankton and detrital material suggests benthic feeding habits. Together with utilisation of other non-plant food items, the species position in the food web structure of the lake is discussed in relation to environmental changes which may impact fish ecology. This latter part is continued in **Chapter 8** which looks specifically at the increasing influence of water hyacinth in Lake Victoria.

An overall summary and synthesis of the results from this study is made in **Chapter 9**.

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## Chapter 2.1

## The Lake Victoria environment: its fisheries and its wetlands - A Review[*]

### ABSTRACT

Recent ecological changes in the Lake Victoria ecosystem have been attributed to the role of species stockings and, in particular, from predation pressure by the Nile perch. Evidence for the decline of haplochromines due to predation by the Nile perch, while overwhelming, does not necessarily account for these gross ecological changes. Ecological theory predicts that natural fluctuations would occur in a fisheries where predator and prey species could alternate in abundance. The absence of a substantial recovery of endemic species within cyclical abundance patterns in Lake Victoria (even though they could be delayed), particularly in the pelagic and profundal zones, points to other casual factors.

Ecological changes have occurred in Lake Victoria since the turn of the century when modern fishing methods and techniques were introduced. As the human population increased and the catchment became more exposed to diverse socio-economic activities, further pressure on the ecological functioning of the lake was compounded by exotic species stockings. Thus, declining fisheries, wetland degradation and eutrophication are part of gross environmental changes which are likely to become more manifest with the increasing impact of the water hyacinth. It therefore seems appropriate to consider the ecological changes at both temporal and spatial scales and to re-examine some of the paradigms for ecological change.

Although catacyclismic impacts may have occurred between the 1960's and the early 1980's, the basic cause of ecological changes at least in the inshore zone appears to be the impact of human activity partly associated with a degradation of the riparian wetlands that exposes the aquatic ecosystem to catchment activities. Over-exploitation and a reduction in habitat quality and quantity in this zone could be major factors in the ecological transformations. However, the importance of the littoral zone and the ecological impact of the Nile tilapia, another stocked species, are hardly known. An additional hypothesis is therefore put forward to show whether or not wetland vegetation types in Lake Victoria are important fish habitats. This hypothesis allows for testing several interrelated sub-hypotheses on questions regarding relationships between wetland vegetation and the ecology of the Nile tilapia. The water hyacinth, a recent feature of the shoreline and an additional strain to the already endangered buffer zone, may have to be regarded as a dynamic but permanent part of most of the littoral zone.

### INTRODUCTION

Lake Victoria, (2.5°S to 1.5°N) is the world's second largest freshwater body (surface area = about 68,500 km$^2$; max. depth = 84 m), has an adjoining catchment area of 184,000 km$^2$, and has a shoreline length of 3,440 km (Beadle, 1972; Kite, 1982; Hecky and Bugenyi, 1992). The coastline is very irregular, and the entire lake is shared between Uganda (43%), Tanzania (51%) and Kenya (6%) (Fig. 1). Numerous seasonal streams are a characteristic feature associated with

extensive but presently threatened wetland vegetation that fringes the shoreline. The Lake Victoria basin has been the single most important source of protein (fish) and a major economic resource for its densely populated basin. It is estimated that in 1990, the lake accounted for 25% of the total inland catch in the whole of Africa (IDRC mimeo, 1992). Judging by an earlier study (Kudhongania and Cordone, 1974), a significant fraction of the ichthyomass (14%) was derived from the shallow (0 - 9 m depth; 8% of total area of the Tanzanian part of Lake Victoria) zone also frequently referred to as the tilapia zone or the artisanal fishery zone. Systematic observations carried out at a transect in the Mwanza gulf between 1977 and 1991 indicate that in spite of the changes in the fisheries since the 1980's the shallow area still contains a higher fish species diversity and production potential than offshore deeper areas (Witte and Goudswaard 1984 and Witte et al.; 1992).
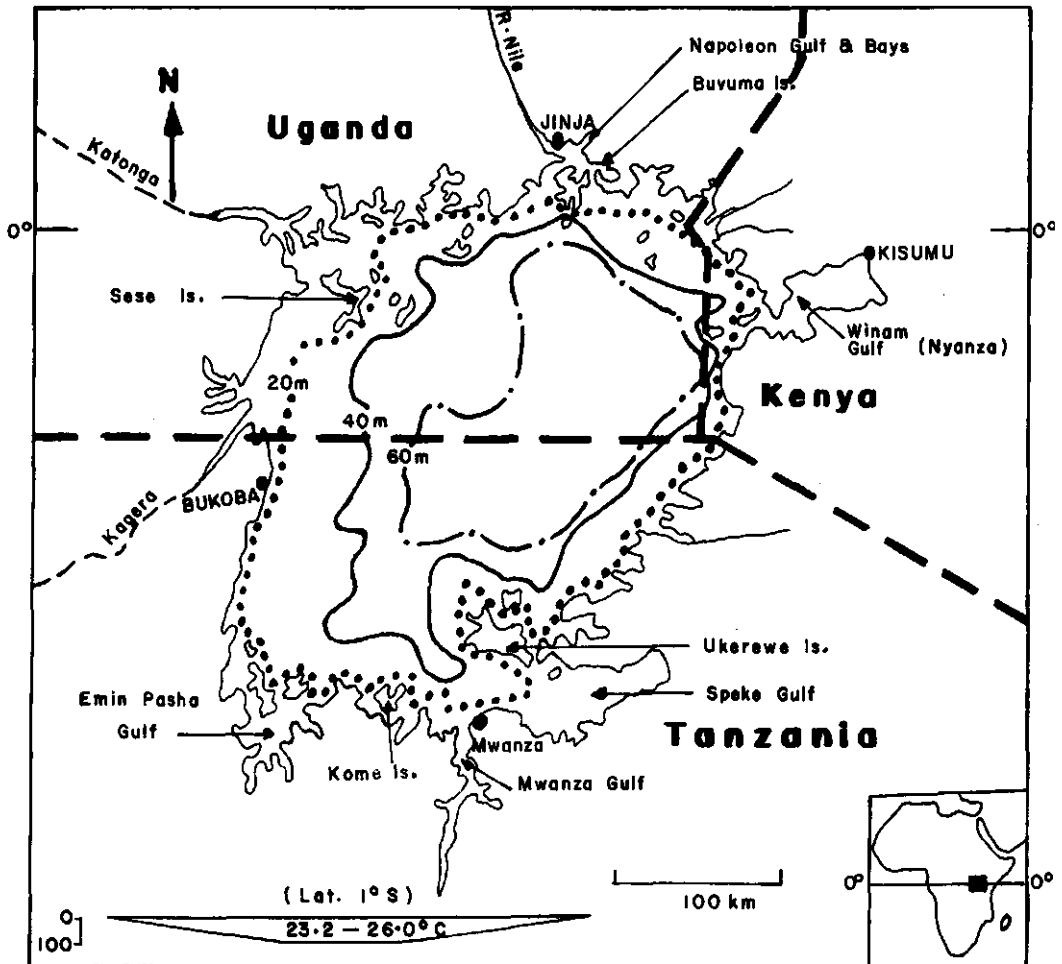


Fig. 1.    Bathymetric map of Lake Victoria and its location (inset) with some of its physical features depicted in the bottom left.

## The fisheries

The fact that fisheries catch data from the lake also includes landings from the floodplain and the marginal wetland zone sources is often overlooked. For practical purposes e.g., for marketing, the catch irrespective of source, is pooled at fish landings or disappears into local outlets closest to fishing grounds. This catch from outside the open lake surface may be large. Welcomme (1972) estimated that wetland and floodplain-related catches contribute about 40% of the total freshwater catch of the African continent. Marginal wetlands and floodplains may contribute to catches in the following aspects:

(a)  Flood-plains and wetlands form temporary fish feeding habitats especially during periods when they are inundated;

(b)  Wetlands and, to some extent, flood-plains may form spawning and nursery habitats for some fish;

(c)  Many are sites of small-scale fisheries which still rely on this inshore zone for their livelihood by gill-netting, angling and trapping fish; the swamp fisheries such as at lake edges are of much greater direct importance to local communities than open lake catches;

(d)  Wetlands may be a major source of materials and substances that enhance fish production in the adjacent (shallow) lake zone and therefore act as regulators of water quality for aquatic ecosystems.

Apart from fisheries, wetlands and floodplains may be intensely used as grazing and agricultural areas (especially as market gardens) and are among the first areas to be impacted by man (Loffler, 1990). Thus, the various roles to which wetlands may be subjected gives rise to conflicting demands which may be detrimental to entire aquatic ecosystems and their dependent fisheries. In some landlocked countries (e.g., Uganda) with extensive wetland systems surrounding commercially large lake fisheries, the stability of wetlands may be important in sustaining the viability of the fisheries apart from the other wetland functions. It is therefore not surprising that wetland degradation could be contributing to the uncertain future of Lake Victoria.

## The ecological transformations of Lake Victoria

Uncertainty about Lake Victoria is a result of several factors: (a) alien fish stockings, (b) over-exploitation of the fisheries, (c) a rise in lake level during 1960's, (d) regional climate changes, (e) increased nutrient inputs from the atmosphere and catchment, (f) reduction and reclamation of the buffer wetland zone, and, (g) colonisation of the lake by the water hyacinth. However, apart from (a) and (b) many of these factors are only beginning to be considered as critical in the transformation of the lake (Coulter *et al.* 1986; Bugenyi and Balirwa, 1989; Hecky, 1993; Bootsma and Hecky, 1993). It is thus not surprising that, until

recently, all changes (especially in the productivity of Lake Victoria) were considered primarily in terms of fisheries management. For instance, a major objective of stocking the lake with the Nile perch and the tilapias was to increase the fish yield and encourage a return to the use of appropriate gear (Hamblyn, 1960; Anderson, 1961; Gee, 1965). This is understandable given the declining catches at the time and the central role the lake plays in the livelihood of residents in its densely populated watershed. Lowe-Mconnell (1994) suggests that lake management urgently needs a unified Lake Victoria Fisheries Commission, to unify statistics and legislation in the three riparian states, and that the use of the lake's bays to culture tilapias and other species already in the lake would be more advisable than further fish introductions. However, owing to the complexity of the once multi-species fisheries, the unresolved interrelationships between the fish faunal changes and the eutrophication (Lowe-McConnell, 1992), and the failure of previous attempts at effective unified management (Kudhongania, *et al.*, 1992), it appears that *fisheries management* has approached its limits.

There are various factors, especially human activity, that have become associated with a simplification of the Lake Victoria ecosystem (Bugenyi and Balirwa, 1989; Kaufman, 1992; Bootsma and Hecky, 1993; Hecky, 1993; Lowe-McConnell, 1994). Apart from anthropogenic use of the wetland buffer zone, the rapid spread of the water hyacinth (*Eichhornia crassipes* (Martius, Solms - Laubach) along the lake margins (Twongo *et al.*, 1992) is a recent phenomenon which adds further uncertainty to the sustainabilty of the fisheries. There is therefore need to look at other factors apart from fisheries management that could be addressed to improve the conditions and to check further deterioration of the Lake Victoria system.

An important problem is to understand the importance of riparian wetlands to ecological processes of the near shore environments, especially as the shoreline is increasingly influenced by human activities and the water hyacinth (an exotic). A study of wetlands is logical for the benefit of both fisheries and water quality.

This review paper is part of the research which will examine the influence of wetland type on the ecology of *Oreochromis niloticus*. By focusing on the littoral zone, wetlands and a fish of commercial importance, it is hoped that the study will hopefully stimulate additional research into the ecological importance of wetlands and their management in a framework that includes various other concerns such as sewage disposal, agriculture and maintenance of local biodiversity. A review of previous studies is given and gaps in ecological theory that account for a deterioration of the Lake Victoria ecosystem as a whole are highlighted. In subsequent contributions, the major wetland vegetation types that represent the larger scale wetland landscape of Lake Victoria will be characterised and important fishery zones identified.

## Wetlands and their management

Many freshwater ecosystems are dynamically dependent on the riparian zone, and knowledge of links between fish and land/inland water ecotones should be of great importance in improving understanding of processes in aquatic habitats. Wetlands may be considered as ecotones, which are transition zones between adjacent ecological systems, having sets of characteristics uniquely defined by space and time scales and by the strengths of interactions between adjacent systems (Holland, 1988). As a result of their complexity, various functions/uses are associated with wetlands (Carter, 1955; Denny, 1985; Welcomme, 1985; Loffler, 1990; Zalewski *et al.* 1991). Table 1 is a summary of the major functions and the human values associated with wetlands. Common fauna of the tropical African wetlands have been described by Bugenyi (1991) and include various bird species, hippo, crocodile, sitatunga, and a variety of fish species which may either utilise wetlands for part of the year or are permanent residents adapted to living in the packed vegetation-water matrix with conditions of low dissolved oxygen.

Table 1.    Major wetlands functions and human values.

| wetland function | human values |
| --- | --- |
| 1. High species diversity of fauna and flora | Gene pool; Recreation |
| 2. Habitats: for fish as nursery, feeding and refuge areas | Fish as food |
| 3. Nutrient retention | Biofilters (nutrient strippers) |
| 4. Agricultural buffer zones (irrigation and drainage) | Food crops especially during dry periods |
| 5. Biomass export | Fuel, building materials and handicrafts |
| 6. Water source | For domestic and livestock use |
| 7. Presence of pests (undesirable organisms) | Disease vectors e.g. mosquitoes, snails |

The stability of wetlands can be especially important to the ecological functioning of inland waters such as lakes. Figure 2 (redrawn from Loffler, 1990) summarizes the kinds of global uses of wetlands by man. The figure suggests the importance of fisheries while the same author discusses the variety of wetlands plants used by man as food and their nutritional composition. Other uses of wetlands in landscape ecology include the capture, storage and gradual release of rain water and run off; ground water recharge and influence on microclimate.

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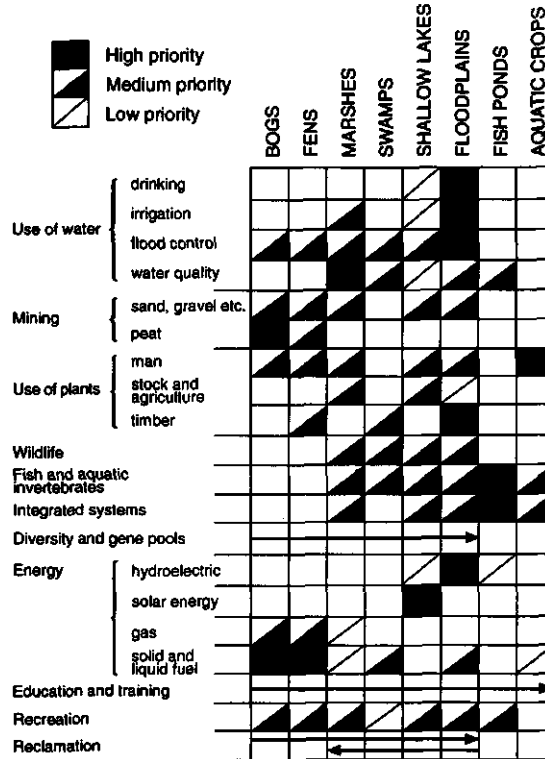
Fig. 2.    Major global wetland uses (after Loffler 1990).

A major question on Lake Victoria now concerns the role of wetlands in aquatic biodiversity on one hand and, on the other, genuine socio-economic uses of the wetlands such as fisheries, biomass export, agriculture and wastewater treatment. Hecky (1993) suggested that population growth is the basic cause of aquatic impacts from primitive agriculture, intense animal husbandry and shoreline access for fishing. Sustainable use of the aquatic resources requires a substantially increased ecological research base if applicable ecotechnological solutions are to be found for the entire lake basin.

Studies of the ecology of African wetlands are few (Denny, 1985) and most of the information available on the structure and function of wetlands is about temperate communities. Results of community studies of European wetlands e.g., Dutch wetland systems, are at a level where management options have been tried and evaluated (Wirdum, 1991; Verhoeven; 1992; Wigbels, 1992; Balirwa, 1993; Van Vierssen; 1993). In such situations it is possible to evaluate the benefits and costs of wetland management and conservation, although environmental conservation and ecological restoration have been the main focus of activity.

Several studies in what can be regarded as pioneering works on tropical wetlands include those on nutrients (e.g. Viner, 1975; Gaudet, 1978, 1979; Chale, 1984) and productivity (Muturi et al. 1989). Denny (1985) reviewed the ecology and management options for African wetlands while Wolff and Smit (1990) and Wolff et al. (1993) analyzed the ecological structure and functioning of The Banc d'Argiun wetland area of Mauritania, West Africa, with an emphasis on the area as an environment for birds. However, to my knowledge, there is hardly any published information on how wetland structure and function might affect fishes and fisheries in Lake Victoria - one of the Great Lakes in Africa under threat from human activity (Hecky, 1993). Howard-Williams and Thompson (1985) observed that wetland conservation in general is not a priority in tropical countries while Bugenyi (1991) suggested relating wetland conservation and management options to economic issues of individual countries. In many of these countries particularly in the region of the Great Lakes of Africa, fish is food for millions of people and the sustainability of the fishing industry may be the key to coupling wetland management and conservation to other benefits such as water supply for drinking, agriculture and industry; aesthetic and scientific value. Lake Victoria for example provides essential resources to more than thirty million people in East Africa and supports a commercial fishery valued at nearly three hundred million dollars per year (Kaufman, 1992). Wetland management and conservation could therefore be related to sustaining fisheries of socio-economic importance, an option which would also serve other values such as regulated biomass harvests, nutrient stripping and biodiversity concerns.

### The state of the Lake Victoria fisheries
Early research based at EAFRO[1], later EAFFRO[2], UFFRO[3] and presently FIRI[4] was instrumental in documenting the development of the fisheries from the very first survey of the lake by Graham (1929). The original fish community of Lake Victoria included at least 300 species, mostly comprised of haplochromine cichlids (van Oijen et al., 1981), and at least 14 cyprinids (mostly Barbus species; Balirwa, 1984). Besides the ecologically dominant haplochromines, 11 other genera supported continuously or intermittently a significant fishery (CIFA, 1984). By the 1950's when the catches of most target species (especially Oreochromis esculentus, O. variabilis and Labeo victorianus) had drastically declined due to overfishing, several tilapias (O. niloticus, O. leucostictus and Tilapia zillii) and a predator (the Nile perch -Lates niloticus), were stocked to boost the fisheries (EAFRO/EAFFRO, 1959; Garrod, 1961; Gee, 1965; Welcomme, 1981, 1988).

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[1]EAFRO = East African Fisheries Research Organization
[2]EAFFRO = East African Freshwater Fisheries Research Organization
[3]UFFRO = Uganda Freshwater Fisheries Research Organization
[4]FIRI = Fisheries Research Institute

A recovery of the endemic tilapiines attributed to the exceptionally heavy rains of the 1960's (Welcomme, 1966a, b). Thereafter, an apparent improvement in the fisheries from the early 1980's boosted by the stocked Nile perch and *Oreochromis niloticus* was accompanied by a drastic reduction in the fish species diversity especially of the haplochromine cichlids (Witte *et al.*, 1992a, b). Other significant ecological changes include increased algal biomass (especially of cyanobacteria) and reduced oxygen levels approaching anoxia in bottom waters (Bugenyi and Hecky, 1992; Mugidde, 1993).

Eutrophication in Lake Victoria was observed while the fish community was changing (Hecky, 1993) and there is concern about what should be done to "clean up the lake" (Baskin, 1992). For all practical purposes, the Lake Victoria fisheries are presently based on three species: a small native pelagic cyprinid called *mukene* in Uganda (*Rastrineobola argentea*); the introduced Nile perch (*Lates niloticus*) and Nile tilapia (*Oreochromis niloticus*). The relatively recent colonization of the lake by *Eichhornia crassipes* (Twongo *et al.*, 1992) is considered as a long term threat to the fisheries (Willoughby *et al.*, 1993). However, from the seemingly its well established nature, *Eichhornia* might as well be regarded as permanent but dynamic, feature of Lake Victoria's shoreline.

**Perturbations of the Lake Victoria ecosystem**
Ecological research at EAFRO undertaken in 1949-1953 identified the major fish faunal assemblages of Lake Victoria and included basic limnological data on water chemistry, lake stratification, phytoplankton, invertebrates important as fish food, ecology of indigenous tilapias, haplochromines and non-cichlids was undertaken (EAFRO/EAFFRO, Ann. Rep (1949 - 1964). This earlier research includes evidence for changes in the hydrochemistry, primary productivity and fisheries of the lake. These studies suggested (Beauchamp, 1952) that removing too many herbivores from the lake (particularly the tilapias) would slow the rate of biological production. The annual reports also include accounts of the positive impact on the fisheries of an abnormal rise in lake level following the heavy rains of the 1960's (Welcomme, 1964a, b; 1966; 1967).

It is not clear if the increase in nutrient concentrations were caused by short-lived rise in lake level that caused increased fish populations, or the excessive fishing effort which reduced the herbivore biomass. Since that period however, the lake level seems to have stabilised (after another rise in the period 1978/79; Kite, 1982) at a lower level and some previously submerged are now terrestrial patches and no longer available as fish habitats.

Other recent limnological data from both offshore and inshore stations of the lake indicate changed conditions of temperature and dissolved oxygen profiles and algae between about 1960 (Fish, 1957; Talling, 1966) and 1990 (Hecky and Bugenyi, 1992; Hecky, 1993; Mugidde, 1992). These studies suggest that even before the Nile perch explosion of the late 1970's and early 1980's. Moreover, one of the possible consequences of regional climatic changes or changes in water yield from

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the catchment (Hecky *et al.* 1993) is the increased stability of thermal stratification leading to a reduction of deep water oxygen concentration (Hecky, 1993; Hecky *et al.* 1993). This would result in a reduction of the habitable space (Hecky, 1993) and the fish kills reported by Ochumba and Kibaara (1989). It is also probable that some factors of historical significance apart from over-exploitation, and now presently indicated in the sediment record would help elucidate forces that are partly responsible for the present ecological state of the lake. There is a remote, but possible role for some cataclysmically selective phenomenon in a geologically infinitely short period (2 decades).

The effects of predation were initially thought to account for the rapid (within 10 years from the timing of the Nile perch upsurge) and almost total decimation of the endemic fauna pointed to predation pressure by the Nile perch (e.g., Okemwa, 1984; Barel *et al.*, 1985 Goudswaard and Witte, 1985; Ogari, 1985; Ogutu-Ohwayo, 1985, 1988, 1990a; Okaranon *et al.*, 1985; Balon and Bruton, 1986; Hughes, 1986; Goudswaard and Ligtvoet, 1988; Ogari and Dadzie, 1988). While the impact of predation by the Nile perch is undeniable (Witte et al. 1992a, b), some authors (Lowe-McConnell, 1975; Marten, 1979; Ssentongo and Welcomme, 1985; Acere, 1988; Kudhongania *et al.*, 1988; Kudhongania *et al.* 1992) have attempted to put into perspective other earlier accounts (e.g Beauchamp, 1955; Cadwalladr, 1965; Fryer, 1976; Mann, 1970) of forces (especially over-exploitation leading to growth and recruitment overfishing) that at least account for the initial decline in the originally abundant inshore and riverine endemic species particularly *O. esculentus, O. variabilis* and *Labeo victorianus*. This suggests that the disappearance most haplochromines may be strongly related with predation by the Nile perch. This has, in fact, been demonstrated by studies on the feeding habits of the species in Lake Victoria (Ogari, 1985; Ogari and Dadzi, 1988; Goudswaard and Ligtvoet, 1988; Ogutu-Ohwayo, 1985; 1990b) that also indicate both size and depth related patterns in prey-selection (Witte *et al.* 1992a, b). Willoughby *et al.* (1993) demonstrated that haplochromines are still the dominant group in inshore habitats despite the population expansion of the introduced species, *Oreochromis niloticus* and *Lates niloticus*. It was also shown by the study that haplochromines were breeding in these inshore areas, whereas the introduced species were not found in breeding condition in the vicinity.

A major conclusion which can be drawn from these studies with regard to the impact of the Nile perch is that the predator seems to have been most effective in reducing those species of *Haplochromis* in the habitats frequented by the piscivorous phase of the predator - principally from the sub-littoral to the deep waters including the off-shore pelagic zone. In these two zones the impact of Nile perch predation could have also affected stocks of several non- cichlid fishes such as *Bagrus docmak, Synodontis victoriae, Xenoclarias eupogon* and lacustrine populations of the anadromous species *Barbus altianalis* and *Clarias gariepinus*. In such a scenario, other environmental factors could be seen as fuelling the impact of predation e.g through habitat reduction and increased competitive interactions. The occasional landings of large-sized specimens of *C. gariepinus* and *Protopterus*

*aethiopicus* (or of their juveniles) which are basically inshore species indicates the presence of suitable habitats in which viable populations still occur. However, even research in the littoral areas sampled by the *Haplochromis* Ecology Survey Team (HEST) group working out of Mwanza does not give a full indication of all the groups of the purely inshore littoral species which may have escaped predation pressure by the Nile perch. Relatively fewer investigations have been carried out in the littoral zone and its wetland buffer zone.

The ecological effects of the other stocked and successful *O.niloticus* are hardly known apart from possible interspecific competition and reported instances of hybridisation and competition with some of the native tilapiines (EAFRO/EAFFRO, 1959; Welcomme, 1964b, 1966; Kudhongania *et al.*, 1992; Twongo, 1992). Thus questions remain regarding those elements of the fishery which were not directly threatened by perch predation, and the ecological impact of *O. niloticus*. Hecky (1993) suggested that the increasing turbidity and deoxygenation, caused by the eutrophication, broke down the complexly balanced food web through a combination of demersal haplochromine displacement and increased vertebrate abundances finally resulting into a cascade of trophic effects leading to a decimation of haplochromines by the adult Nile perch population.

The above background serves to show the complexity of the dynamics of the Lake Victoria ecosystem and how several factors both biotic and abiotic could have interacted sometimes with unpredictable consequences for the ecosystem. It is now acknowledged that individual factors, e.g., predation pressure, are inadequate by themselves to account for the evolution of present day fisheries and ecological status of the lake. Some publications now focus on combinations and interactions of factors (Bugenyi and Balirwa, 1989; Coulter *et al.*, 1986; Bruton, 1990; Kudhongania *et al.*, 1992; Kaufman, 1992; Hecky and Bugenyi, 1992; Mugidde, 1992; Bootsma and Hecky, 1993; Hecky, 1993), and Lowe-McConnell (1994) points to the likelihood that many of the threats to the fisheries will act synergistically.

Three major causes of environmental change are highlighted by local and international scientists (summarised by CIFA, 1992):
(i)     An increased input of nutrients from external sources, particularly from the atmosphere, but also from run off from the catchment;
(ii)    A change in the regional climate associated with an increase in temperature leading to prolonged periods of thermal stratification and anoxia at the bottom of the water column;
(iii)   Species stockings of the Nile perch and Nile tilapia which have led to a disruption of energy flow patterns.

It is, however, not clear whether or not research based on only these hypotheses could resolve which single most important factor accounts for the changes in ecosystem behaviour, and yet, they have been used as the basis for research formulation. Even if these factors were considered to be operating synergistically,

it seems surprising that certain other potential influences of direct human impact (habitat reduction and degradation) have not been appreciated to the same extent. For example, the first factor would only make sense if run-off from the catchment were seen as having increased above background levels. In addition, other factors such as ineffective management or over-exploitation (Lowe-McConnell, 1994) with destructive gears (Kudhongania *et al.*, 1992) should be considered.

A reduction in fish production between 1970's and 1980's is clearly indicated (Fig. 3) from the results of a comparison of haplochromine catch rates (kg.hr$^{-1}$) between 1970's and 1980's (Kudhongania and Cordone, 1974; Goudswaard and Witte, 1985; Okaronon *et al.*, 1985; Goudswaard, 1988) and changes in species composition (Witte *et.al.*, 1992). However, no account of increased effort was made as a result of the poor statistical system for the analysis of long term trends in catches. Yet, it is obvious that the fishery has become more mechanised, more expanded and more commercial. When such factors are not taken into account, it is possible the apparent increase in catches could obscure other factors which have and continue to play a role in the transformations of the fishery and ecology of the lake as a whole.
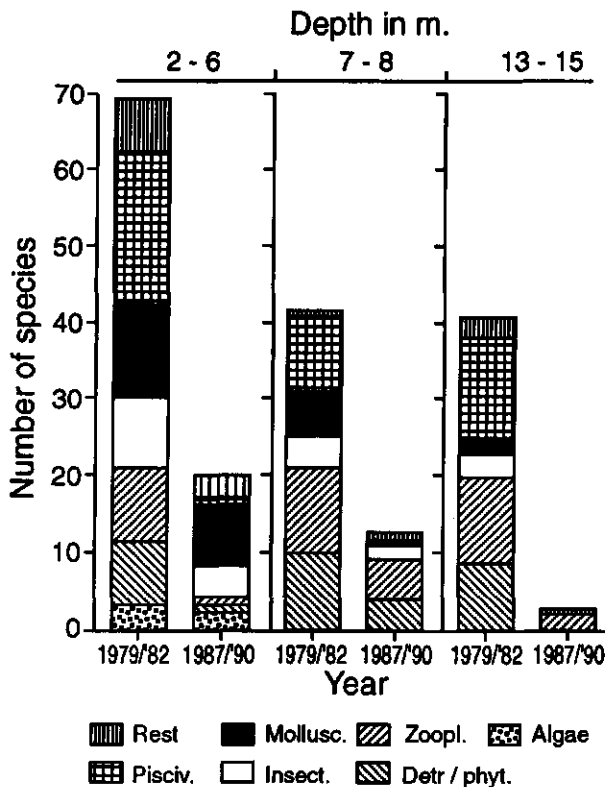


Fig. 3.        Changes in species composition by trophic group between 1979 and 1990 (after Witte *et al.* 1992).

Human impact could exert ecological effects in some subtle ways. For instance, human population growth and direct demands on the watershed could be a major cause of deterioration of water quality and consequently of fish habitat. Human exploitation of fish habitat (e.g., wetlands) or the recent invasion of the lake shoreline by the water hyacinth could directly conflict with the various ecological requirements for fish habitat. Wetland drainage for agriculture, combined with use of fertilisers and pesticides, introductions of exotic species and escapes from fish culture, can engender extinctions through predation, habitat alteration, or spread of disease (Lowe-McConnel, 1994). A combination of all these factors could result in a simplification of shoreline habitats. The effects of several factors acting together on the diversity of fish communities of wetlands could be more important than has been appreciated. The delayed response of fish communities to such changes could be explained in terms of ecological succession. Thus, a fourth hypothesis to test the importance or non-importance of wetland vegetation in the ecology of fish could be added to those which have been suggested above, and could be stated as:

"Direct human influences resulted in a simplification of shoreline habitats and a reduction in fish and fish diversity associated with wetlands".

### The marginal wetlands of Lake Victoria: structure and function

Wetlands, particularly papyrus swamps, are a prominent feature of the marginal zones of Lake Victoria in Uganda (Carter, 1955). They owe their origin to the uplifting of the earth's crust and reversal of the previously east-west flowing rivers and streams in the present day Lake Victoria basin (Greenwood, 1966; Beadle, 1972). As a result of reversal of the drainage patterns, the lake swamps developed due to the rivers being stopped in their flow patterns by the lake formation, forcing many of them to become sluggish and fill with papyrus swamp plants (Beadle, 1972; Taylor, unpubl.) Thus slow moving water seems to have been a major factor in the formation of the lake wetlands. This suggests that alteration of the flow regime in the old pattern e.g., by reclamation of the wetland belt, could negatively affect the swamp.

Just as in many parts of the world, the wetland zone of Lake Victoria can be defined in terms of both water depth and associated characteristic vegetation collectively referred to as marginal macrophytes. This area is equivalent to the littoral zone as defined by Odum (1971) i.e., the shallow-water region where light penetrates to the bottom and is typically occupied by rooted plants. Swamps can be defined as wetland with large macrophytes like papyrus and tall grasses. Thus aquatic macrophytes are more than just the plants found in underwater habitats.

In Lake Victoria, aquatic macrophytes extending from land to a water depth 1 to 2 m are subjected to wave action and water level variations. As an interface zone between the sub-littoral and terrestrial ecosystems, it fits the definition of ecotone defined by Holland (1988) and Naiman *et al.* (1989), and used by Zalewski *et al.* (1991) or, as the littoral zone (Odum, 1971). In terms of width, the distance from

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the shore is variable from a few metres (20-50 m) on rocky shores, to 100-200 m or more in some of the sheltered bays and over sandy beaches. In Lake Victoria this zone is further associated with inundation of the lake shore following the heavy rains of the 1960's that resulted into a series of beaches and lagoons (Welcomme, 1964a, b; 1965). Some authors (Witte *et al.* 1992a, b), have, however, used a depth zone of 0-6 m as representing the littoral zone but this may include elements of the fishery outside the influence of aquatic macrophytes and a depth of about 3 m as indicated by secchi transparency.

Meteorological data and analysis of Lake Victoria levels of recent years show a decrease in water level from the peak attained in the 1960's. The level rose from 1136.3 m above sea level in January 1960 to 1139.8 m in June 1964, a rise of 3.5 m (Fig. 4). This indicates that certain areas such as lagoons, which were originally under water, have been recolonised. Wetlands, if not for human impacts, would probably cover a much larger area than before 1964. The area, depth and water quality of wetlands due to the seasonal alternation of the flood and dry phase associated with the rainy and dry seasons would also be different.



Jinja gauge - beginning of year Lake Victoria level
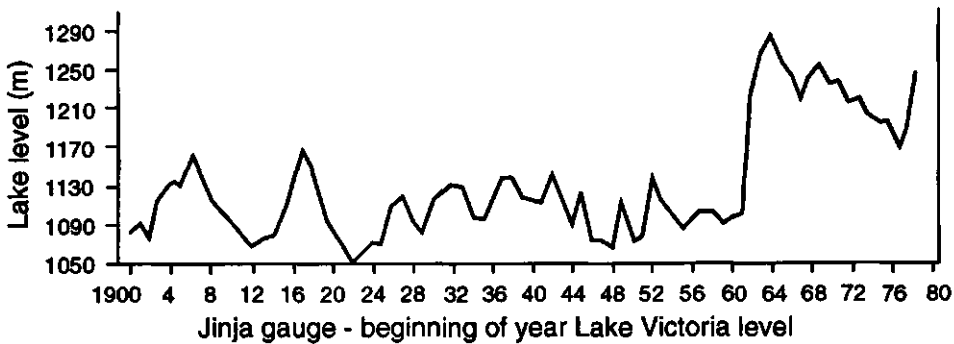
Fig. 4.      Lake Victoria water level readings (after Kite 1982).

The inshore areas as implied in many fishery studies on Lake Victoria appear to be based largely on the range of distances covered by unmotorised canoes operated within sight of the numerous boat landings. The littoral zone including wetlands is on the other hand a strip of interface area as defined by Odum (1971), and is composed of various faunal and floral assemblages.

The Lake Victoria wetlands often contain vegetation (Fig. 5) characteristic of bottom type, slope and water depth. The most visually distinct categories of shoreline wetland include what is usually referred to as swamp such as *Cyperus* (Papyrus), *Phragmites* (Reeds), *Typha* (Bullrush), and *Vossia* (Hippo grass). However, in some areas swamp vegetation includes admixtures of other higher plants or may be interrupted by dense and uniform stands of other species such as

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the swamp shrubs *Sesbania, Hibiscus* and *Mimosa*, the grass *Miscanthidium* or ferns and climbers (*Ipomoea*). For purposes of typology however, the more important aquatic macrophytes zones (Denny, 1985) in Lake Victoria are:

**(a) Euhydrophytes**
- Floating-leaved species such as *Nymphaea* and *Eichhornia* (depending on depth).
- Submerged species such as *Ceratophyllum* and *Potamogeton*.

**(b) Surface - Floating macrophytes**
- *Lemna, Pistia*, and *Eichhornia*.

**(c) Emergent marginal macrophytes**
- Usually the dominant shoreline vegetation type with such species as *Cyperus, Phragmites, Typha* and *Vossia*.

In Lake Victoria, *Eichhornia crassipes* complicates the above typology because of its dynamic character: permanent in some locations but prone to dislocation and drifting in others.
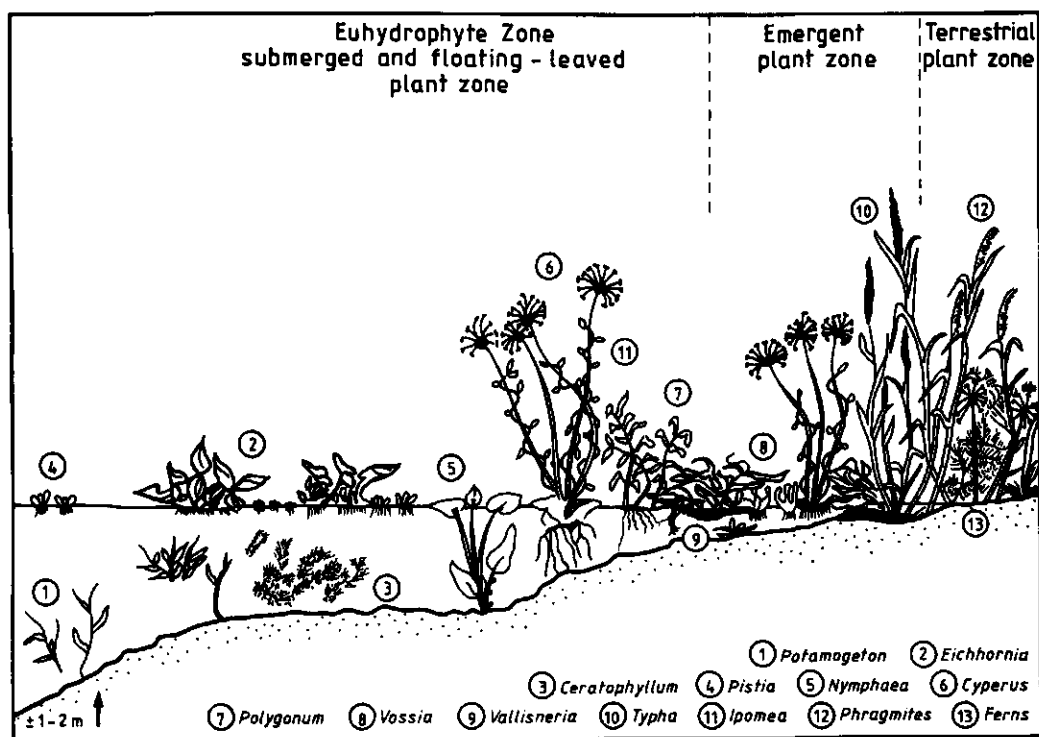


Fig. 5.     Zonation pattern and characteristic vegetation in Lake Victoria wetlands.

**Some studies conducted on Lake Victoria wetlands and their significance**
The inshore waters of Lake Victoria and other East African lakes have been described as the typical habitat for tilapia (Graham, 1929; Lowe-McConnell, 1958, 1975; Welcomme, 1965, 1966; Kudhongania and Cordone, 1974) and *Oreochromis niloticus* is now the main commercially important species caught in the inshore zone. However, it appears that previous investigations have tended to assume an obvious relationship between tilapias and wetlands. Early investigations by EAFRO (1953) pointed to the unsuitability of papyrus swamps for fish except those that can breathe air (e.g., *Protopterus aethiopicus* and *C. gariepinus*) because of low dissolved oxygen and high carbon dioxide concentrations. On the other hand, it was also considered that the increase in tilapia catches associated with the rain season is a result of "foul water" from the swamps driving fish into the open water.

There are indirect references to the influence of wetlands for fish (EAFRO, 1953, 1956/57). In one study, 7 out of 12 stations sampled for population studies, can be considered as representing shallow wetland zones in which at least 10 species of fish were encountered including *Haplochromis* spp, *Tilapia*, *Bagrus*, *Labeo*, *Barbus*, *Mormyrus* spp, *Gnathonemus*, *Alestes* (*Brycinus*), *Clarias* and *Protopterus*. A major limitation of the above studies was not to distinguish between vegetation categories associated with fish habitat and the relative importance of each habitat. However, Welcomme (1964) observed that *Pistia* packed beaches and papyrus swamps support very few fishes mostly *Aplocheilichthys*, *Ctenopoma* and small *Clarias*. These studies were also limited by the duration over which experiments were conducted. In other studies, Welcomme (1964b, 1965, 1966) observed that the expansion of habitats associated with the 1960's flooding of the shoreline vegetation was beneficial to the stocks of *Tilapia*. These investigations were conducted under conditions of exceptionally high water; they do not represent average conditions but do indicate the importance the flooded phase. It also seems that a major focus of this study was on the utilisation by the introduced species of Tilapia of the inundated shoreline, and especially lagoons. With a recession in water level, lagoons and flooded swamps are no longer a common feature.

In a recent study (Willoughby *et al.*, in press) demonstrated that contrary to results of earlier reports, and following the overall reduction in species diversity which has been associated with the previous hypotheses, fish fauna were richer in papyrus swamps, *Vossia* and *Typha* than the open shoreline and *Eichhornia*. *Eichhornia* was seen as a long term threat to the ecology and fisheries of the lake because it had the least number of species and fish biomass. Although the study was limited  to one month and therefore cannot reveal seasonal influences, it gives a first quantitative picture of the importance of shoreline vegetation to fish.

Balirwa and Bugenyi (unpubl.) have attempted to reconstruct the impact of habitat reduction (Fig. 6) on fish that seem particularly relevant for swamp and seasonal stream populations. In the first stage (a), Lake Victoria is shown as being fringed by a wetland buffer zone that is progressively exposed to human impacts. This is a direct result of increasing population pressure and attendant demand for arable land and grazing pastures. What follows is a combination of effects which translate into ecological changes initially manifested in the littoral zone. In stage (c), agricultural run-off contributes to increased nutrient and silt loading of the inshore littoral zone. The final stage (d) is a disappearance of the potamon stream zone and fringing buffer zone, as well as fish habitat degradation. Pollution due to eutrophication also adds to a simplification of the inshore fish habitats and an alteration of the entire trophic structure. Populations of those species originally dependent for breeding in the littoral zone and related lotic conditions in the streams could collapse.

From the above studies, it is clear that fringing wetlands like those of Lake Victoria may be vital habitats for fish apart from regulating material transport to the lake. This provides the justification for increased understanding of the relationships between fish especially the commercially important species like *O. niloticus* and the dynamics at the water/land boundary.

As a starting point, a hypothesis to examine the importance of wetlands in the ecology of fish is: "Shoreline wetland vegetation has no influence on the ecology of the Nile tilapia (*Oreochromis niloticus*) in Lake Victoria." Nile tilapia is used because it is a key species of commercial importance which could lead to recognition of the management potential for shoreline wetlands. This hypothesis is flexible and would allow for testing several closely related hypotheses which would answer pertinent questions such as:

a.  What are the major shoreline wetland vegetation types in Lake Victoria and to what extent do they represent the large scale shoreline landscape?
b.  To what extent are these wetland types important fish habitats?
c.  How are the life cycle features and ecology related to the assumed importance of shoreline wetland vegetation; do wetlands serve as breeding, nursery, feeding and refuge areas?
d.  Do wetlands provide physical-chemical or biotic influences of ecological importance for the Nile tilapia?
e.  Are there any seasonal influences governing wetland use by fish?
f.  How does wetland modification (degradation) affect fish?

## SUMMARY AND CONCLUSIONS

1. The Lake Victoria ecosystem has been changing and changes in the ecology of the lake predate species introductions. However, species introductions which also have contributed to the uncertainty of the aquatic resources are at present the basis of the fisheries of socio-economic importance.
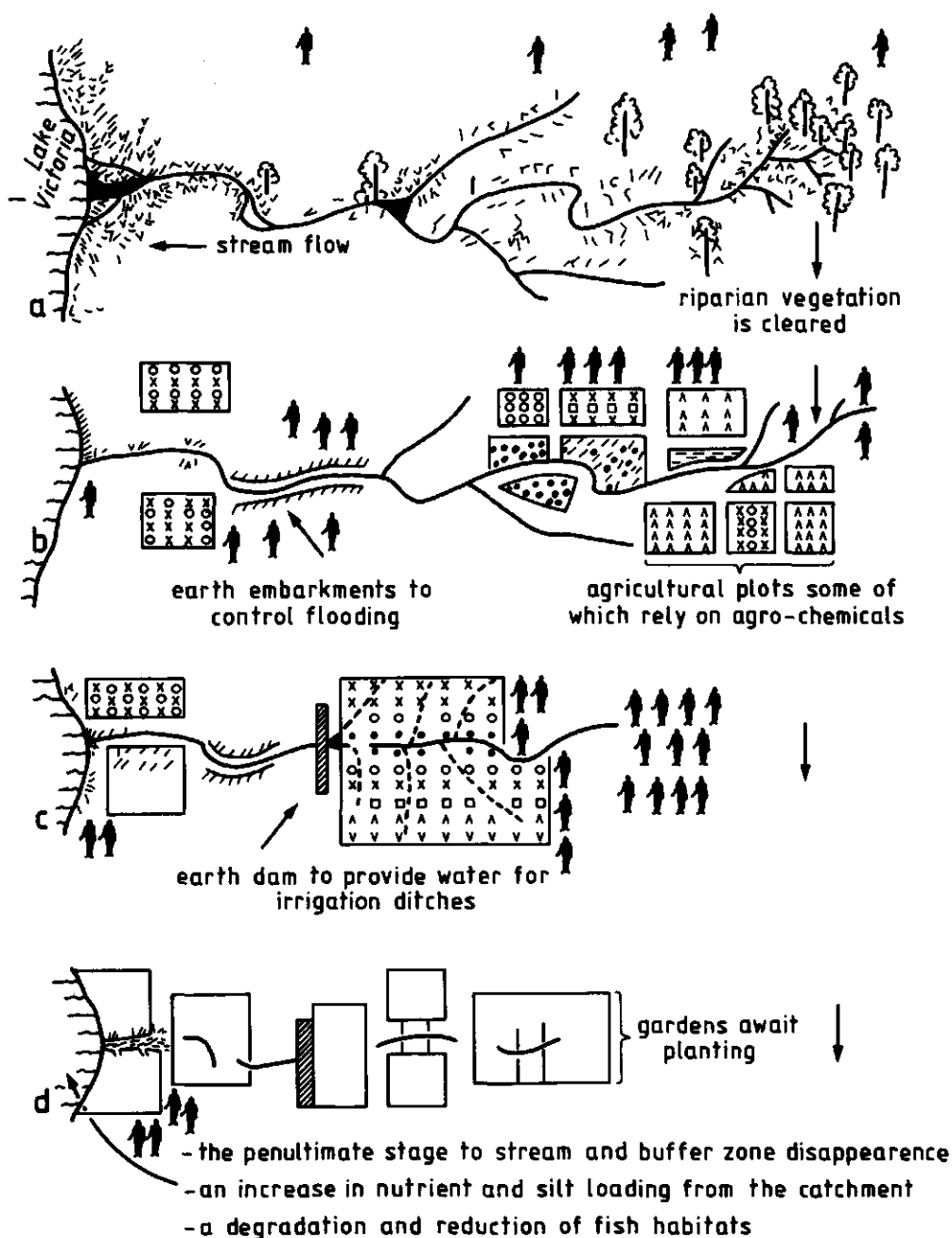
Fig. 6.     Schematic trends in the degradation of wetland habitats in the Lake Victoria basin.

2. The present limnological status over the entire lake is different from what it was in the 1960's and an evolution towards the present state cannot be ascribed to predation pressure alone; the possibility of some cataclysmic phenomenon of unknown duration (masked by apparent climatic and limnological changes) cannot be ruled out.

3. Nile perch (*Lates niloticus*) is probably the main factor responsible for a major part of the endemic haplochromine fauna in Lake Victoria. How big this part may be is still unresolved, but mostly comprises of populations in the sub-littoral zone. The deep water offshore zone seems to have been similarly affected by the Nile perch upsurge, but data are insufficient to relate changes in fish stocks to Nile perch densities and trophic characteristics.

4. The over-exploitation of the inshore stocks seems to be an ever present threat because standard fishery methods appear to have limited success in an environment characterised by open access to the aquatic resources.

5. The littoral zone, particularly the wetland fringe, has been under intense pressure from human activities. this pressure is likely the major cause of fish habitat degradation of wetlands and inlet streams, and ultimately for the fisheries as a whole. Negative impacts for the littoral zone include: habitat reduction, reduced breeding and spawning activity, eutrophication, algal blooms, reduced dissolved oxygen and increased carbon dioxide concentrations, fish kills, suppression of under-water plants by increased turbidity, algal shading and allelopathic substance-limiting effects on the under water plants. The wetland zone is related to water quality in the lake; so there is need to control the quality of the water leaving the swamps.

6. As an area of immense ecological importance for the fisheries and water quality of the lake, there is need for increased understanding of the role of wetlands in the ecology of fish such as the commercially important Nile tilapia.

7. The Nile tilapia is thought to occur in inshore littoral zone habitats associated with wetland vegetation; so there is need to establish the nature of the relationship if any between fish populations and wetland zone factors.

8. A working hypothesis is offered for a study of shoreline wetland vegetation in relation to the ecology of fish. The hypothesis allows for answering several related questions regarding the assumed importance of wetlands for fish. The water hyacinth may have to be regarded as a dynamic and permanent feature of the Lake Victoria shoreline.

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# Chapter 2.2

# The evolution of the fishery of *Oreochromis niloticus* (Pisces: Cichlidae) in Lake Victoria[*]

## ABSTRACT
The Lake Victoria ecosystem has experienced changes associated with fishing levels, a rise in lake level in the 1960s, fish introductions, and human activities in the drainage basin. Following the fish introductions of the 1950s and early 1960s, *Oreochromis niloticus* has become the most abundant and commercially important species among the tilapiines, and the only species which has managed to co-exist with the Nile perch in Lakes Victoria and Kyoga. There is, however, little published information on the biology and ecology of the specie in the new habitats. It has therefore been found necessary to initiate studies on the characteristics of O. *niloticus* in Lake Victoria.

## INTRODUCTION
*Oreochromis niloticus* LINNÉ' is a cichlid of the tilapiine group (Trewavas, 1983). The species is presently common in many parts of the world. It occurs together with *Sarotherodon galilaeus* LINNÉ and *Tilapia zillii* Gervais throughout much of its natural range in Palestine, in the Nile and across to West Africa, and in Lakes Rudolf (Turkana) and Albert in East Africa (Lowe-McConnell, 1958).

Following its introduction in Uganda in the early 1950s, *O. niloticus* has become the most abundant and commercially important tilapiine in Lake Victoria north, and it contrasts sharply with the tilapias of the 1950s and 1960s which were *O. esculentus* and *O. variabilis*. The mainstay of the commercial fishery of both Lakes Victoria and Kyoga are *Oreochromis niloticus* and *Lates niloticus*, (the Nile perch) - another introduced species (Ogutu-Ohwayo, 1984; 1988; Acere, 1988). From the mid-seventies to date, the two species have comprised on average 60% of the catch at Masese (Lake Victoria north) (Table 1). However, while *L. niloticus* has received much attention in the past due to its impact on the lake fishery (Ogutu-Ohwayo, 1984, 1988; Acere, 1985, 1988; Ogari, 1984; Okaronon *et al.*, 1984; Ssentongo and Welcomme, 1985; Hughes, 1986; Goudswaard and Ligtvoet, 1988) there is little published information on *O. niloticus* in Lake Victoria. This chapter gives a preliminary assessment of *O. niloticus* fisheries in the northern waters of the Lake.

### The introduction of *O. niloticus* in Lake Victoria
The first introduction of *O. niloticus* into Lake Victoria probably occurred in the early 1950s. Welcomme (1966a, b; 1967) reports that *O. niloticus* was stocked into Kagera river (Uganda part) in 1954 via the Koki lakes which had been stocked in 1936 from Lake Bunyonyi. The origin of these stockings was Lake Edward. The species was reported from the new habitat in the same year of the Kagera stocking. There followed further stockings of Lake Victoria in Kenya and Tanzania waters between 1956 and 1958 with fry from Kajjansi Fish Ponds. More stockings were carried out from Entebbe (Uganda) between 1961 and 1962. The latter were massive, involving tens of thousands of fry whose origin is not well documented.

The Lakes Albert-Edward origin of *O. niloticus* represents *O. niloticus eduardianus* (Trewavas, 1983).

Table 1.    Fish production by species for some years at Masese landing.

| Species | 1974 | 1976 | 1977 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 |
|---|---|---|---|---|---|---|---|---|---|---|
| *Oreochromis niloticus* | 34.2 | 38.8 | 38.2 | 37.0 | 50.6 | 55.2 | 18.1 | 42.5 | 22.9 | 37.8 |
| *Lates niloticus* | 26.7 | 20.1 | 3.4 | 34.8 | 30.7 | 41.0 | 71.4 | 44.6 | 69.9 | 59.8 |
| *Tilapia zilli* | 1.3 | 0.2 | 0.2 | 0.6 | 2.1 | 0.5 | 5.9 | 5.4 | 5.2 | 0.1 |
| *Oreochromis leucostictus* | 1.6 | 1.5 | 0.9 | 1.2 | 0.3 | 0.1 | 0.4 | 0.4 | 0.1 | - |
| *Oreochromis esculentus* | 0.01 | 0.01 | 0.01 | - | · | · | - | - | · | · |
| *Oreochromis variabilis* | 3.6 | 8.8 | 15.7 | 15.2 | - | - | · | · | | |
| *Bagrus* | 10.2 | 5.6 | 11.6 | 1.8 | · | - | - | · | - | - |
| *Momyrus* | 0.7 | 0.4 | 1.2 | 0.4 | 2.0 | 0.3 | 0.5 | 0.3 | 0.2 | 0.1 |
| *Barbus* | 0.8 | 0.3 | 2.1 | 0.3 | 1.0 | 0.3 | 0.2 | 0.3 | 0.1 | - |
| *Protopterus aetheropicus* | 9.2 | 10.5 | 11.7 | 7.0 | 8.0 | 1.9 | 1.6 | 4.9 | 1.2 | 0.6 |
| *Clarias gariepinus* | 11.3 | 12.0 | 12.0 | 2.1 | 5.5 | 0.6 | 1.9 | 1.6 | 0.6 | 0.8 |
| *Synodontis* | 0.001 | - | 0.01 | · | - | · | - | · | · | · |
| *Haplochromis* | 0.2 | 1.1 | 2.4 | - | - | - | - | · | - | · |
| *Labeo* | · | 0.7 | - | - | - | - | - | · | - | · |

Source: (Compiled from monthly production statistics of Uganda Fisheries Department Office, Jinja).

Apart from *Oreochromis niloticus,* other tilapiines introduced into Lake Victoria between 1951 and 1962 were *O. leucostictus, T. zillii* and *S. melanotheron ( = T. rendalli)* - the last originating from Zambia. The picture of introductions is somewhat confused as Trewavas (1983) suggests that *O. leucostictus* came originally, by accident, with *T. zillii* from Lake Albert. She also points out that the lake was stocked with the Lake Turkana subspecies of *O. niloticus ( = O. niloticus vulcani).*

### Past trends in the Tilapia fishery of Lake Victoria
The history of the fishing industry on Lake Victoria up to the mid-sixties is given by Mann (1969). Even in absence of catch records, there was virtually no impact on the stocks by subsistance requirements up to the I900s when gill-nets were introduced as a new fishing technique. Lake Victoria then contained large stocks of *Oreochromis esculentus.* With the introduction of the gill-net, coupled with the growth of urban centres and communications around the lake, the fishing industry assumed a commercial role. By 1916, the catch rate per net per night (c.p.n.) ranged from 25 to 100 *O. esculentus* in a 5 inch (127 mm) net of 50 yards (C. 45 m) (EAFFRO, 1955/56). The gill-nets became so popular that by the mid-1920s, the number of tilapia (essentially *O. esculentus)* had declined to 5 (c.p.n.) in Nyanza Gulf, and 4-7 elsewhere (EAFFRO 1954/55; Mann. 1969).

Following a survey of the Lake Victoria fisheries, Graham (1929) recommended a mesh-size limit of 5 inches (127 mm) to protect *O. esculentus,* and a lakewide authority responsible for fishery regulation and catch-data collection. These were initiated in 1933 and the Lake Victoria Fisheries Service was established in 1947 (Mann, 1969). In spite of these measures and the economic depression following

the world war, the catch per net per night of *O. esculentus* dropped from 3.1 between 1933-37 to 1.9 by 1945 and 1.2 in 1955 (Mann, op. cit.). As *O. esculentus* was marketed by numbers rather than by weight, this encouraged fishermen to fish with undersized gill-nets. Thus, from 1956 gill nets of 4.5 inch (114 mm) mesh appeared. This resulted in a considerable increase in profits to the fishermen and catches of *O. esculentus* were restored.

The smaller meshed-nets of 3" to 4.5" became widespread in the late 50s and early 60s. They mainly captured stocks of *Oreochromis variabilis* which had been shown to grow to a smaller size and have a lower growth rate than *O. esculentus* (EAFFRO, 1958/59). With increased fishing effort, *O. variabilis* declined over a relatively shorter period than did *O. esculentus.* A compensatory factor was the appearance of the introduced *O. leucostictus* and *T. zillii,* though *O. variabilis* still dominated the commercial catch in 1962 (EAFFRO, 1965).

The period 1961-1963 was characterised by exceptionally heavy rains which led to a rise in the water level of the Lake. The effects were a flooding of marginal areas of the lake and the creation of new beaches and lagoons, leading to improvements in tilapia stocks (Welcomme,1965). All the tilapiines (both endemic and introduced species) featured in commercial catches.

### The growth of the fishery for *O. niloticus*
*Oreochromis niloticus* appeared in the commercial records in 1960 (Welcomme, 1967). Since the species grows to a large size, its stocking in Lake Victoria in the 1950s and 1960s had been expected to lead to a return of the use of the 5-inch (127 mm) mesh gill nets and, to increase the commercial fishery. However, this objective had not been fulfilled by 1963 and the species constituted less than 1 per cent of the commercial catch (Welcomme, 1965). However, from 1965 on, it started featuring prominently in the commercial catches. There were varying degrees of prominence, reflecting the geographical location of fishing ground and approximate period of stocking (Table 2). It appears that the species first established itself to the west of the lake followed by an eastward trend towards Entebbe. Tables 1 and 2 show clearly that, from the late 1960s up to present, *O. niloticus* has assumed a major role in the commercial fishery of Lake Victoria and has encouraged a return to the use of the 5-inch gill net.

### Factors favouring the growth of the *O. niloticus* fishery of Lake Victoria
The massive 1960s stockings off Entebbe followed by the rising lake level could have enhanced the spread of *O. niloticus,* because of the appearance of new breeding areas. An additional factor favouring *O. niloticus* was the reduced competition for space by the reduced levels of the endemic *O. esculentus* and *O. variabilis;* by oveffishing with small mesh gill nets of 3 " to 4.5 " (76-114 mm), and unrestricted use of beach seines. The introduced *O. leucostictus* and *T. zillii* made a temporary impact but were also apparently overfished in the early sixties.

Furthermore, the inshore zone of Lake Victoria has been influenced by human activity in the drainage basin (Bugenyi and Balirwa, 1988), such as clearance of swamp and marginal vegetation, and nutrients transported to the lake via run-offs. The effects of swamp clearance could have been an increase in spawning areas for *O. niloticus*. On the other hand, the disappearance of water lillies and other aquatic weeds reduced the nursery grounds for *O. esculentus* and the feeding niche of higher plant material *(Potamogeton* and *Ceratophyllum)* which are ingested by T. *zillii* (Welcomme, 1967).

Table 2.  Mean percentage of the Tilapia catch by species in 1965 in the 4-inch (102 mm) mesh gillnets from various landings of Lake Victoria in Uganda.

| Landing | Year | Total catch (Nos) | O. esculentus | O. variabilis | T. zillii | O. niloticus | O. leucostictus |
|---------|------|-------------------|---------------|---------------|-----------|--------------|-----------------|
| Bukakata | 1965 | 667351 | 87.14 | 9.81 | 2.26 | 0.69 | 0.09 |
| | 1966* | 38801 | 61.40 | 30.00 | 4.50 | 3.50 | 0.60 |
| Katebo | 1965 | 502752 | 83.38 | 8.78 | 1.05 | 6.79 | - |
| | 1966 | 178815 | 77.50 | 10.56 | 1.23 | 10.71 | - |
| Masese | 1965 | 8830340 | 81.20 | 11.30 | 6.29 | 0.57 | 0.64 |
| | 1966 | 6083314 | 69.30 | 13.80 | 7.70 | 3.20 | 6.00 |
| Namirembe | 1965 | 106748 | 57.09 | 4.59 | 4.06 | 34.26 | - |
| | 1966 | 108176 | 18.12 | 10.50 | 0.67 | 70.71 | - |

* Based on one month's catch. Extracted from Welcomme (1967).

Welcomme (1967) observed that in Lake Victoria, *O. niloticus* feeds on plankton and bottom deposits (i.e. planktonic rain of debris). Studies in progress suggest that the Lake Victoria *O. niloticus* is best described as an opportunistic omnivore. Its food consists of a broad spectrum of items including detritus, crustaceans, mollusc eggs and insects. Flagellates and rotifers and at least 16 species of phytoplankton associated with detritus, have all been found in the gut. The feeding habits of *O. niloticus* are therefore probably of higher survival value in Lake Victoria than those of other tilapiines.

Following the establishment of the Nile perch *(Lates niloticus)* in Lake Victoria, there has been an obvious reduction in ichthyofaunal diversity (Ogutu-Ohwayo, 1984; Ogari, 1984; Hughes, 1986; Goudswaard, 1987). The magnitude of this factor likely promoted the spread of *O. niloticus*. Its co-existence with *L. niloticus* in both the endemic and introduced habitats may be due to an ecological separation which has evolved over a long time.

Tilapias are known to interbreed under both natural and artificial conditions (Lowe-McConnell, 1958, 1959; Elder and Garrod, 1961; Elder *et al.,* 1971; Welcomme, 1967). From such studies, Welcomme (op. cit.) reported two naturally occurring hybrids - *S. melanotheron x T. zillii* and *O. variabilis x O. niloticus* hybrids, while *O. esculentus x O. niloticus* hybridized under experimental conditions (Lowe-McConnell, 1958). On the basis of preliminary studies in the northern waters

of Lake Victoria, it is apparent that such hybrids are common here. A characteristic feature of all hybrids is the dominance of *O. niloticus* morphologic features. Therefore, for all practical purposes, the common tilapia in Lake Victoria north at present is some form of *O. niloticus*.

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# Chapter 3

# Structural characterisation of shoreline wetlands bordering Lake Victoria (Uganda)[*]

## ABSTRACT

Lake Victoria is bordered by extensive stretches of wetlands which are a part of the lake's geomorphological history and its ecology. The lake's ecology could rapidly be transformed further from human impacts in the catchment but mechanisms to stem that process may heavily depend on in-depth knowledge of the ecology of the interface zone. The objective of this study, which was carried out between 1993 and 1996 was to characterise the shoreline interface of northern Lake Victoria with respect to wetland vegetation, and other structural features (water quality, sediments, phytoplankton, macrofauna) of the adjoining littoral zone. From the more than 40 wetland plant species identified along a 110 km stretch of shoreline, five plant communities (*Cyperus papyrus*, *Vossia cuspidata*, *Typha domingensis* and *Phragmites mauritianus*) could be distinguished according to the dominant emergent species at the shore. A comparison of map data for the period between 1950/60 and 1993 showed that wetland cover had declined by at least 5 % in that period, indicating the probable significance of human activity. An exotic weed, the water hyacinth (*Eichhornia crassipes*) appeared in the study area during the period, and rapidly increased in cover by 200 % to justifying it as a new but dynamic wetland type in the lake. Although the biomass of the different plant dominants varied widely within and among replicate sites, the dominant vegetation patterns appeared stable enough to still be used as habitat types. Average concentrations of 350 $\mu$g.l-1 Si, 50 $\mu$g.l-1 tot.-P, 20 $\mu$g.l-1 chl-a, and conductivity of 108 $\mu$S.cm-1 characterised the shallower ($<$ 2 m deep) parts abutting to the vegetation, in contrast to 70 $\mu$g.l-1 Si, 1.5 $\mu$g.l-1 tot.-P, 5 $\mu$g.l-1 chl-a and a conductivity of 94 $\mu$S.cm-1 in deeper (4-6 m deep) open water habitats which were more than 300 m away from the shore. In some physico-chemical factors (Si, soluble reactive-P, chl-a, temperature, pH, electrical conductivity), significant (p$<$0.05) variation was explained most by hydrology, hence the seasonal differences according to the climatic regime in the study area. In other factors, vegetation type explained most of the variation regarding tot.-P concentration, while interaction between vegetation type and season was significant with respect to $NO_3$-N and dissolved oxygen. In addition to vegetation, shallow habitats could be distinguished on the basis of mean depth, slope and sediment composition into 2 major types: *Cyperus - Eichhornia* dominated habitats, and the *Vossia - Typha - Phragmites* type, both of which appeared to be separated from the outer limit of the littoral zone by a region of varying width with a silt dominated bottom in about 4 - 6 m deep water. This classification corresponded to patterns reflected in distribution and relative abundance of macrofauna of which molluscs and chironomids were the most represented. Human impacts could follow a sequence associated with this classification.

## INTRODUCTION

Shoreline wetlands in much of the large lakes' area of East Africa are a product of receding water levels (Lind and Visser, 1962) as well as river capture through tectonic movements since the Miocene (Beadle, 1981). These wetlands are of a herbaceous type (Denny, 1993). In the Lake Victoria basin, the rainfall pattern and the slow-flowing water conditions in the old river beds have been important factors

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in the development of wetlands especially to the west and north of the lake (Fig. 1). The interface between the swamp fringes and open water is probably the most important zone for inland freshwater fisheries, wildlife and other values (Denny, 1985, 1993; Balirwa, 1995). However, in contrast to open water, much less is known about the lake's shoreline wetlands probably due to their structural complexity and inaccessibility. As these buffer zones are not yet grossly drained or altered except near urban centres, the ecological effects of swamp vegetation development extend to some distance towards the open water; but how far in the open water they are manifested is not known. The effects are mediated through gradients and dynamics in structural components such as via inlet water through streams (Gaudet, 1977; 1979) or land drainage through rain leaching.
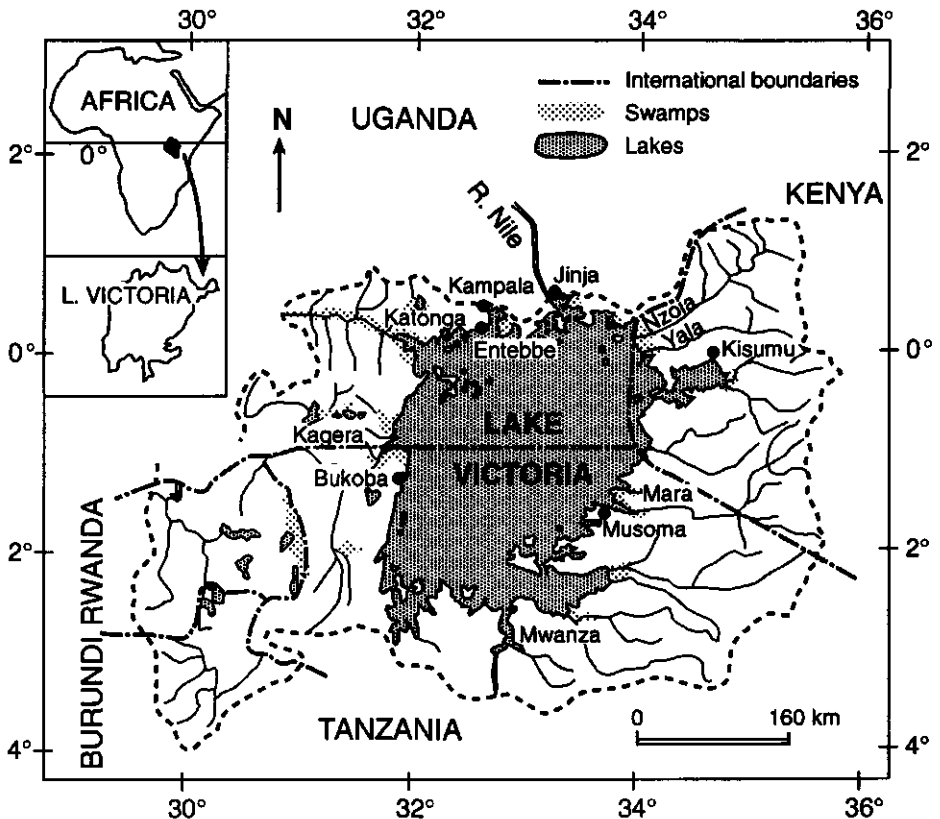


Fig. 1. The Lake Victoria environment including its catchment boundary.

As the largest tropical lake in terms of surface area (*c*. 68,500 km²), Lake Victoria has a long and diverse shoreline (3,440 km). A great variety of shores are present which differ in degree of exposure and range from wave-beaten rocky or sandy beaches to shallow, sheltered and papyrus-lined bays (Welcomme, 1966). The

waters within about 60 m of the lake's edges are considered here an integral part of the lake's wetlands (Balirwa, 1995). The interface, also referred to as the littoral zone (Odum, 1971; Denny, 1985), has not attracted much scientific study till recently. Interest in the area seems to have been prompted by water quality deterioration and decline in fish species abundance which have been partially linked to human activities and degradation of wetland buffers (Bugenyi and Balirwa, 1989; Hecky, 1993). Lowe-McConnell (1994) recognised that wetland drainage for agriculture combined with use of fertilisers and pesticides can engender fish extinctions through habitat alterations but practically no data are available since the work of Welcomme (1966) showed the effects of climatic changes on the biology of fish. From their studies on swamp nutrients, Muthuri and Jones (1997) observed that large scale exploitation of papyrus could have significant ecological implications for the swamps and adjacent wetland systems. Other sources of habitat change may be caused by point sources of municipal effluent or by the increasing influence of exotic weeds such as the water hyacinth. Clearly, the increasing human population in the Lake Victoria basin may be partly responsible for the rapid loss of wetland cover, and some of the changes in the adjacent shallow water habitats. The present rate of wetland reduction or degradation probably compares with the previous rate of loss for tropical forest cover. There is therefore need for quantitative information on the interrelationships between wetland zones and fisheries. Such information is generally lacking for tropical aquatic ecosystems, and yet is essential for management of aquatic resources and, for monitoring changes in the ecosystems.

The fisheries are socio-economically most important (Kaufman, 1992) but are vulnerable. Any aspect which might be related to the quality of fish habitat requires detailed knowledge which in the case of Lake Victoria's wetlands is scanty. Macrophytes are an integral part of the vegetation dominated continuum from land to below water to a depth at which further plant growth is light limited. In Lake Victoria, this is about 2 m at maximum and encloses an area within 50 - 70 m from the shoreline. This is an area of the lake for which there are no comparative data. The rich life found there (invertebrates, fish, waterfowl, mammals) as in the Upper Nile swamps is thought to be a result of the release of nutrients at the swamp edges (Rzóska, 1971). Excess nutrients from swamps (municipal discharges and silt from agriculture) can be detrimental to habitat quality especially over the shallow regions in inland waters. That is why it is essential to establish the ecological characteristics of lake shore wetland zones and how far into the lake their influence is manifested. Apart from the influence of macrophytes on water quality at the interface, phytoplankton and benthic organisms (macrofauna) are among the important components in the trophic ecology of the fishes. Studies of the lake's ecology particularly phytoplankton (Talling, 1957; 1966, Akiyama *et al.*, 1971) and benthic organisms (Macdonald, 1956; Corbet, 1958; Okedi, 1990) have emphasised the sub-littoral zone rather than the lake's wetland interface. Apart from the extensive studies of haplochromine ecology to the south of the lake (e.g., van Oijen *et al.*, 1981; Witte, 1981; Witte and van Oijen, 1990) and riverine investigations (e.g., Welcomme, 1969; Balirwa, 1984), the majority of fish studies

have mainly looked at individual species biology without much reference to specific habitat characterisation. A major question that remains concerns the structure, and the biotic-abiotic relationships in the littoral, which could influence fish populations, species diversity and ecology, and what role the terrestrial watershed plays.

The area of lake wetlands in Lake Victoria as defined by Beadle (1981) includes those parts of the shoreline with emergent vegetation (*Cyperus papyrus*, *Vossia cuspidata*, *Typha domingensis* and *Phragmites mauritianus*) which he called "shaded" i.e shaded from sunlight and wind, and others in shallow water supporting submerged and floating plants (*Nymphaea*, *Ceratophyllum*, etc.) which he regarded as "unshaded swamps". In this study as well as in the concept of Lake Victoria wetlands (Balirwa, 1995), the two ("shaded and unshaded") are taken as a mosaic of interacting elements. The interface zone stretching from the shoreline emergent plants (Denny, 1985) over a platform of water of the littoral zone (Odum, 1971; Balirwa, 1995) was used in these studies.
Following from the review of Lake Victoria wetlands (Balirwa, 1995), the objective of this study was to identify and characterise shoreline wetlands (swamps) in a particular area of the lake by the wetlands' biotic and abiotic features which may serve as indicators of ecological importance to fish. From the identified features, the study also aimed at providing more insight into possible sources of ecological changes in the shallow wetland habitats in relation to human activities in the catchment. Hence, the shoreline plant communities are characterized here by an inventory, the dominant patterns are established and, above and below water plant biomass of the dominant species are compared. Seasonal patterns in water quality variables are evaluated. In order to assess the influence of plant nutrient status with the general ecology of the littoral zone, water quality and physico-chemical conditions of the littoral zone are compared with the nutrient composition of the plants and sediments. Also quantified are the major phytoplankton and macrofauna taxa. Special attention is given to horizontal and seasonal patterns of distribution of the abiotic and biotic components particularly in the papyrus- and *Eichhornia*-dominated habitats because they are the most extensive. As there are virtually no comparable data on Lake Victoria wetlands as defined above, the hypothesis that wetland types (habitats) associated with dominant vegetation stands show homogeneous and stable biotic-abiotic relationships irrespective of temporal and spatial (catchment) influences and horizontal distances is examined.

## STUDY AREA
The area investigated lies to the northern part of lake Victoria in Napoleon Gulf comprising several bays and islands. It is located between Latitudes 0° 22'N and 0° 30'N and Longitudes 33° 10'E and 33° 26'E (Figure 2). The total length of the shoreline including islands in this area is about 110 km while the surface area of the open water is about 133 km$^2$.

The study area lies in the vicinity of Jinja town to the north of Lake Victoria near the outflow of the River Nile (Figure 2). Originally, this area was dominated by a forest-savanna mosaic occurring at medium altitudes. Preliminary surveys in 1993

and 1994 of much of the shoreline of the lake in Uganda indicated that despite human occupancy, the Jinja area still contains many of the characteristic physical and physiognomic features of the entire shoreline, and can therefore be assumed to represent the large-scale landscape.
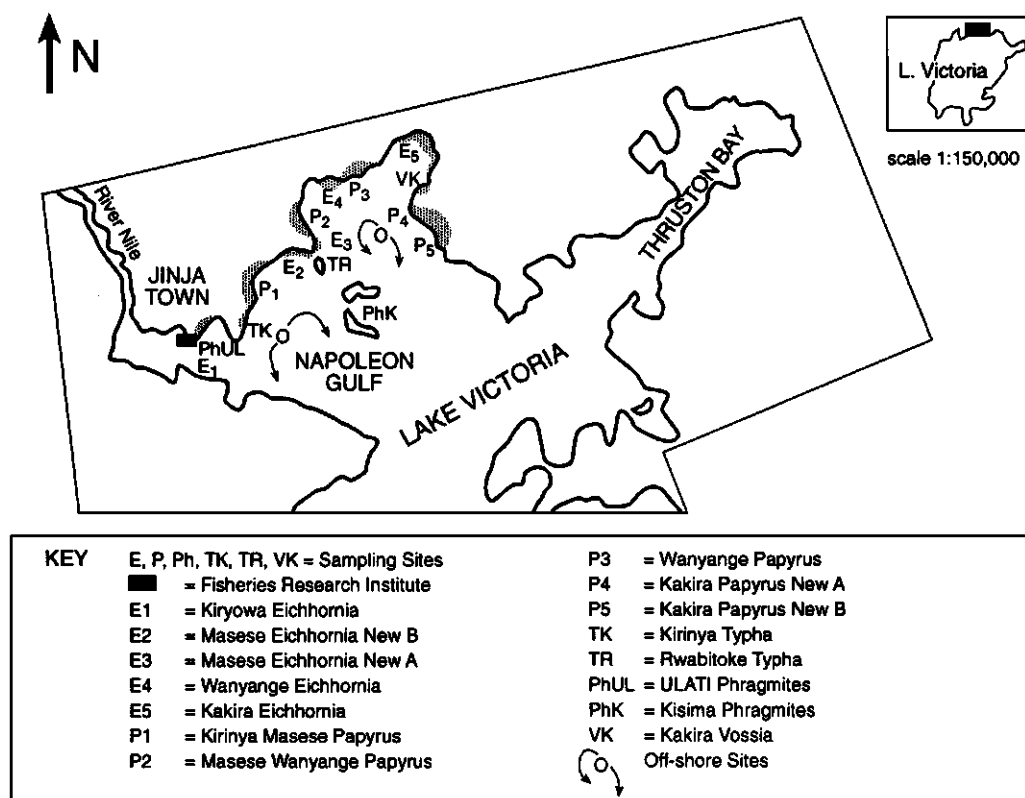


Fig. 2. The research area: the Napoleon Gulf near Jinja, Uganda. The stands used to characterize the five vegetation types are indicated.

According to Velle and Drichi (1992) the area is mostly underlain by argillites, basal quarzites and amphibolites. In some parts, the soils are similar to those found in the Kampala - Entebbe belt and include the brown to yellow-red sandy clay loams with laterite horizons on flat ridge tops. There are also alluvial, recent lacustrine deposits, latosols and shallow stony types. Hence, it appears that the study area is part of a geomorphologically uniform belt extending at least to the west and east of the lake. Among the main geographical features surrounding the study area are the flat topped hills with steep slopes, an extensive agricultural landscape including a large sugar cane plantation to the north and north west. To the east, the population is urban with Jinja (population 290,000 and population density of 428 inhabitants.km$^{-2}$ as at the 1991 census) as the main centre of activity. Farmland and built-up areas comprise at least 40 % of the landscape. Numerous landings dot

the highly irregular and indented shoreline which is associated with sheltered bays (e.g Masese, Kafunda, Fielding and Thruston). Large patches of the wetland fringe comprise various plant species associated with beaches some of which formed the sampling sites. To the west of the area, the landscape still contains extensive areas of natural forest and woodland.

## MATERIALS AND METHODS

### Identification of recurrent vegetation types

To evaluate temporal changes in wetland landscape between previous periods and the present landscape, a SPOT satellite image taken in 1992 was acquired from The National Biomass Project, Kampala and used to identify different patterns in shoreline vegetation. A mapping process described by Velle and Drichi (1992) was used. For gross landscape changes on the scale of the study area, forest and wetland cover changes were used as the main indicators of landuse changes.

Old topographic maps (1950/60) based on photographs were used to infer the same geographical features of interest at an earlier period. The maps were first processed into overlayer sheets, reduced to the scale 1:35,000 and reproduced using the PC-ARC.INFO Version 3.4D software. The resultant map was then used in global comparisons with the similarly GIS processed SPOT image.

Next a preliminary survey of the shoreline in the study area was done early 1993. In total 38 sites were studied. Site selection and replication were based primarily on the presence of intact vegetation free from human activity up to the water mark. Following Moore (1962) the assessment scale for cover abundance (Table 1) was used to generate impressions of the importance (frequency, constancy, associations and degree of dominance) of the different species encountered. Quantification of the importance of plant species in terms of cover took into account size, numbers of individuals, spatial coverage and homogeneity of stands. The resulting scores for the most important taxa are given in Appendix 1.

Table 1.　　Assessment scale for cover and abundance of the macrophytes.
R = Rare, Oc = Occasional, LF = Locally frequent, F = Frequent, LAb = Locally abundant, A = Abundant, LD = Locally Dominant and D = Dominant.

| Score | Descriptor | Label |
|-------|-----------|-------|
| + | species sparsely present (cover small) $< 1$ % of area | R |
| 1 | any number of individuals covering $> 1 < 5$ % of area | OC |
| 2 | any number of individuals covering 5-25 % of area | LF |
| 3 | any number of individuals covering 26-50 % of area | F |
| 4 | any number of individuals covering 51-75 % of area | LAb & A |
| 5 | any number of individuals covering 76-100 % of area | LD & D |

**Characterization of the sites**
For the characterization of five vegetation types 16 stands were selected (5 *Cyperus papyrus*, 2 *Phragmites*, 2 *Typha*, 2 *Vossia* and 5 *Eichhornia crassipes* sites) (Appendix 2). To examine whether or not the five vegetation types were consistently different types, multiple comparison tests (Tukey option, following ANOVA) were used on sediment characteristics (total-N, total-P, total organic content) to evaluate differences within replicate stands. For the same purpose vegetation analyses were compared. Some of the 16 stands were subsequently left out due to, among others, the increasing influence and dynamic character of water hyacinth.
Each of the sites was investigated for physical and chemical variables, phytoplankton, macrophytes and macrofauna from 1993 till 1996. Along a 45 m stretch parallel to the swamp edge of each of the sites, macrophyte samples were drawn from the vegetation edge to 10 m inland.
Water, phytoplankton and macrofauna samples were taken along transects from the shoreline (0 m) to about 40-60 m into the water; open water samples for the same variables were taken about 350-500 m away from the shoreline. Distances at the various points along these transects were determined from a marked nylon rope which was tied at the shore and fixed to a boat anchored in open water. The pattern of sampling was the same for all sites. Samples were in triplicate.

*Physical and chemical characterization*  ˙
Physical and chemical characterization of the vegetation stands was done once every season during one year (May 1995, July 1995, October 1995, February 1996). The seasons were based on the climatic regime in the northern part of lake Victoria. The main characteristic seasonal patterns are: December - March (dry season), March - June (main wet season), July - September (short dry season), September - November ( short wet season). However, the onset and intensity of the rains, and the duration of the seasons are subject to considerable variation between years (Welcomme, 1966; also see ch. 1, Fig. 4) which may explain the unexpected wet conditions for part of February, 1996. The climatic pattern may further be complicated by maritime influence on large-scale controls (Nicholson, 1966) leading to a breakdown of established seasonality in some years. Water temperature (°C), dissolved oxygen (mg.l$^{-1}$), pH, conductivity ($\mu$S.cm$^{-1}$) and oxidation reduction potential (ORP) or redox potentials (millivolts) were determined in the field with a HYDROLAB SURVEYOR II (Hydrolab$^{TM}$ Environmental Data System - SONDE UNIT Model SVR2-SU) for both subsurface and just off the bottom conditions and the results averaged. At times these variables were assessed by a WTW pH meter and a WTW LF323-A for conductivity which also included an oxygen probe. Transparency of the water column was determined with a Secchi disk.

Water samples for chemical analyses were taken with a bucket from the edge of the vegetation (0 m), 10 m, 20 m, 40 m and about 350 m from the shoreline in triplicate. Samples were dispensed into  plastic containers. These were wrapped in black polythene bags and kept in a cooler until ready for analyses at the

laboratory. Chemical analyses were performed on 0.45 $\mu$m membrane filtered (alkalinity; $NO_3$-N; SRP) and unfiltered (Si; TP) samples within 48 h of collection according to standard procedures (Stainton *et al.*, 1977; APHA, 1992; Novosamsky *et al.*, 1983; Houba *et al.*, 1995).

Diurnal measurements of water temperature, dissolved oxygen, pH, conductivity and oxidation reduction potential were carried out between 08.30 and 18.00 h during February and May of 1996.

Sediments were collected on three occasions (October 1994, May 1995, July 1996) by Ponar Grab with a jaw opening of 245 $cm^2$. Size fractions of the sediments were determined by visual observation and by percentage estimates of clay, silt and sand fractions (after sieving and weighing the oven dried material, 105 °C for 24 h). Percent organic matter was determined separately.

For chemical characterization sediment samples were divided into two fractions: one was oven dried at 45 °C for 24 h, ground and analyzed for total nitrogen and total phosphorus. The second fraction was oven dried at 105 °C for 24 h and ashed in a muffle furnace at 550 °C for 3 h after which ashfree dry weight ( = total organic content) was calculated.

The slope of the sampling site was computed as the X-coefficient from a regression of depths at the edge, 10 m, 20 m, 40 m and about 350 m from the edge towards open water. Depths were measured at approximately 2.5 m intervals for the first 45 m from the edge of each site studied.

### Phytoplankton

Phytoplankton was sampled once every season during one year (May 1995, July 1995, October 1995 and February 1996).

Part of the water sample (250 ml) was fixed for phytoplankton identifications (with 3 ml of Lugol and 2 ml of 5 % formaldehyde). The samples were stored in the dark for at least 4 weeks to allow for natural sedimentation. After concentration the algae were counted in triplicate using a Sedgewick counting chamber.

Phytoplankton was identified up to genus level using several checklists (Nygaard 1976; Olsen and Blomqvist, 1981; Mosille, 1984; Talling, 1987).

Chlorophyll-a was analyzed according to the methanol method (Vollenweider, 1968). All analyses were in duplicate.

Algal biomass, expressed as ashfree dry weight, was determined as follows. A known volume of water sample was concentrated over pre-weighed Whatman glass fibre filters (W1). The filters were dried (105 °C, 24h) and weighed again (W2). Next, the filters were ashed (540 °C, 3h) and weighed (W3). The difference between W2 and W3 (DW-AW) is the ashfree dry weight (AFDW). Percent AFDW is AFDW/W2 * 100. All analyses were done in triplicate.

### Macrophytes

Plant material was harvested from the edge and at 2 - 20 m inside the vegetation. Biomass estimates were made at four different times during the study period, i.e. August 1993 (*Cyperus, Typha, Vossia, Phragmites*), February 1994 (*Cyperus*),

August 1995 (*Eichhornia, Cyperus*) and May 1996 (*Eichhornia, Cyperus, Typha, Vossia, Phragmites*).

At each of the stands, all vegetation within 3-5 random 1 m² quadrats was harvested. A smaller 0.5 m² quadrat was used to harvest below water biomass. The material harvested was systematically sorted into species, enumerated and weighed. Green fresh material was separated from dry litter and weighed separately. Subsamples of above and below water biomass were treated similarly. Samples were oven dried (105 °C for 24 h) and ashed (540 °C, 3 h).

The 5 dominant species (*Eichhornia crassipes, Cyperus papyrus, Typha domingensis, Vossia cuspidata* and *Phragmites mauritianus*) were analyzed for their nutrient content. The plant material was divided into above and below water biomass and these were chopped into smaller pieces. These were oven dried (45 °C, 24 h) and analyzed for total nitrogen, total phosphorus and ashfree dry weight. Chemical analyses of the plant material was done according to the same methods used for sediment analyses.

**Macrofauna**

Benthic macrofauna from the sediments were collected once (June 1996) with a Ponar Grab (with jaw size of 245 cm²) in triplicate from sites investigated for physico-chemical variables and phytoplankton. Other samples were collected at about 350 m to 500 m off the shoreline, corresponding to the transects used in the fish studies. Samples were transported in black polythene bags to the laboratory for further analyses. The samples were washed several times through a macrofauna sieve of 0.5 mm mesh, sorted, classified and grouped (Chironomidae, Oligochaeta, Ephemeroptera, Trichoptera, Odonata, Gastropoda and Bivalvia) counted and weighed (fresh weights and dry weights).

In 1995 an *Eichhornia crassipes* stand and a *Cyperus papyrus* stand have been studied more frequently (in May, July and October).

Data analyses were generally based on arithmetic means ± standard error. Sites were compared by ANOVA and multiple comparisons among means were done with Tukey's option.

## RESULTS

**Identification of recurrent vegetation types**

A map of the study area depicting the situation in 1950/1960 is given in Fig. 3. Fig. 4 gives the situation for 1992.

At least 40 plant species were observed in the wetlands along the Jinja shoreline of Lake Victoria. It is likely that more species will be added to this list especially if belt transects are to be used in detailed investigations of the vegetation.

On the basis of dominance, cover abundance and plant associations, six plant communities were distinguished (Table 2). Apart from *Eichhornia*, the majority of stands contained secondary species whose diversity and abundance was variable. Communities were identifiable by dominant species or by groups of species which form more or less discrete associations.
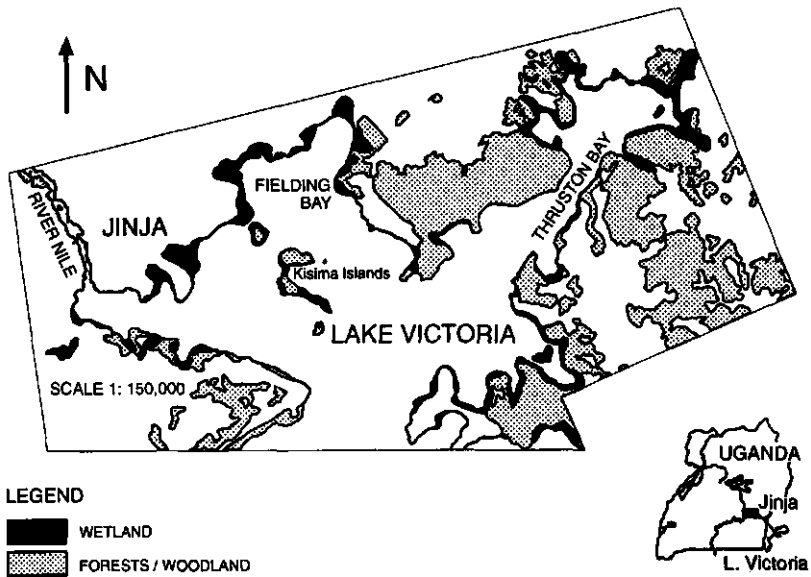
Fig. 3. Wetlands and forests/woodland in the research area near Jinja: 1950/1960 period.
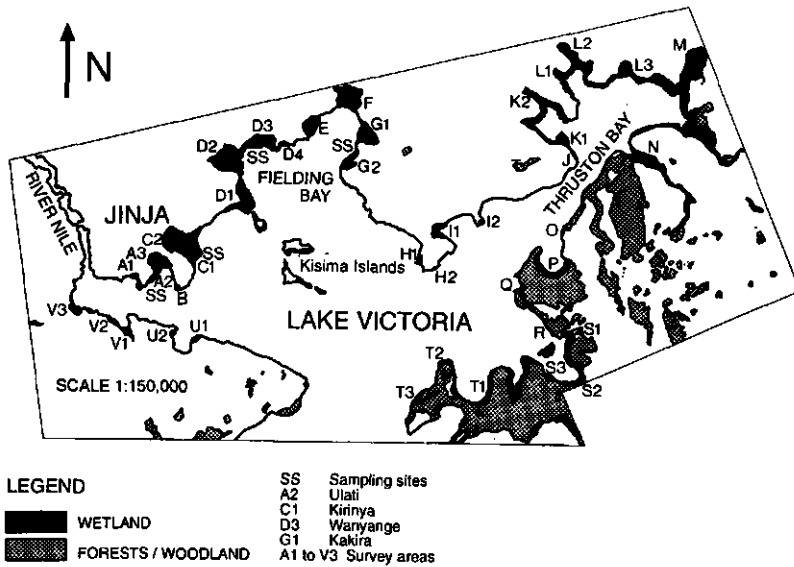


Fig. 4. Wetlands and forests/woodland in the research area near Jinja: 1992 period. The stands investigated during the preliminary survey are indicated.

From the water side, eight species or combination of species can be categorised as being the most common taxa in the 38 vegetation stands of the study area (Table 3). However, their inland species composition patterns differ only a short distance from the water's edge.

Five of the six dominant species of fringing vegetation were selected for further characterization. These were from water to land: *Eichhornia crassipes, Vossia cuspidata, Typha domingensis, Cyperus papyrus* and *Phragmites mauritianus*. Being singularly dominant in particular locations (Appendix 2) and occupying considerable stretches, they were used as identifiers of shoreline vegetation type.

Table 2.      Major plant communities identified by the dominant angiosperm taxa of the Lake Victoria wetland fringe in the Jinja study area.

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1. *Cyperus papyrus* in association with:
    a. *Phragmites mauritianus* and *Typha domingensis* in background
    b. *Ipomoea, Melanthera, Cyphostema* and other climbers and twiners
    c. *Vossia cuspidata* in the foreground
    d. ferns, *Polygonum, Cynodon* and other herbaceous species

2. *Phragmites mauritianus*: usually on higher ground and frequently in association with *Cyperus, Hibiscus* and other arborescent dicots especially *Melanthera*.

3. *Vossia cuspidata*: with *Cyperus* in the background

4. *Typha domingensis* with: *Cyperus* in association with *Phragmites* in the background or in small pure stands

5. *Sesbania sesban/micrantha*: occasionally in association with *Aeschynomene* (ambatch) and *Kotschya africana* particularly between *Cyperus* and *Phragmites* stands.

6. *Eichhornia crassipes*:
    a. sheltered bays
    b. shorelines exposed to on-shore winds in association with *Cyperus, Typha* or *Vossia*.

---

**Characterization of the sites**
*Physical and chemical characterization*
In Table 4 the size distribution of the sediments is given for the five vegetation types. Multiple comparison tests on sediment characteristics showed that there were no significant differences ($p > 0.05$) within replicate sites of the five vegetation types, indicating that the sites were representative of habitat types.

Table 3.     Species frequency in the 38 wetland stands studied.

| Taxon | Percentage occ. in sites |
|---|---|
| *Hibiscus/Melanthera* species | 100 |
| *Eichhornia crassipes* (water hyacinth) | 95 |
| *Cyperus papyrus* (papyrus) | 92 |
| *Vossia cuspidata* (hippo grass) | 92 |
| *Cyphostema-Ipomoea* mixture | 84 |
| *Phragmites mauritianus* (reed) | 79 |
| *Sesbania sesban/micrantha* | 66 |
| *Typha domingensis* (cattail) | 53 |

Table 4.     Pooled sediment characteristics of dominant vegetation type habitats.

| | pH | organic matter (%) | sand (%) | clay (%) | silt (%) |
|---|---|---|---|---|---|
| *E. crassipes* | | | | | |
| 0 m | | <---------------- coarse plant litter ------------------> | | | |
| 10 m | | <---------------- coarse plant litter ------------------> | | | |
| 20 m | | <---------------- coarse plant litter ------------------> | | | |
| 40 m | 6.2 | 13.9 | 27.2 | 52.0 | 20.8 |
| 350 m | 5.8 | 14.7 | 40.3 | 39.2 | 20.5 |
| *C. papyrus* | | | | | |
| 0 m | 6.4 | <---------------- coarse plant litter ------------------> | | | |
| 10 m | | <---------------- coarse plant litter ------------------> | | | |
| 20 m | 6.0 | <---------------- coarse plant litter ------------------> | | | |
| 40 m | 6.0 | <---------------- coarse plant litter ------------------> | | | |
| 350 m | 5.8 | 14.7 | 40.3 | 39.2 | 20.5 |
| *T. domingensis* | | | | | |
| 0 m | | <---------------- mostly sand ------------------------> | | | |
| 10 m | | <---------------- mostly sand ------------------------> | | | |
| *V. cuspidata* | | | | | |
| 0 m | 6.8 | 4.3 | 50.6 | 30.2 | 19.2 |
| 20 m | 7.4 | 0.6 | 70.4 | 8.3 | 21.3 |
| *P. mauritianus* | | | | | |
| 0 m | 7.0 | 1.0 | 50.2 | 12.2 | 37.6 |
| 40 m | 6.5 | 1.5 | 52.4 | 2.4 | 36.2 |

With regard to sediment texture (Table 4), shoreline bottoms within 10-40 m of the shoreline in *Eichhornia* and *Cyperus* dominated habitats tend to be overlain with coarse plant material. On the basis of textural analyses, two main sediment types characterise the habitats: those in which sediments with a high clay content are dominant (*Cyperus papyrus* and *Eichhornia*) and those which are sandy (*Vossia*, *Phragmites* and *Typha*) but in general clay and silt are well represented in the 20-40 m sections off the vegetation of all the habitats.

The mean seasonal N- and P-content of the sediments (mg.g$^{-1}$) for October (1994), May (1995) and July (1996) are shown in Fig. 5a-f. In Table 5 the mean seasonal total-N/total-P ratio (from mg.g$^{-1}$) of the sediments is given for the five vegetation types. The total organic matter content of the sediments is given in Table 6.

Table 5.    Mean seasonal total-N/total-P ratio (from mg.g$^{-1}$) of the sediments for the five vegetation types. O = October 1994; M = May 1995; J = July 1996.

|  | -5 m | | | 0 m | | | 10 m | | | 20 m | | | 40 m | | | open water | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | O | M | J | O | M | J | O | M | J | O | M | J | O | M | J | O | M | J |
| *Eichhornia* | - | 67 | 18 | 11 | 46 | 19 | 13 | 27 | 14 | 5 | 25 | 18 | 12 | 37 | 21 | 14 | 10 | 15 |
| *Cyperus* | - | - | - | 17 | 24 | 22 | 19 | 30 | 23 | 20 | 26 | 21 | 15 | 20 | 21 | 20 | 13 | 17 |
| *Typha* | - | - | - | 1 | 15 | 5 | 1 | 10 | 6 | 1 | 23 | 7 | 2 | 15 | 6 | 14 | 7 | 10 |
| *Vossia* | - | - | - | 8 | 2 | 4 | 9 | 1 | 8 | 8 | 1 | 1 | 7 | - | 2 | 13 | 8 | - |
| *Phragmites* | - | - | - | 2 | 3 | 4 | 5 | 12 | 4 | 9 | 28 | 5 | 7 | 15 | 6 | 20 | 8 | 14 |

Table 6.    Seasonal total organic matter of the sediments (A: as %; B: as g.m$^{-2}$, mean and standard error) from transects of the investigated vegetation types. O = October 1994; M = May 1995; J = July 1996.

|  | -5 m | | | 0 m | | | 10 m | | | 20 m | | | 40 m | | | open water | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | O | M | J | O | M | J | O | M | J | O | M | J | O | M | J | O | M | J |
| **A.** | | | | | | | | | | | | | | | | | | |
| *Eichhornia* | - | 38 | 60 | 76 | 50 | 53 | 72 | 44 | 40 | 60 | 32 | 53 | 64 | 41 | 55 | 35 | 41 | 36 |
| *Cyperus* | - | - | - | 87 | 83 | 81 | 87 | 67 | 72 | 85 | 60 | 62 | 67 | 55 | 54 | 45 | 38 | 43 |
| *Typha* | - | - | - | 1 | 1 | 1 | 1 | 1 | 2 | 32 | 3 | 2 | 6 | 1 | 1 | 32 | 36 | 29 |
| *Vossia* | - | - | - | 39 | 12 | 16 | 43 | 15 | 15 | 36 | 13 | 9 | 36 | 22 | 11 | 45 | 32 | - |
| *Phragmites* | - | - | - | 6 | 5 | 5 | 5 | 6 | 6 | 17 | 8 | 5 | 16 | 10 | 8 | 35 | 22 | 43 |

**B. May 1995**

|  | -5 m | 0 m | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| *Eichhornia* | 3232 ± 260 | 4006 ± 310 | 4021 ± 348 | 3688 ± 778 | 2804 ± 540 | 3232 ± 126 |
| *Cyperus* | - | 4102 ± 743 | 4092 ± 310 | 4489 ± 399 | 8650 ±2935 | 3155 ± 148 |
| *Typha* | - | 108 ± 40 | 52 ± 17 | 770 ± 379 | 211 ± 75 | 2787 ± 212 |
| *Vossia* | - | 1826 ± 203 | 2279 ± 485 | 2090 ± 971 | 1254 ± 329 | 3096 ± 87 |
| *Phragmites* | - | 1381 ± 504 | 718 ± 138 | 2036 ± 947 | 1412 ± 193 | 1989 ± 478 |

In May 1995 the ashfree dry weight also has been determined per square meter (Table 6b, Fig. 6).
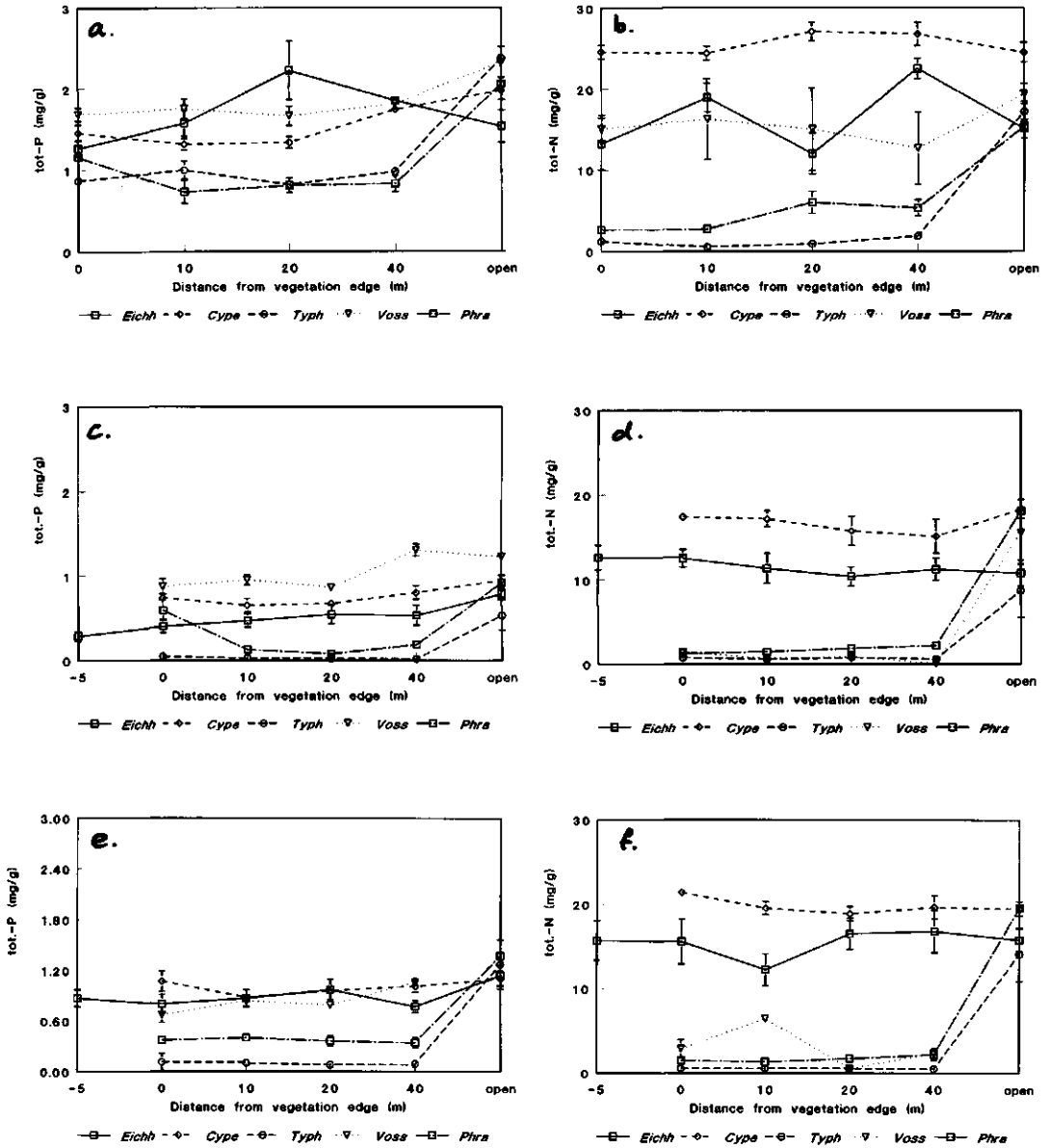
Fig. 5.    The mean seasonal total-P and total-N content of the sediments (mg.g⁻¹) according to the distance from the edge (0 m) of the vegetation (open = 350-500 m off the edge).
a and b: October 1994; c and d: May 1995; e and f: July 1996.
*Eichh = Eichhornia, Cype = Cyperus, Typh = Typha; Phra = Phragmites.*
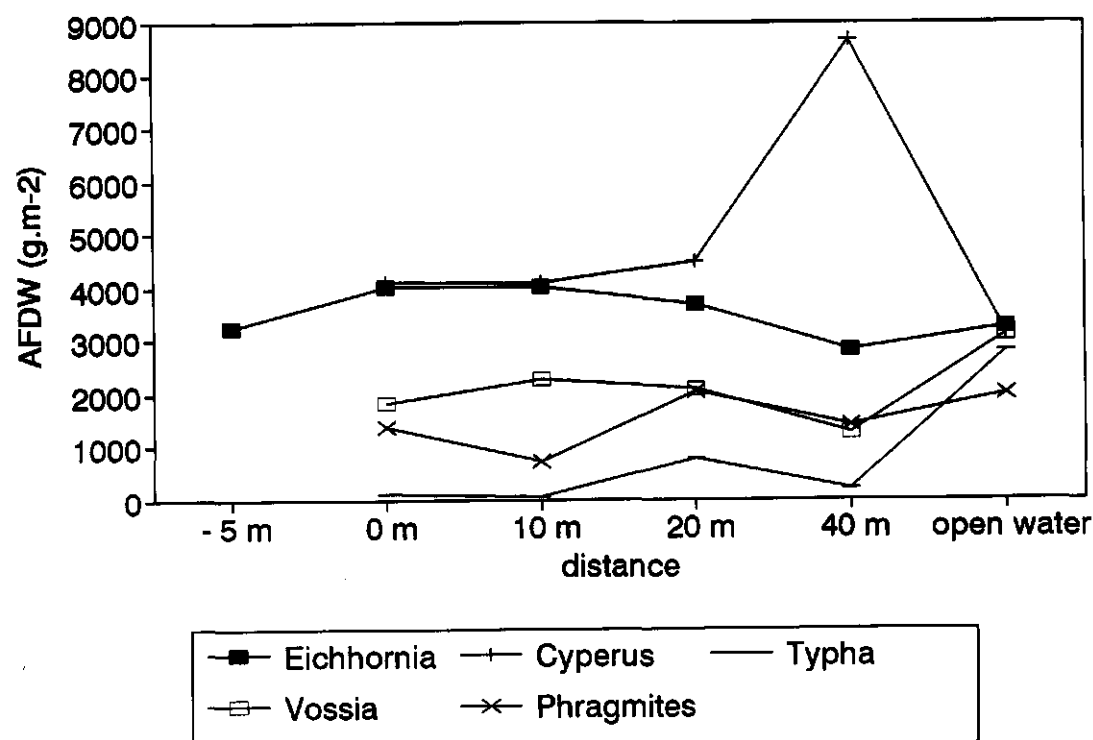
Fig. 6.    Total organic matter (AFDW in g.m$^{-2}$) of the sediments at different distances from the edge for the five vegetation types.

Fig. 7 gives a schematic drawing of transects through typical stands of four vegetation types, i.e. *Cyperus papyrus*, *Phragmites mauritianus*, *Vossia cuspidata* and *Typha domingensis*.

Data on physical and chemical variables of the water are given in Appendix 3a-d. To make an evaluation easier, the data from the 10, 20 and 40 m samples have been averaged in those situations that differences were minimal (e.g. papyrus and water hyacinth stands). Results of a two-way ANOVA showed significant effects of vegetation type, season and interaction of these two (vegetation*season) on most of the investigated variables (Table 7). Although the three factors were significant in explaining the variation in physico-chemical characteristics, seasonal effects tended to explain most variation in most variables. For tot.-P, most variation was explained by vegetation type, hence habitat differences, while for dissolved oxygen and NO$_3$-N, interaction accounted for the most variation.
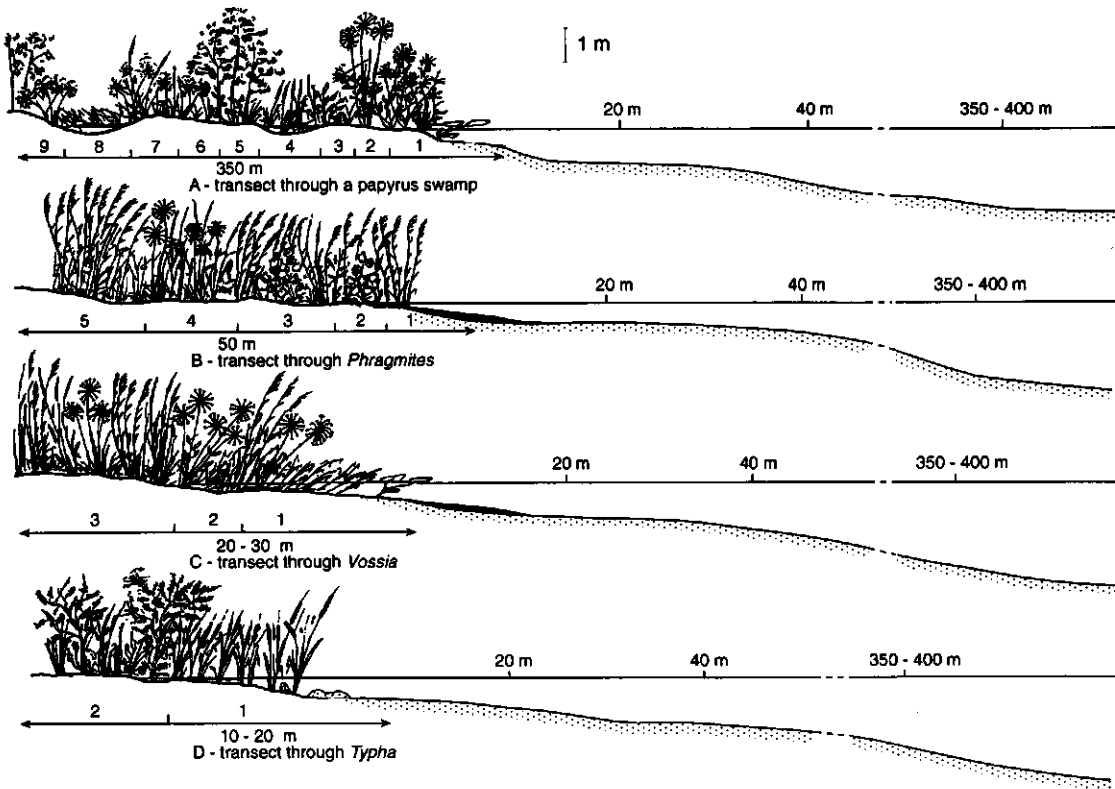
Fig. 7. Schematic presentation of transects in typical stands of four vegetation types.

In Fig. 8 data on Si, SRP, tot.-P, $NO_3$-N and chlorophyll-a are presented. The data are pooled across the vegetation types (Fig. 8a) as well as across the seasons (Fig. 8b).

Mean values for algal biomass (seston DW), temperature, pH, oxygen, EC and redox for the five vegetation types are given in Table 8.

Table 8. Mean values ($\pm$ standard error) for algal biomass (mg DW.l$^{-1}$), temperature (°C), pH, oxygen (mg.l$^{-1}$), Electric Conductivity ($\mu$S.cm$^{-1}$) and redox (mV) for the five vegetation types. Different characters show significant differences (p < 0.05).

| | algal biomass | temperature | pH | oxygen | EC | redox |
|---|---|---|---|---|---|---|
| Cyperus | 11.8 ± 0.3 a | 26.6 ± 0.1 | 8.2 ± 0.1 b | 6.9 ± 0.2 | 110 ± 1.0 b | 0.14 ± 0.004 |
| Eichhornia | 11.1 ± 0.2 a | 26.5 ± 0.1 | 7.7 ± 0.0 a | 6.7 ± 0.1 | 110 ± 1.0 b | 0.24 ± 0.003 |
| Vossia | 16.9 ± 1.3 c | - | 8.2 ± 0.5 ab | 6.6 ± 0.7 | 94 ± 2.0 a | - |
| Typha | 16.4 ± 0.4 bc | - | 8.3 ± 0.2 ab | 7.1 ± 0.3 | 95 ± 1.0 a | - |
| Phragmites | 12.2 ± 0.4 ab | - | 8.0 ± 0.2 ab | 7.3 ± 0.5 | 95 ± 1.0 a | - |

52
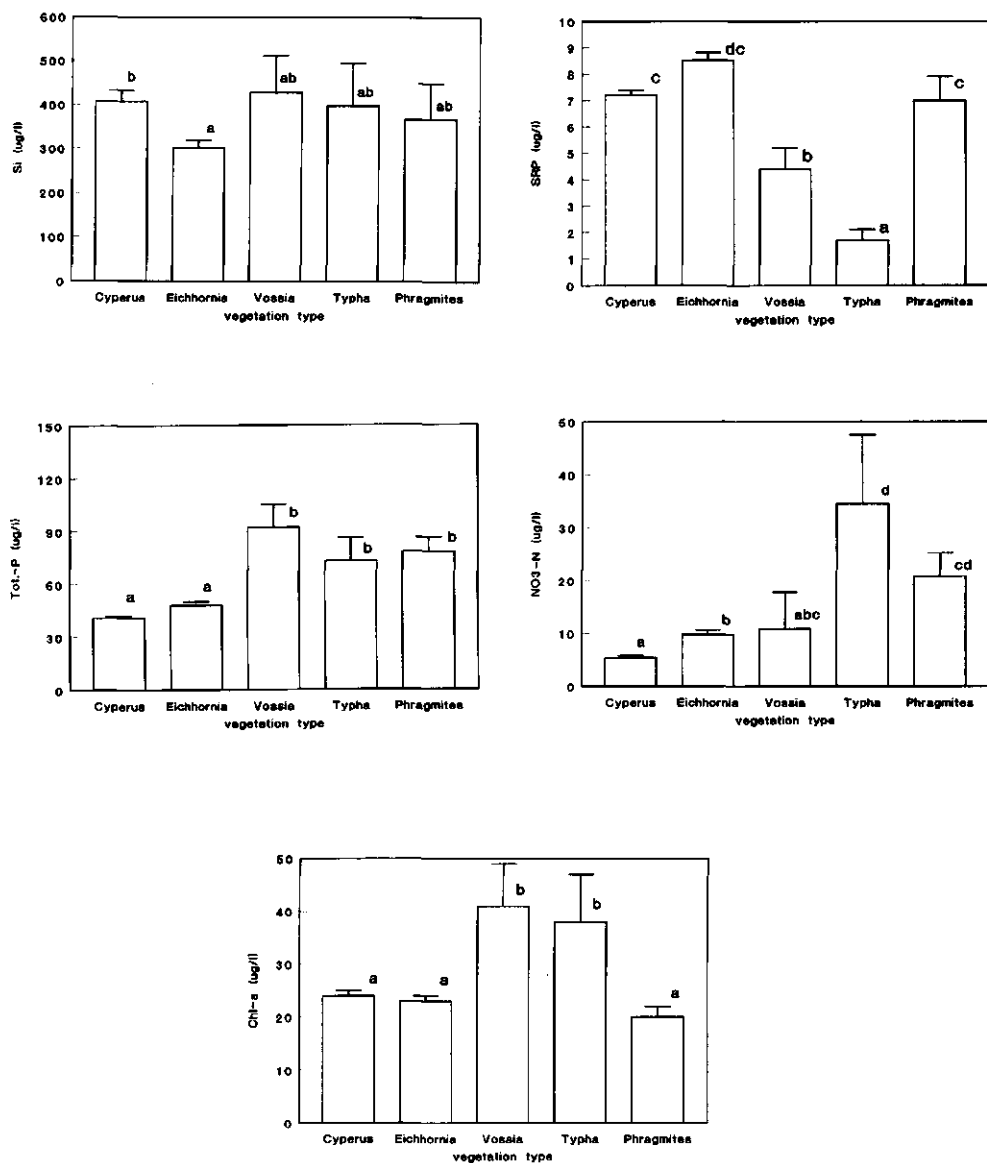
Fig. 8a. Mean concentrations (± s.e.) of Si, SRP, total-P, $NO_3$-N and chlor.-a concentrations pooled across the habitats; seasonal means that are not significantly different share a common letter.
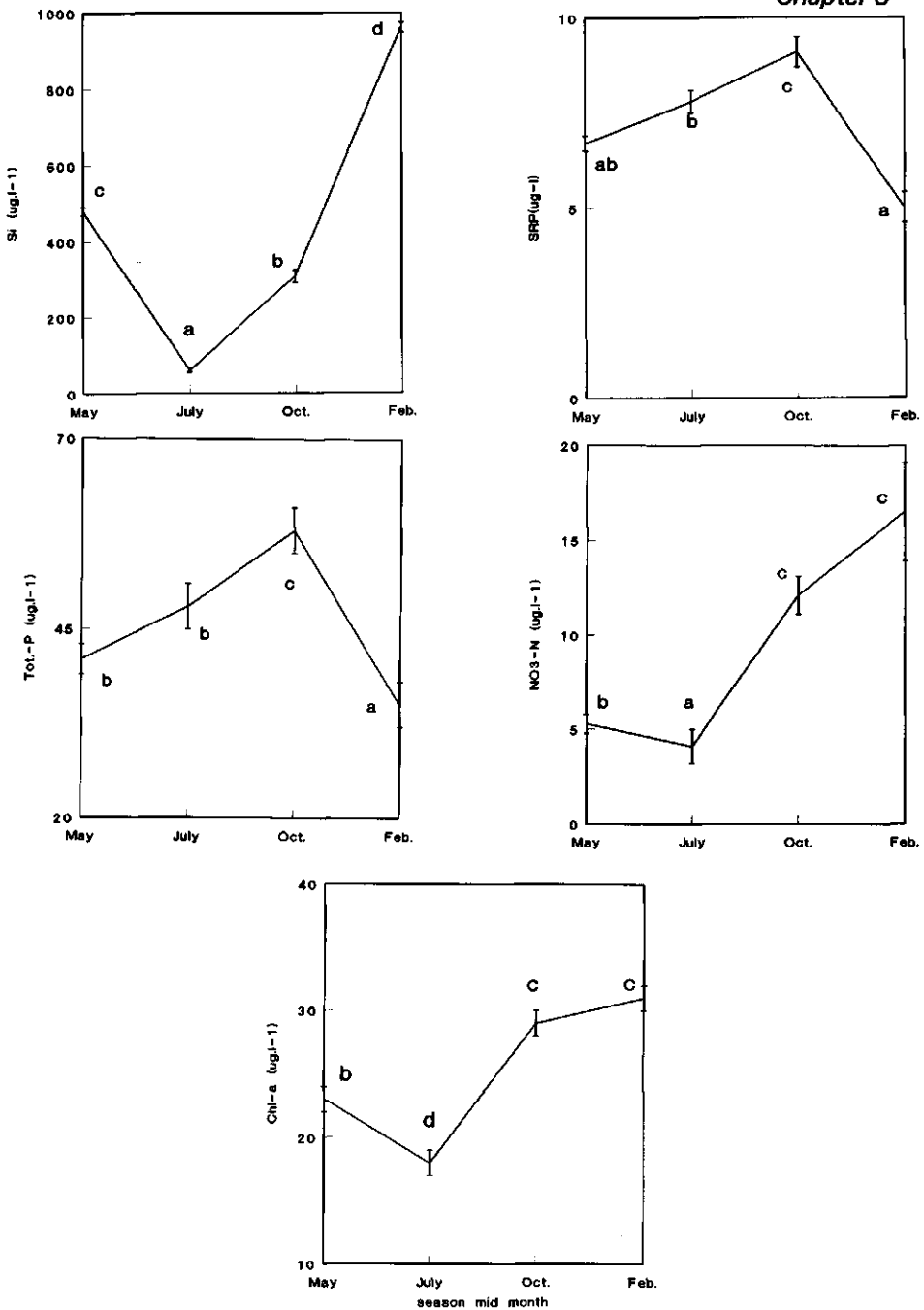
Fig. 8b. Mean concentrations (± s.e.) of Si, SRP, total-P, $NO_3$-N and chlor.-a concentrations pooled across the seasons from the investigated littoral habitats; habitat means that are not significantly different share a common letter.

Table 7.    Two-way ANOVA on some chemical, physical and biological variables to analyze effects of vegetation type, season and the interaction of these two.
Four levels of significance are indicated: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*) and $p > 0.05$ (ns = not significant).
F = factor ss; E = explained ss (F/E % = a measure of variation explained by that factor).

|  | vegetation | | season | | interaction | |
|---|---|---|---|---|---|---|
|  | p | F/E | p | F/E | p | F/E |
| Si | *** | 2 | *** | 95 | *** | 1 |
| SRP | *** | 31 | *** | 64 | * | 12 |
| tot.-P | *** | 60 | *** | 14 | ** | 10 |
| $NO_3$-N | *** | 22 | *** | 36 | *** | 47 |
| chlor.-a | ns | 1 | *** | 95 | ns | 2 |
| seston DW | ns | 0.8 | * | 98 | ns | 2 |
| temp. | ** | 2 | *** | 98 | * | 1 |
| pH | *** | 29 | *** | 72 | *** | 6 |
| oxygen | ns | 1 | ns | 5 | *** | 94 |
| EC | ns | <0.1 | *** | 55 | *** | 45 |
| redox | *** | 22 | *** | 57 | *** | 25 |

The seasonal patterns as shown by algal biomass (seston DW), temperature, pH, oxygen, EC and redox are given in Table 9.

Table 9.    Mean values (standard error) for algal biomass (mg DW.$l^{-1}$), temperature (°C), pH, oxygen (mg.$l^{-1}$), Electric Conductivity ($\mu S.cm^{-1}$) and redox (mV) for the seasons. Different characters show significant differences ($p < 0.05$).

|  | algal biomass | | | temperature | | | pH | | | oxygen | | | EC | | | redox | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| May | - | | | 27.5 | ± | 0.0 c | 8.0 | ± | 0.0 c | 6.6 | ± | 0.2 a | 108 | ± | 0.5 b | 0.31 | ± | 0.040 c |
| July | 10.9 | ± | 0.3 a | 25.2 | ± | 0.0 a | 7.4 | ± | 0.0 a | 6.7 | ± | 0.1 b | 112 | ± | 2.0 b | 0.18 | ± | 0.003 b |
| October | 12.1 | ± | 0.3 b | 26.9 | ± | 0.1 b | 8.4 | ± | 0.1 b | 6.6 | ± | 0.7 ab | 106 | ± | 0.4 a | 0.10 | ± | 0.005 a |
| February | 12.1 | ± | 0.3 b | - | | | - | | | - | | | - | | | - | | |

For all stands higher concentrations of silica (500-1000 $\mu g.l^{-1}$) are associated with the rainy periods (e.g. February and May) in contrast to July (200-500 $\mu g.l^{-1}$) The silica concentrations in October are intermediate (250 $\mu g.l^{-1}$) between the May and July periods for water hyacinth and papyrus stands. For *Typha*, *Vossia* and *Phragmites* the October (700-1000 $\mu g.l^{-1}$) and July (70-150 $\mu g.l^{-1}$) silica concentrations are comparatively higher than in water hyacinth and papyrus edges. February data for water hyacinth and papyrus show unexpectedly high silica
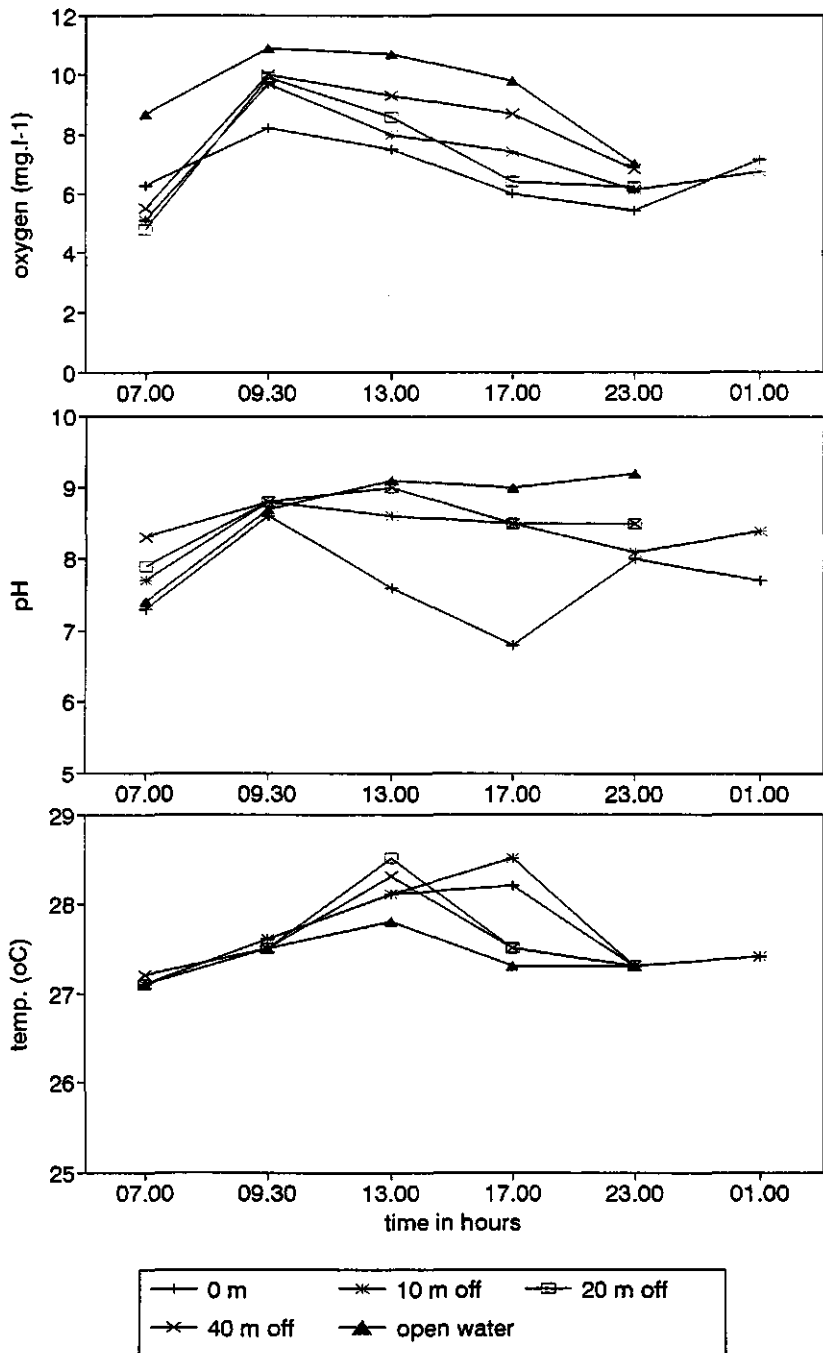
Fig. 9.     Diurnal changes in some variables in a *Cyperus papyrus* stand (Masese-
            Wanyange). February 1996.
            Top: Oxygen (mg.l-1); middle: pH; below: Temperature (°C).

concentrations (900-1000 $\mu$g.l^{-1}) when dry conditions prevail. The data show major differences between 5 m into water hyacinth, the edge and the open water sites.

Data on diurnal variations in temperature, oxygen and pH for February 1996 and May 1996 respectively, can be summarized as follows. In general, horizontal gradients in temperature, pH and dissolved oxygen appeared to be both distance and time dependent in all the investigated habitats (e.g. 4.0 - 6.0 mg $O_2$.l[-1], irrespective of time of the day). There were clear trends in the other habitats: temperature was lowest (25 - 27 °C) at 07.00 h rising to 26 - 28 °C between 13.00 - 17.00 h; pH 6.0 - 7.0 increased to 7.6 - 9.0 during the same period. Low oxygen values (4.0 - 6.5 mg.l^{-1}) were associated with 07.00 h readings in all the habitats. Fig. 9 showing the diurnal patterns in a *Cyperus papyrus* (Masese-Wanyange; February 1996) provides an example:

- Temperature at 07.00 h was uniform (27 °C) at all distances of the transect *i.e. from the vegetation fringe to open water sites. It reached a maximum (28.1 - 28.5 °C) between 13.00 - 17.00 h, and subsequently decreased to 27 °C.
- pH had increased from 7.0 to 9.0 by 13.00 h, and was still high (8.5 - 9.0) by 17.00 h.
- Oxygen was at 07.00 h low (4.5 - 6.0 mg.l^{-1}) at the vegetation fringe, in comparison to 8.7 mg.l^{-1} in open water sites. Between 09.30 h and 13.00 h there was an increase in dissolved oxygen (7.5 - 9.0 mg.l^{-1}) in the shallower end, and (11.0 mg.l^{-1}) in the open water sites. There appeared to be a subsequent decrease, and by 17.00 h the pattern was similar to what was observed in the morning .

There are other patterns in variations and changes in temperature and oxygen with respect to surface and bottom conditions and time of the day in the different habitats. For example, surface temperatures in *Phragmites*-dominated habitats are lower than bottom conditions at the start of the day, while they are uniform in *Cyperus papyrus*-dominated habitats. In open water sites, surface temperature in *Phragmites* is higher than in *C. papyrus* habitats, but the reverse is true for bottom temperatures. *Typha* habitats behaved similarly. Oxygen concentrations are higher in *Phragmites* and *Typha* habitats than in *Cyperus papyrus* and in *E. crassipes*. The higher values are obtained in open water sites for the same periods. By 15.00 h *Phragmites* and *Typha* sites show reduced oxygen concentrations in comparison to *C. papyrus*.

### Phytoplankton
A total of 42 phytoplankton genera were identified from the sampling sites. Generally, phytoplankton was dominated by genera belonging to the Cyanobacteria and Chlorophyceae (Table 10).

The habitats had a high dominance of Cyanobacteria in April, while diatoms dominated in September. Fig. 10 illustrates the relative importance of the three major algal groups in April and September for a *Cyperus papyrus* stand (Kakira new B). *Typha domingensis* and *Phragmites mauritianus* habitats had the highest algal
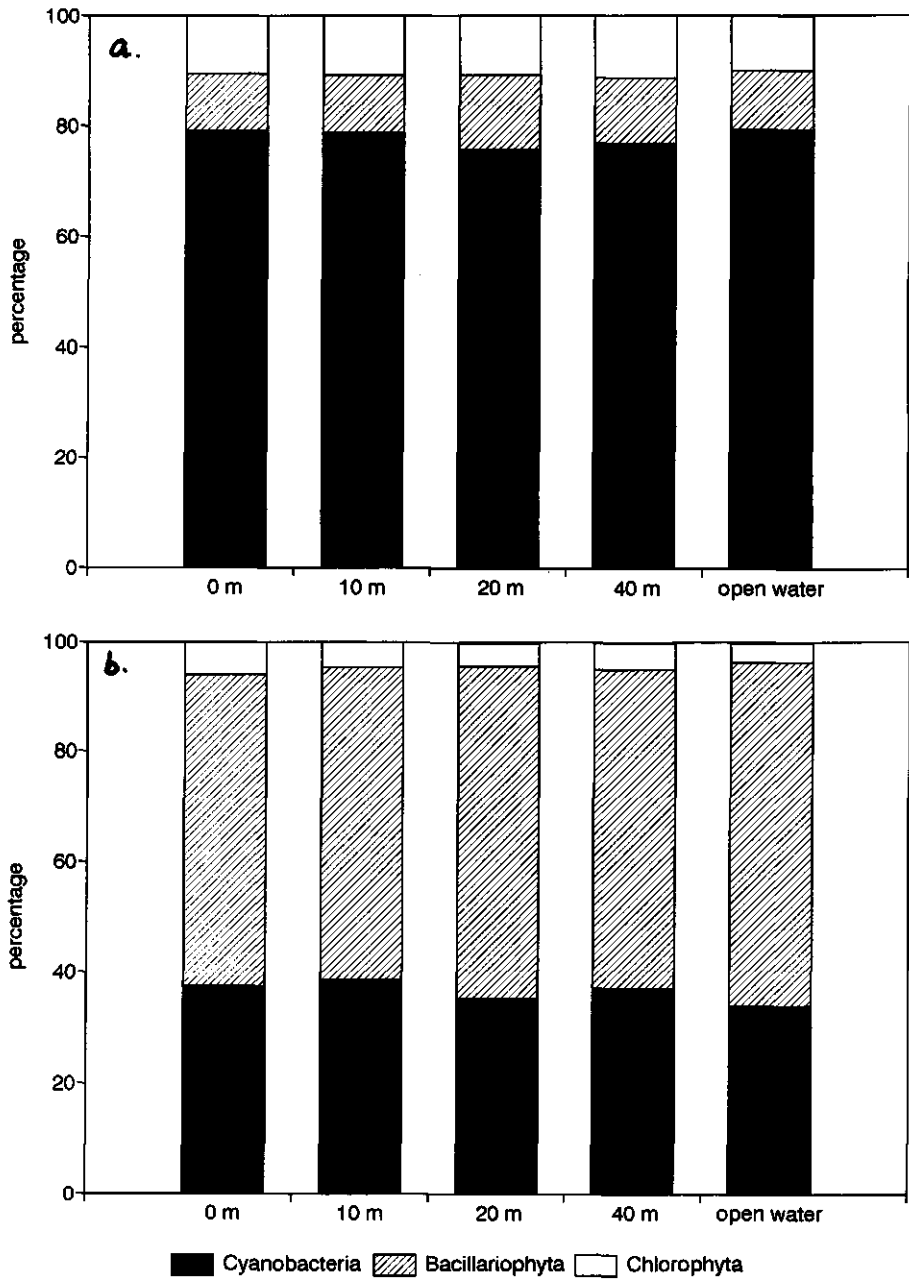
Fig. 10.    Relative importance of the three major phytoplankton groups
(Cyanobacteria, Bacillariophyta, Chlorophyta), expressed as
percentages of the total number of individuals in a *Cyperus papyrus*
stand (Masese-Wanyange).
a. April 1995; b. September 1995.

abundance (ind. of genera.$l^{-1}$, not shown). These patterns were also reflected in seston (Table 7).

Table 10.   Common phytoplankton genera found in samples from the Jinja study sites during April and September 1995; evaluation was based on number of cells per litre.

| Bacillariophyceae | Cyanobacteria | Chlorophyceae |
|---|---|---|
| *Nitzschia* | *Anabaena* | *Sphaerocystis* |
| | *Lyngbya* | *Scenedesmus* |
| | *Merismopedia* | *Ankistrodesmus* |
| | *Microcystis* | |
| | *Oscillatoria* | |

To evaluate further the horizontal and seasonal patterns of phytoplankton biomass, averaged results of chlorophyll-a measurements for *Eichhornia crassipes* and *Cyperus papyrus* stands are presented in Table 11.

Table 11.   Chlorophyll-a ($\mu$g.$l^{-1}$) in *Eichhornia crassipes* and *Cyperus papyrus* transects (mean values and standard error). The wet and dry seasons have been indicated.

| | May 1995 (wet) | July 1995 (dry) | October 1995 (wet) | February 1996 (dry) |
|---|---|---|---|---|
| *Eichhornia crassipes* | | | | |
| shoreline | 23.0 ± 1.9 | 16.1 ± 1.2 | 23.7 ± 2.4 | 16.7 ± 0.5 |
| 10 - 40 m off | 21.1 ± 0.7 | 18.7 ± 0.7 | 26.5 ± 1.3 | 20.2 ± 0.7 |
| open water | 21.6 ± 0.9 | 20.5 ± 3.0 | 24.5 ± 2.9 | 45.9 |
| *Cyperus papyrus* | | | | |
| shoreline | 22.4 ± 1.1 | 16.6 ± 1.9 | 25.1 ± 2.6 | 31.1 ± 2.9 |
| 10 - 40 m off | 20.6 ± 2.0 | 18.5 ± 1.2 | 25.2 ± 1.3 | 36.4 ± 1.4 |
| open water | 22.1 ± 1.4 | 21.1 ± 2.5 | 29.9 ± 0.0 | 40.7 ± 2.2 |

As can be seen from the table, the chlorophyll-a content was higher during the wet seasons; the open water sites appeared to also have higher concentrations than the shallower parts of the transects.

To find out whether or not the patterns (Table 11) related to spatial and seasonal differences, pH values for the same period are presented in Table 12. The evaluation assumes that a higher pH indicates a higher phytoplankton productivity (Talling, 1976) and thus a higher chlorophyll-a content.

Table 12. The pH in *Eichhornia crassipes* and *Cyperus papyrus* transects (mean values and standard error). The wet and dry seasons have been indicated.

|  | May 1995 (wet) | July 1995 (dry) | October 1995 (wet) | February 1996 (dry) |
|---|---|---|---|---|
| *Eichhornia crassipes* |  |  |  |  |
| shoreline | 7.7 ± 0.1 | 7.1 ± 0.1 | 7.7 ± 0.1 | - |
| 10 - 40 m off | 7.9 ± 0.1 | 7.4 ± 0.1 | 8.2 ± 0.2 | - |
| open water | 8.1 ± 0.3 | 7.5 | 8.9 ± 0.1 | - |
| *Cyperus papyrus* |  |  |  |  |
| shoreline | 8.0 ± 0.2 | 7.5 ± 0.1 | 8.7 ± 0.1 | - |
| 10 - 40 m off | 8.1 ± 0.1 | 7.6 ± 0.1 | 8.8 ± 0.1 | - |
| open water | 6.7 ± 1.7 | 7.6 ± 0.4 | 8.9 ± 0.0 | - |

The tables 11 and 12 indicate a higher phytoplankton productivity in the open water sites compared to the (near) shoreline sites. In the wet seasons the pH is higher at all sites than it was during the dry season.

**Macrophytes**
In Table 13 the biomass of the five vegetation types is given for August 1993, February 1994, August 1995 and August 1996.

*C. papyrus* carried the highest biomass irrespective of time of sampling, followed by *P. mauritianus* and *E. crassipes*. It is notable that over the period of investigations the biomass of *T. domingensis* and *V. cuspidata* declined. *E. crassipes*, which earlier had not been among the most frequent species (Table 3), rapidly increased in 1995 but had declined in biomass in the 1996 measurements. The above water biomass in *C. papyrus* is relatively lower than the below water fraction in contrast to *E. crassipes*; it is highest at the shoreline while that of *E. crassipes* reaches maximum development 5 - 10 m inside. In general however, the biomass in each of the vegetation types was highly variable within sites and among seasons.

Table 13.  Biomass (mean ± standard error in g AFDW.m$^{-2}$) of the dominant plant species in the five vegetation types. The biomass is given for the above water parts as well as for the below water parts at 0 m (swamp edge), 5, 10 and 20 m towards dry land.

| | Aug. '93 | Feb. '94 | Aug. '95 | | | May '96 | | |
|---|---|---|---|---|---|---|---|---|
| *Eichhornia crassipes* | | | | | | | | |
| shoreline | | | | | | | | |
| above | . | . | 2404 | ± | 420 | 1026 | ± | 73 |
| below | . | . | 1114 | ± | 155 | 1094 | ± | 144 |
| 5 m in | | | | | | | | |
| above | . | . | 2035 | ± | 511 | 1814 | ± | 395 |
| below | . | . | 1023 | ± | 175 | 1360 | ± | 288 |
| 10 m in | | | | | | | | |
| above | . | . | 2412 | ± | 370 | 1281 | ± | 168 |
| below | . | . | 1496 | ± | 292 | 1263 | ± | 145 |
| *Cyperus papyrus* | | | | | | | | |
| shoreline | | | | | | | | |
| above | 2889 | 4291 | 3104 | | | 4573 | ± | 751 |
| below | 14527 | 23247 | 5036 | | | 6131 | ± | 2085 |
| 5 m in | | | | | | | | |
| above | . | . | 9326 | | | 1672 | ± | 224 |
| below | . | . | 10457 | | | 2342 | ± | 317 |
| 10 m in | | | | | | | | |
| above | 1033 | 2131 | 10808 | | | 2558 | ± | 810 |
| below | 5260 | 9445 | 15997 | | | 8386 | ± | 2098 |
| 20 m in | | | | | | | | |
| above | . | . | . | | | 2836 | ± | 593 |
| below | . | . | . | | | 12230 | ± | 1870 |
| *Typha domingensis* | | | | | | | | |
| shoreline | | | | | | | | |
| above | 486 | . | . | | | 13 | ± | 10 |
| below | 173 | . | . | | | 14 | ± | 12 |
| 10 m in | | | | | | | | |
| above | 149 | . | . | | | 33 | ± | 18 |
| below | 40 | . | . | | | 0 | | |
| *Vossia cuspidata* | | | | | | | | |
| shoreline | | | | | | | | |
| above | 947 | . | . | | | 490 | ± | 50 |
| below | 459 | . | . | | | 2 | ± | 0.1 |
| 5 m in | | | | | | | | |
| above | . | . | . | | | 700 | ± | 270 |
| below | . | . | . | | | 3 | ± | 0.6 |
| 10 m in | | | | | | | | |
| above | 4228 | . | . | | | 903 | ± | 11 |
| below | 2149 | . | . | | | . | | |
| *Phragmites mauritianus* | | | | | | | | |
| shoreline | | | | | | | | |
| above | 3999 | . | . | | | 3222 | ± | 694 |
| below | 0 | . | . | | | 4117 | ± | 786 |
| 5 m in | | | | | | | | |
| above | 2560 | . | . | | | 2553 | ± | 1102 |
| below | 0 | . | . | | | 3646 | ± | 1370 |

Table 14 considers the total biomass of the secondary plant species and that of litter within the first 10 m into the vegetation stands.

Table 14.    Total biomass of secondary species and litter (g AFDW.m$^{-2}$) in the investigated vegetation types.

|  | secondary species | | litter | total |
|---|---|---|---|---|
|  | n | biomass | biomass | biomass |
| *Eichhornia crassipes* | 0 | 0 | 0 | 0 |
| *Cyperus papyrus* | 5 | 196 | 1705 | 1901 |
| *Typha domingensis* | 8 | 1479 | 1627 | 3106 |
| *Vossia cuspidata* | 0 | 0 | 0 | 0 |
| *Phragmites mauritianus* | 4 | 225 | 766 | 991 |

Both   *C. papyrus* and *T. domingensis* stands carried the highest biomass of secondary species. The most important secondary species considered are climbers such as *Ipomoea* and *Cyphostema*. Other species such as *Hibiscus*, *Commelina*, *Dryopteris* and *Cynodon* were equally important. *Eichhornia*, *Phragmites* and *Echinochloa* were also important secondary species in other vegetation types, especially in habitats such as *Typha* that were increasingly coming under influence of *Eichhornia crassipes*. In *Typha* dominated habitats, an increase in secondary species appeared to be correlated with a reduction in the biomass of the dominant between 1993 and 1996 (Table 13).

**Macrofauna**
In Table 15 the taxa encountered in the macrofauna samples are given.

Table 15.   Benthic macrofauna taxa from wetland habitats of lake Victoria.

| Class | Taxa |
|---|---|
| Mollusca | *Bellamya, Mellanoides, Coelatura, Pisidium* |
| Insecta | Chironomidae,   Chaoboridae,   Odonanta, Trichoptera, Ephemeroptera |
| Crustacea | *Caridina* |
| Annelida | Oligochaeta, Hirudinea |

Of these macrofauna, nine taxa commonly identified in bottom samples, were recovered in sufficient numbers to allow further analysis. These data are summarized in Table 16 for the five vegetation types.

Data on the temporal distribution patterns of the same macrofaunal groups in an *Eichhornia crassipes* and a *Cyperus papyrus* stand are summarized in Table 17 (May, July and October 1995).

Table 16. Mean abundance (individuals .m⁻²) of benthic organisms in the five vegetation types investigated June 1996).

*Eichhornia crassipes:*

|  | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| Bivalvia | 151 | 246 | 96 | 369 | 205 | 0 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 0 | 0 | 0 | 14 | 0 | 0 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | 233 | 615 | 96 | 123 | 123 | 123 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 14 | 0 | 0 | 14 | 0 | 0 |
| Oligochaeta | 0 | 0 | 55 | 14 | 0 | 0 |
| Trichoptera | 0 | 0 | 0 | 41 | 14 | 41 |

*Cyperus papyrus:*

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 110 | 192 | 14 | 28 | 52 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 28 | 14 | 82 | 0 | 31 |
| Ephemeroptera | 28 | 0 | 0 | 0 | 0 |
| Gastropoda | 96 | 369 | 233 | 287 | 123 |
| Hirudinea | 0 | 0 | 0 | 0 | 10 |
| Odonata | 9 | 0 | 14 | 0 | 0 |
| Oligochaeta | 0 | 0 | 0 | 0 | 0 |
| Trichoptera | 14 | 0 | 0 | 0 | 10 |

*Typha domingensis:*

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 41 | 410 | 205 | 287 | 0 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 205 | 0 | 21 | 41 | 0 |
| Ephemeroptera | 0 | 0 | 41 | 0 | 0 |
| Gastropoda | 41 | 0 | 21 | 0 | 41 |
| Hirudinea | 0 | 0 | 21 | 21 | 0 |
| Odonata | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | 41 | 0 | 144 | 82 | 0 |
| Trichoptera | 861 | 41 | 246 | 308 | 0 |

*Phragmites mauritianus:*

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 431 | 123 | 308 | 267 | 41 |
| Chaoboridae | 205 | 0 | 0 | 0 | 0 |
| Chironomidae | 123 | 1374 | 62 | 62 | 41 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 41 |
| Gastropoda | 123 | 0 | 123 | 451 | 103 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 7 | 0 | 0 |
| Oligochaeta | 0 | 164 | 21 | 21 | 21 |
| Trichoptera | 1005 | 554 | 123 | 103 | 21 |

*Vossia cuspidata:*

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 0 | 615 | 1025 | 0 | |
| Chaoboridae | 0 | 0 | 0 | 0 | |
| Chironomidae | 1763 | 0 | 328 | 123 | |
| Ephemeroptera | 246 | 0 | 123 | 0 | |
| Gastropoda | 82 | 164 | 82 | 41 | |
| Hirudinea | 0 | 0 | 41 | 0 | |
| Odonata | 0 | 0 | 0 | 41 | |
| Oligochaeta | 0 | 0 | 0 | 41 | |
| Trichoptera | 205 | 205 | 1353 | 41 | |

**Table 17.** Seasonal changes in mean abundance (individuals.m$^{-2}$) of benthic organisms from an *Eichhornia crassipes* and a *Cyperus papyrus* stand.

*Eichhornia crassipes*: May 1995

| | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 0 | 0 | 7 | 16 | 21 | 25 | 0 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 0 | 0 | 7 | 16 | 0 | 0 | 8 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | 0 | 0 | 62 | 66 | 103 | 123 | 139 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 7 | 0 | 7 | 0 | 0 |
| Oligochaeta | 0 | 0 | 0 | 25 | 7 | 8 | 16 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Eichhornia crassipes*: July 1995

| | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 57 | 155 | 141 | 570 | 948 | 69 | 402 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 0 | 0 | 0 | 5 | 5 | 5 | 29 |
| Ephemeroptera | 0 | 7 | 5 | 0 | 0 | 0 | 0 |
| Gastropoda | 25 | 41 | 137 | 96 | 137 | 274 | 16 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 9 | 9 | 9 | 5 | 0 | 21 |
| Oligochaeta | 16 | 14 | 28 | 46 | 28 | 14 | 28 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Eichhornia crassipes*: October 1995

| | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 0 | 129 | 73 | 23 | 250 | 182 | 14 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 0 | 6 | 0 | 9 | 14 | 0 | 14 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | 28 | 35 | 41 | 69 | 219 | 114 | 69 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | 0 | 6 | 41 | 41 | 41 | 14 | 18 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Cyperus papyrus*: May 1995

| | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 21 | 89 | 267 | 137 | 0 |
| Chaoboridae | 0 | 0 | 0 | 0 | 192 |
| Chironomidae | 649 | 14 | 7 | 0 | 28 |
| Ephemeroptera | 164 | 7 | 0 | 0 | 0 |
| Gastropoda | 116 | 260 | 779 | 349 | 41 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 |
| Odonata | 41 | 7 | 7 | 21 | 14 |
| Oligochaeta | 28 | 62 | 14 | 7 | 7 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 |

*Cyperus papyrus*: July 1995

| | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 67 | 155 | 192 | 297 | 132 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 73 | 5 | 14 | 31 | 69 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 14 |
| Gastropoda | 0 | 301 | 283 | 151 | 223 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 |
| Odonata | 16 | 9 | 14 | 0 | 18 |
| Oligochaeta | 5 | 28 | 14 | 21 | 9 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 |

*Cyperus papyrus*: October 1995

| | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 50 | 401 | 401 | 497 | 82 |
| Chaoboridae | 0 | 0 | 0 | 0 | 0 |
| Chironomidae | 23 | 14 | 5 | 16 | 12 |
| Ephemeroptera | 55 | 0 | 0 | 0 | 0 |
| Gastropoda | 87 | 328 | 164 | 267 | 98 |
| Hirudinea | 0 | 0 | 0 | 0 | 0 |
| Odonata | 14 | 14 | 7 | 0 | 0 |
| Oligochaeta | 14 | 28 | 9 | 16 | 12 |
| Trichoptera | 0 | 0 | 0 | 0 | 0 |

In Table 18 data of all sampling stations, pooled for each vegetation type, are given for six taxa.

Table 18.              Summary of ANOVA- analysis for pooled macrofauna numbers (ind.m$_{.2}$) for each of the vegetation types.
a, b, c, d refer to differences (the sequence a - d indicates increasing trends) between the vegetation types tested with one-way ANOVA. The same character is given to any combination which is not significantly different. Different characters show significant differences ($p < 0.05$).

| | taxa | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| **Number of samples** | | | | | | | |
| open water | 48 | cd | b | a | a | b | a |
| C. papyrus | 134 | b | a | a | a | ab | a |
| E. crassipes | 161 | a | a | a | a | a | a |
| P. mauritianus | 10 | abc | a | a | b | a | a |
| T. domingensis | 10 | d | a | a | b | ab | a |
| V. cuspidata | 5 | d | a | a | b | ab | b |

1 = Chironomidae, 2 = Chaoboridae, 3 = Oligochaeta, 4 = Trichoptera, 5 = Gastropoda, 6 = Bivalvia

From Table 18 it can be seen that the *T. domingensis* and *V. cuspidata* stands were very similar in macrofauna abundance and only differed in the number of bivalves. They also showed a similarity with the open water sites (400 - 500 m offshore). ANOVA for five *Cyperus papyrus* replicate sites showed similar patterns of distribution and abundance ($p > > 0.10$). Among the *Eichhornia crassipes* beds, one site was significantly different ($p < 0.05$) from others. Averages from *Typha domingensis* and *Phragmites mauritianus* were also similar, while only one permanent *Vossia cuspidata* site was included. Vegetation types, therefore, appeared to represent different invertebrate communities.
Molluscs were well represented in all habitats with peak abundance of 615 ind.m$^{-2}$ at the edge of *Eichhornia crassipes* mats, while the highest number of bivalves (1025) was recorded at 20 m off *Vossia cuspidata*. *V. cuspidata* carried the highest number (1760) of chironomids, although the group was well represented at 10 m off *P. mauritianus* (1370) and at the edge of *T. domingensis* (505). Although distributed at most distances from *C. papyrus*, chironomids were absent from *E. crassipes*. Trichoptera were particularly abundant (860 - 1350 ind.m$^{-2}$) in *T. domingensis, P. mauritianus* and *V. cuspidata* habitats. They were much fewer 10 - 40) and more sparsely distributed off *E. crassipes* and *C. papyrus*. Oligochaetes were mostly associated with *T. domingensis* (40 - 140 ind.m$^{-2}$) at 20 - 40 m off the edge of the vegetation. The general trend from the data for all habitats investigated shows that numbers of individuals and of taxa tend to peak between 20 - 40 m off

the edge of vegetation. A secondary peak in numbers and diversity was observed at 400 m in comparison to 500 m off the edge of the vegetation (Table 21).

As there were more replicate samples between *Eichhornia* and *Cyperus papyrus* sites, a two-way ANOVA was carried out to test the significance ($p < 0.05$) of vegetation, distance from the vegetation edge and the interaction (vegetation * distance) on seven of the benthic macrofauna taxa (Table 19).

Table 19.   ANOVA's of the effects of vegetation, distance from the vegetation edge and the interaction of these two on distribution of seven benthic macrofauna taxa in *Eichhornia crassipes* and *Cyperus papyrus* sites. Four levels of significance are indicated: $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*) and $p > 0.05$ (ns = not significant). F = factor ss; E = explained ss (F/E % = a measure of variation explained by that factor).

| | vegetation | | distance | | interaction | |
|---|---|---|---|---|---|---|
| | p | F/E (%) | p | F/E (%) | p | F/E (%) |
| Bivalves | *** | 30 | ** | 38 | ** | 29 |
| Chironomidae | * | 13 | ** | 45 | ** | 43 |
| Ephemeroptera | ns | | ns | | ns | |
| Gastropoda | *** | 25 | ** | 37 | ** | 35 |
| Hirudinea | ns | | ns | | ns | |
| Odonata | ns | | ns | | ns | |
| Oligochaeta | * | 22 | ns | | ns | |

The table shows that for three taxa (Bivalvia, Chironomidae and Gastropoda) both vegetation and distance affect their distribution and a large proportion (30 - 40 %) of the interaction is due to distance. Oligochaeta appear to be strongly affected by vegetation but no effects of distance were significant ($p = 0.05$) for other groups.

Table 20 presents the distribution patterns of the taxa influenced by vegetation and distance (Bivalvia, Chironomidae and Gastropoda) in *Cyperus papyrus* habitats. The table shows that Chironomidae were more abundant closer to the shore while Bivalvia and Gastropoda appeared to be more abundant between 10-40 m from the vegetation edge. After the 350 m area, there appeared to be a secondary pattern between 400-500 m of the edge of vegetation (Table 21).

Table 20. Distribution of Bivalvia, Chironomidae and Gastropoda (ind.m$^{-2}$ ± s.e.) off the edge of the *Cyperus papyrus* sites (n = 6). Different characters show significant differences (p < 0.05).

| distance (m) | Chironomidae | Bivalvia | Gastropoda |
|---|---|---|---|
| 0 | 648 ± 291 b | 21 ± 12 ab | 115 ± 57 ab |
| 10 | 21 ± 8 a | 90 ± 29 abc | 258 ± 94 ab |
| 20 | 8 ± 8 a | 267 ± 90 c | 787 ± 189 b |
| 40 | 0 a | 135 ± 45 bc | 385 ± 98 ab |
| 350 | 29 ± 12 a | - | 41 ± 25 a |

Table 21. Benthic macrofauna (individuals per square metre) in open water stations.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| 400 m off | 107 | 29 | 15 | 4 | 0 | 271 | 58 | 21 | 15 |
| 500 m off | 48 | 21 | 10 | 7 | 7 | 232 | 40 | 0 | 6 |

1 = Chironomidae, 2 = Chaoboridae, 3 = Oligochaeta, 4 = Odonata, 5 = Ephemeroptera, 6 = Gastropoda, 7 = Bivalvia, 8 = Hirudinea, 9 = Trichoptera

In Table 22 the mean dry weights are given for the different macrofauna taxa. With the help of this table the biomass could be computed (DW in g.m$^{-2}$ in Appendix 4).

Table 22. Mean dry weight per individual of the most common macrofauna taxa.

| taxon | dry weight (g) |
|---|---|
| Gastropoda | 0.052 |
| Bivalvia | 0.052 |
| Odonata | 0.030 |
| Trichoptera | 0.021 |
| *Caridina* | 0.010 |
| Oligochaeta | 0.004 |
| Hirudinea | 0.004 |
| Chironomidae | 0.001 |
| Chaoboridae | 0.001 |
| Ephemeroptera | 0.001 |

## Changes in the wetland landscape

Fig. 3 and 4 illustrate changes in the landscape of the study area between 1950/60 and 1992. Comparing Fig. 3 with Fig. 4 shows that distinct changes have occurred particularly to the east and west of Jinja. In these areas, large parts of forests and wetlands appear to have been cleared. Along the eastern shores of Thruston Bay and the islands, both forest and wetlands have considerably reduced.

Table 23 provides a quantification of the main changes in the landscape between 1950/60 and 1992.

Table 23. Changes in the Lake Victoria landscape (1950/60 and 1992) in the Jinja study area. Data represent area in $km^2$ as well as percentages of the total area (between brackets).

|  | historic (1950/60) |  | modern (1992) |  |
| --- | --- | --- | --- | --- |
| total area | 367.4 |  | 367.4 |  |
| surface water | 127.8 | (34.8) | 133.1 | (36.2) |
| forest/woodland | 67.0 | (18.2) | 23.5 | (6.4) |
| wetlands | 15.4 | (4.2) | 14.8 | (4.0) |
| others | 157.2 | (42.8) | 195.9 | (53.3) |

The table shows a 30 % reduction in forest/woodland, and about 5 % decrease in wetlands. The increase in the category "others" is due to agricultural and built-up areas. Wetland loss appears small on the scale of resolution used in the assessments.

## DISCUSSION

In Lake Victoria, the interface between wetland buffers and the associated open water has been assumed to be ecologically important for fisheries. The wetland buffers have also been regarded as a major factor in the water quality of the lake (e.g., Crul, 1995) and structural diversity of shallow water habitats (this chapter). As these interface habitats in the lake are most likely to be the first to experience changes in the catchment, the degree to which such habitats may respond depends on knowledge of their structure and function. In Lake Victoria, lake shore wetlands and the adjoining shallow aquatic habitats are commonly only regarded as swamps. Therefore, major questions remain regarding the composition of the swamps, and whether they are characterised by special conditions which distinguish them from open water. In addition, until this study, hydrological changes associated with the lake level rise in the 1960s, and, an increase in the human population in the catchment as sources of major ecological influences which may affect wetlands as fish habitats were not fully appreciated. The exotic weed, *Eichhornia crassipes* was unknown and water plants had commonly been reported (e.g., Lind and Visser, 1962; Beadle, 1981). The area investigated was considered as representative of

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a large part of the lake's vegetated shoreline in which various influences could be characterised. Additionally, the area was found to be part of a wider belt of geomorphologically similar features as described by Velle and Drichi (1962).

### Identification of recurrent vegetation types

The more than 40 plant species identified during the study have been grouped into six major plant communities (Table 2). A plant community for the purpose of this study could be defined as a group of plant species which normally grow together in a particular habitat and form a recognisable type of vegetation identifiable by dominant species or discrete associations. Although *C. papyrus* was the most extensively distributed dominant plant species in the study area, the presence of other community types (Table 2) in specific locations along the shoreline indicates special abiotic features in those locations. As originally shown by Moore (1962), differences in species cover abundance often observed in plant associations may be related to specific habitat factors. In Lake Victoria, Lind and Visser (1962) suggested that the important factors related to plant zonation in lake swamps were water levels, slope and mineral concentrations, while Welcomme (1965; 1966) used slope, water level and wind exposure to distinguish between gradient and non-gradient beaches among the shallow aquatic habitats. From the study of vegetation patterns along the shoreline, it appears that dominant emergent plant species may also be used to distinguish shallow aquatic habitats into various types. In Lake Victoria, these habitats would include *C. papyrus*, *V. cuspidata*, *T. domingensis* and *P. mauritianus* dominated types. As a new but dominant species associated with shallow areas, *E. crassipes* could also qualify to be regarded as a distinct habitat type, even though it occurs mostly as a floating species. The discerned pattern may also account for structural diversity in other factors including mineral concentrations, water level, slope, and, subsequently in fish populations.

The influence of plant patterns at the shore on water and habitat quality may be partly due to their proximity to the water medium and to their biomass characteristics. Being emergents and in transitional zones between land and water, the plant communities' influence is probably confined to the interface area between the vegetation fringes and the limit of the littoral zone. In the study area, this part of the lake was defined as an area lying within about 50-70 m from the shoreline. Beyond this zone, there appears to be a transitional zone (about 300 to 500 m off the vegetation fringe towards open water) in which there may be considerable interchanges between the inner shallower littoral and an outer sub-littoral zone. Although some species of fish (e.g. *Oreochromis* spp.) may be caught some distance away from the shoreline and have therefore been frequently referred to as occurring in inshore areas in a majority of studies, such species could actually be habitat specific as shown in studies to the south of the lake (Witte, 1981). Therefore, any changes in the type, cover abundance or other features of the vegetation at the shore are likely to be manifested more prominently, initially in the ecology of fish populations and other organisms in the inner littoral habitats at the lake shore.

**Changes in the wetland landscape**

The use of different methods in generating spatial differences has the main limitation that scales cannot be reproduced with the desired level of accuracy. This applies particularly to comparisons between satellite images and topographic maps. However, it was considered that for gross landscape changes on the scale of the study area, a sufficiently reliable impression could be obtained relating to land use and wetland cover changes.

Heavy rains (1961/64) modified the earlier mapped landscape. The increase in the surface area of water is part of the rise in lake level. The creation of lagoons within the papyrus fringes by the rising level (Welcomme, 1966) is an example of this modification. However small the reduction in woodland and wetland cover may appear to be (Table 23), it is likely that without the exceptionally heavy rains and a 2 m rise in lake level, the absolute cover change would be greater. It is probable that the present shoreline wetland landscape may still be partly under the influence of past lake level changes. However, human impacts such as biomass harvests, agriculture and human settlements, and the impact of stocked fish (Welcomme, 1965; 1966) have also contributed to the present structure of the shallow aquatic habitats. The present fauna of the habitats is therefore likely to be undergoing succession resulting from cover change and related impacts. For example, in small community types, secondary succession is more rapid. In *Typha*, this could lead to rapid modification of the habitat due to colonisation by *Eichhornia*, *Vossia*, *Echinochloa* and several shrubs. In *Vossia*, the influence of *Eichhornia* appeared to be followed by an expansion of floating *Vossia* stems into the open water and a superficial dominance of the species. For fish species where predator avoidance is part of the life history (Crowder and Cooper, 1982), habitat structural complexity as shown in *Typha* stands could be beneficial.

The investigated littoral habitats of northern Lake Victoria's shoreline were characterised by 5 dominant plant communities: *C. papyrus*, *E. crassipes*, *V. cuspidata*, *T. domingensis* and *P. mauritianus*. Of these, *C. papyrus* had the highest biomass, occurred in more than 90 % of stands along the 110 km investigated shoreline, and stretched further inland than the other species. *E. crassipes* first recognised in the lake in 1989 (Twongo, 1991) was rapidly gaining areal importance and was more strongly associated with the coastline off papyrus which is exposed to onshore winds (Appendix 2). Apart from its floating habit, the weed stretched much further into the open water than the other species.

The present investigations also show that there have been profound changes in the areal extent of the vegetation types (Fig. 3 and 4) and of open water (Table 23). These changes have been due to an increased population and landuse, and in the case of open water, a rise in lake level. The impact of lake level rise on the tilapias, particularly the stocked species, was considered beneficial (Welcomme, 1965; 1966). This was due in part to the appearance of lagoons behind papyrus fringes, and more gradient beaches. Though this influence has declined in time as the lake's level receded, some species of fish such as the tilapias probably owe their initial

establishment to this phenomenon. This may account for the suggestion that the effects of swamp clearance could lead to an increase in spawning areas for the Nile tilapia, *Oreochromis niloticus* (Balirwa, 1992). However, as young stages of many of the tilapia species seek habitats in clear shallow water (Welcomme, 1964), succession of the type caused by receding water levels or by invasive weeds may result into the fish species displacement by others, such as the mud dwelling taxa e.g., the clariids and *Protopterus* which can also utilise atmospheric oxygen (Greenwood, 1966).

A major effect of the hydrological changes at present has been the contraction of the littoral zone. As the water receded from the previously flooded marginal areas, the area under water reduced to one which stretches from the present shoreline to about 50 - 70 m off the vegetation fringe, and a reduction of lagoons behind the vegetation fringes. The study also showed that the Jinja area still contains areas of intact wetland patches dominated by the indigenous 4 species and the exotic hyacinth. Dominant vegetation fringes and the seasonal hydrological regime may therefore be major indicators of habitat conditions for fish at present. They are however probably subjected to higher loads of nutrient and other inputs from the watershed and, the increasing infestation with *Eichhornia crassipes*. The effect of vegetation on habitat structure therefore partly depends on the biomass (aerial and below ground), its location with respect to the water surface and on hydrology. The development of the present landuse, in relation to the vegetation characteristics and hydrology (increased nutrient loads) may explain the rare occurrence of euhydrophytes such as *Nymphaea*, *Ceratophyllum* and *Potamogeton* which were commonly observed in the past (Carter, 1955; Lind and Visser, 1962; Beadle, 1981).

## Characterisation of the sites
### Physical and chemical characterization
The investigated habitats were initially distinguished on the basis of recurrent dominant vegetation. In Table 4, the influence of vegetation on sediment composition shows a horizontal gradient in *Eichhornia crassipes* and *Cyperus papyrus* habitats. The two also have the highest coarse plant litter content on the surface sediments. Plant litter content is probably due to the biomass of the plants (Table 13) and their location at the shoreline, and the rate of decomposition. The high proportion of organic matter content (up to 40 m away from the vegetation) in relation to other sediment components (sand, clay, silt) and a higher N:P ratio than for the *Vossia*, *Typha* and *Phragmites* habitats in spite of steeper gradients (Fig. 7) of the former may also be due to these factors.

Based on size fractionation of the sediments (Table 4) two types of sites could be characterized.
Type a): Sites with a dominance of sediments with a high clay content. These sites were characterized by the vegetation types dominated by *Eichhornia crassipes* and/or *Cyperus papyrus*.

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Type b): Sites with sandy sediments, dominated by *Typha domingensis*, *Vossia cuspidata* or *Phragmites mauritianus*.

Table 4 also shows that clay and silt fractions increase with distance from the shoreline to open water sites. These data show that the littoral zone in the study area is structured both by vegetation type and by distance from the vegetation fringe.

The N/P-ratios (by weight, $mg.g^{-1}$) of the sediments (Table 5), also confirms the classification of the sites examined into the two major types: a) *Cyperus papyrus-Eichhornia crassipes* habitats in which the October N/P ratio is generally above 10 and b) *Phragmites-Typha-Vossia* habitats in which the October N/P ratio is less than 10. The May values are higher and of the order of at least 25 for type a and 15 for type b). With respect to the periods examined, the patterns tend to show a relation with the amount of rainfall and, therefore, the influence of transport from land. The average N/P ratio of vascular plants is 10 (Mulligan *et al.*, 1976) and that of sediments fell into the categories recognised above. This suggests a strong vegetation-hydrological effect confirmed by statistical analysis (Table 7). The seasonal total organic matter (AFDW) of the sediments also separates the two types of habitats. From Table 6 it can be seen that a) the total organic matter of the *Cyperus papyrus* and the *Eichhornia crassipes* sediments is high and b) the offshore sediments have about the same organic content.

Further away from the vegetation fringe, the offshore sediments have about the same organic content which lower than that nearer to the vegetation. It appears that despite the uniformity in size fractions and TOC which appear to separate the vegetation types into two habitat categories, the N/P or C/N ratios may determine finer differences among the habitats. For example, although the average N/P ratio of vascular plants is 10 (Mulligan *et al.*, 1976), that of sediments varied with season. In addition, the TOC in *Vossia* stands was generally higher than that in *Typha* and *Phragmites* dominated habitats (Table 6). These differences could be related to factors such as the variable biomass of the dominant vegetation at the shore (Table 13), to the efficiency by the plants in the uptake and release of nitrogen compounds (Muthuri and Jones, 1997), and other factors such as slope and the amount of allochthonous matter leached into the shallow areas from the catchment. In this, lies an additional potential of human impacts (e.g., alteration of run off rates through devegatation) on the shallow aquatic habitats, which has been regarded as a major threat to tropical freshwater fish (Lowe-McConnell, 1994). It is therefore considered that although sediment parameters are largely similar with respect to the two categorised habitat types, other differences among habitats could be governed by the annual sequence of the rains, and may be influenced by human activity in the study area.

Of the analyzed water quality parameters (Table 7, Fig. 8), the hydrological regime (seasonality) accounted for most of the significant variation. Vegetation type (habitat) explained mostly significant effects on tot.-P, SRP and redox while interaction (vegetation type * season) effects explained most variation associated

with $NO_3$-N, dissolved oxygen and conductivity. In pooled samples of all habitat types studied, higher silica concentrations (500 - 1000 $\mu$g,$l^{-1}$) were recorded during rainy periods in comparison to 200 - 500 $\mu$g.$l^{-1}$ during the July - September short dry season (Fig. 8). These findings indicate the complexity and dynamic character of shoreline vegetation dominated habitats. For example, considering the Si, the normally dry period (February) was associated with the highest concentration (Fig. 8b) which could have been a result of the wet conditions during the sampling period. For $NO_3$-N, the interactive effects of vegetation with season may be important but other factors such as phytoplankton (Cyanobacteria) density could play a role in the variations in available $NO_3$-N. However, *Eichhornia* - dominated habitats could be distinguished from the other types in significantly lower Si (302 ± 17 $\mu$g.$l^{-1}$) and higher SRP (8.5 ± 0.3 $\mu$g.$l^{-1}$) considering the width of the littoral zone up to 50 - 70 m away from the vegetation fringe. It has to be noted however, *Eichhornia* habitats stretched further into the water than the four emergent species. Despite this spatial difference, *Eichhornia* and papyrus dominated habitats showed similarities which were significantly different from the other habitat types (Fig. 7). The two (*Eichhornia* and papyrus) habitat types had the lowest mean TP (41 - 48 $\mu$g.$l^{-1}$), $NO_3$-N (5.4 - 9.7 $\mu$g.$l^{-1}$), algal biomass/seston (11.1 - 11.8 $\mu$g.$l^{-1}$) and the highest conductivity (110 $\mu$S.$cm^{-1}$). Although $NH_4$-N was not measured, the low $NO_3$-N could be related to the generally anaerobic conditions in swamp water (Muthuri and Jones, 1997). These results therefore indicate that though season was the main factor explaining most variation in water quality differences, the type of vegetation could be coupled to the influence of season and determine the suitability of habitats for organisms such as invertebrates and fish. As for sediment characteristics (size fractions and TOC), the habitats can also be distinguished from open water habitats along horizontal gradients. Such horizontal differentiation may be increase the strength of water quality differences.

Taking literature data by Hecky and Bugenyi (1989) as reference, it is easily noticed that the water quality of the investigated habitats differs considerably from the generalised Lake Victoria state. For example, literature data give concentrations of 7 - 70 $\mu$g.$l^{-1}$ Si, 0.2 $\mu$g.$l^{-1}$ $NO_3$-N, 0.23 - 0.42 $\mu$g.$l^{-1}$ o-$PO_4$ and 94 - 97 $\mu$S.$cm^{-1}$ conductivity in comparison to much higher values in the width of the sampled area i.e between the vegetation fringes and open water habitats which are 300 - 500 m away (Appendix 5). It is also not clear whether literature data considered seasonal effects which were particularly significant in the presented results from this study (Table 7 and Fig. 7). Seasonal variations in nutrients especially in Si and $NO_3$-N concentrations are correlated with phytoplankton seasonality (Akiyama *et al.*, 1977) may account for seasonal use of the habitats by higher trophic levels especially herbivorous organisms. As a result of human impacts which may be associated with landuse (e.g., vegetation clearance, increased use of fertilisers), hydrological and horizontal effects may either be enhanced, or seasonal patterns of phytoplankton may be dampened out with continuous inputs of substances from the catchment. Considering the effects of vegetation, sediment characteristics, nutrients and seasons, the above elaborated data suggest that the shallow habitats are highly dynamic and respond to mostly to seasonal influences. For aquatic

organisms, the impact of human activity may be the alteration in their behaviour or habitat shifts as some of these influences could however be subordinated by diurnal changes such as in temperature, DO and pH (Fig. 9)

### Phytoplankton

In the shallow habitats investigated, water column structure is expected to be generally more uniform than the deeper areas (6 - 8 m) cited as inshore in previous studies (Fish, 1957; Talling, 1957; 1966; 1987; Akiyama et al., 1977). The emphasis in these studies was to account for the phytoplankton cycles in relation to stratification phenomena. The main sampling sites for the present study were mostly less than 3 m deep. The observed patterns in algal biomass and abundance (Tables 10 and 11) indicate strong hydrological and nutrient effects from the catchment. This is shown by phytoplankton density data (Fig. 10) for April (early in the rain season) and September (end of short dry season). The lower diatom (Nitzschia) density in the rainy season (when silica input is higher) suggests that successional patterns in diatoms and cyanobacteria (Nitzschia, Anabaena, Lyngbya and Microcystis) are more correlated with vertical mixing offshore which follows breakdown of stratification during July-August supported by studies of Talling, (1966; 1987). They could also be due to nutrient limitation resulting from competition between algal species.

Because the investigated littoral habitats are shallow, horizontal differentiation in phytoplankton could also be influenced by sediment characteristics or overhanging vegetation (papyrus). The higher phytoplankton densities in Typha and Phragmites habitats in comparison to those off papyrus and Eichhornia could indicate effects of shading. However, turbulence and resuspension of particulate matter or nutrient competition in Eichhornia-infested habitats could contribute to habitat differences. For phytoplanktivorous fish (Witte, 1981), the observed patterns may indicate preferred feeding grounds (Typha and Phragmites dominated habitats) even though the influence of short term diurnal patterns (Fig. 9) may determine intra-habitat movements observed in the tilapias (Welcomme, 1964).

Among the more common taxa (Table 9), Nitzschia, Merismopedia and Sphaerocystis showed much higher population densities than previously reported by Talling (1966; 1987) and Akiyama et al., (1977). By far, Nitzschia was the most prominent diatom in contrast to Melosira reported in the past investigations. This suggests a long term successional trend paralleled by Sphaerocystis among the green algae. Merismopedia as reported by Talling (1966) is a typically shallow inshore species and was less abundant in open water sites. This is therefore direct evidence for phytoplankton horizontal differentiation. In general, the observed patterns suggest that the most productive areas for phytoplankton are those between 20 and 40 m from the shoreline but loosely attached epiphytic or benthic forms which were not investigated could be important as fish food nearer the vegetation. Hence, for fish, both horizontal and seasonal variations in phytoplankton which are coupled to spatial and temporal differences in abiotic environmental factors could determine the pattern of habitat use especially for

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feeding and the timing of breeding.

### Macrophytes

Both below ground, submerged and aerial macrophyte biomasses were generally high, although variation was considerable especially in papyrus habitats (Table 13). Data for papyrus biomass were particularly high in comparison to literature data (Muthuri *et al.*, 1989). The differences are probably due to habitat specific conditions as much as to sampling in different seasons; also, depending on the sampling design, papyrus biomass may be quite high if for example the more than 1 m downward deep-living entangled rhizome mat is included in estimates as was often the case. The aerial fraction may also be significantly affected if it includes the entire floating fraction of rhizome material as was done in this study. This study therefore shows that part of what is commonly regarded as above water or aerial biomass may in fact be rhizome and should be included in studies of biomass. In any case however, the significance of a high biomass could be related to the high productivity figures reported for the various species (Gaudet, 1979; Wetzel, 1983; Denny, 1985; Muthuri *et al.*, 1989; Bugenyi, 1993). The importance of vegetation and terrestrial watershed-nutrients may derive from a high organic content (Tables 5 and 6) and, the N:P ratio in which *Eichhornia* and papyrus showed significantly higher values than in the other three. However, the areas nearest to the vegetation would respond more both to plant nutrient content and hydrology (Table 7) than areas further away.

For the smaller community types with a lower biomass e.g *Typha* and *Vossia*, other influences come into play. In comparison to both papyrus and *Phragmites* biomass values, those of *Typha* and *Vossia* were much lower but also variable. Shoreline *Typha* biomass was highly unstable over the period (500 g AFDW.m$^{-2}$ in the 1993 dry season and 13 g AFDW.m$^{-2}$ in the 1996 wet season), with similar trends in inland stands. Like *Typha*, there was a higher *Vossia* biomass (950 - 4,200 g AFDW.m$^{-2}$) in the dry period of 1993 than in the wet season (500 - 900 g AFDW.m$^{-2}$) of 1996. Data reported by Muthuri *et al.,* (1989) are not comparable because they dealt with other species (*T. latifolia* and *P. communis*). Further, Lake Victoria *Typha* seems to undergo a seasonal cycle of growth, with maximum biomass during the dry season. In the wet season, young shoots of the species were observed growing out of the water and the products of senescence could be seen littered over the submerged beds of the gentle slope. The consequence of the interaction between vegetation and hydrology in such situations may be an increase in the colonisable surface by epiphytic algae.

In both the *Typha* and *Vossia* habitats, there were already signs of rapid secondary succession shown by a high number of secondary species (Table 14) in contrast to the situation during preliminary investigations. Originally, *Vossia* stands were monospecific but subsequently became associated with *Eichhornia*. In *Typha*, the presence of a high number of secondary species such as *Eichhornia*, *Vossia*, *Echinochloa* and several shrubs could lead to an increase in the biomass and, to rapid modification of the habitat through deposition of sediment in the immediate

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interface with the vegetation. In *Vossia*, the influence of *Eichhornia* appeared to be leading to an expansion of floating stems into the open water and artificial dominance of the species. Originally, *Vossia* stands were monospecific but in time an increase in biomass due to *Eichhornia* could add to the eventual organic content of the sediments. Apart from an increase in shading effects, *Eichhornia* decomposing mats would also result in further sediment loading of otherwise sandy-gravel habitats.

In Lake Victoria, the biennial cycle in *Typha* associated with a phase of degeneration under deep flooding does not affect *Phragmites*. As a result of being on higher ground a large part of its biomass remains erect although both have a much less developed root and rhizome system than papyrus stands. A consequence of this habit is that shoreline *Typha* habitats tend to undergo more rapid ecological succession with secondary colonisers as shown below:

*Eichhornia- > Vossia- > Melanthera- > Echinochloa- > Phragmites- > Hibiscus*

For both *Typha* and *Vossia*, the submergence of part of their biomass along the shallow shorelines increases the area of surface for the colonisation of their structures by epiphytic algae. In addition, a mixture of plant species increases structural complexity of the habitats to the benefit of refuge-seeking fish species (Chick and McIvor, 1994). The variable abundance of *Vossia* can be used as an indication of hydrological instability or high seasonal amplitude (Denny, 1985) but in the study area, it could also be due to the increasing influence of *Eichhornia*. This may have contributed to a lower below water biomass (Table 13) and allowed the younger floating *Vossia* stems to expand into the water without any substantial increase in biomass.

*Eichhornia* was not a prominent feature of the shoreline in 1993. By 1995 the mean total biomass from several habitats dominated by the species was 3,500 g $AFDW.m^{-2}$ about half of it below water. By 1996, this had declined to 2,000 g. This change could have resulted from nutrient limitation as the stands in the study areas had become more or less permanent. Although described as an obligate acropleustophyte (Denny, 1993), the *Eichhornia* of Lake Victoria may either be rooted in very shallow water (e.g among *Typha* stands), or compacted along sheltered shorelines (floating but static). In extensive infestations off the exposed papyrus coastline (Appendix 2), it was mobile (e.g under the influence of wind). The biomass of *Eichhornia* can therefore be highly variable and the data reported represent the situation in semi-permanent mats.

Habitat diversification appeared to be partly dependent on the location of the dominant vegetation with respect to the horizontal axis from land to water. Of the plant communities in the study area, *C. papyrus* was the most extensive and therefore the most typical habitat type of the shoreline wetlands. This is a consequence of the geomorphological history of the basin and the occupancy by *C. papyrus* of the old east-west flowing rivers and streams (Beadle, 1984).

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However, other parts of papyrus lined shores were distinct with respect to their orientation along the shore. By their exposure to on-shore winds, this type of *C. papyrus* habitat was more prone to infestations with water hyacinth. The other communities (*Phragmites*, *Typha* and *Vossia*), also part of several phytochoria in the Lake Victoria mosaic (Denny, 1993), were less extensive. Therefore, the observed distribution patterns of the plant dominants tend seem to explain the influence of slope and depths and the sequence from land to water. Although Denny (1985) observed both *Typha* and *Phragmites* in some herbaceous wetlands behind the papyrus fringe and suggested the sequence: *Typha---> Phragmites---> C. papyrus---> Vossia---> Euhydrophytes*, the present study illustrates that other patterns also occur. *Phragmites* was found over raised sandy-clay banks while *Typha* occurred on more gently sloping sand substrata. *Vossia* on the other hand was observed in the fore ground of *Cyperus papyrus* beds but on a more gravelly substrate than in pure papyrus stands. The characteristic sequence below seems to be typical of the study area:

*Phragmites---> C. papyrus---> Typha ---> Vossia ----> Eichhornia*

### Macrofauna
As the investigated vegetated habitats lie in shallow water, it is to be expected that the assumed ecological importance of the habitats is related to a rich benthic macrofauna as food sources for fish (Crowder and Cooper, 1982; Rasmussen, 1988; Lalonde and Downing, 1992; Brown and Lodge, 1993). The habitats are structured by differences in vegetation types, sediments and water quality. Therefore, differences in both the density and distribution of the macrofauna could be a result of the structural differences in habitat. Of the invertebrate taxa found (Table 15), insects (Chironomidae, Chaoboridae and Trichoptera) and molluscs (gastropods and bivalves) were the most important in density and biomass (Tables 16 and 17) which is consistent with estimates by Mothersill *et al.*, (1979). Three factors (vegetation, distance from vegetation and interaction of the two) significantly explained variations in the patterns of abundance of the Chironomidae, bivalves and gastropods (Table 19). Though most abundant (120-1760 ind. $m^{-2}$) 20 m off *Phragmites* and *Vossia*, chironomids showed a more consistent horizontal trend off papyrus-dominated habitats (Table 20) decreasing with distance from the vegetation edge. Bivalves showed an increasing trend towards more open water but gastropods were more confined to within 40 m of the vegetation. An exceptional feature in the trends was a second similar pattern of abundance at 400-500 m off the edge of vegetation (Table 21). It appears that within each group, there are various patterns reflecting the diversity of the group and of habitat conditions. For example, in the case of the Chironomidae, vegetation development and sediment organic content may have been the important factors yet, the patterns offshore are probably less dependent on vegetation. The observed spatial differences may be correlated with similarities in the diets of some fish species even though they are separated in feeding grounds.

Previous studies have been limited in their assessments of habitat preferences of benthic macrofauna by lack of taxonomic details of the taxa. Apart from the observed patterns, various often similar estimates of invertebrates have been recorded for offshore, near papyrus, in deep and in shallow water and, over various substrata. With regard to chaoborids, open water sites were significantly correlated with the group density (Tables 14 and 16) but the numbers recorded at the edge of *Phragmites* may be anomalous. The chaoborids appear to have both a substrate and depth-dependent relationship. In Lake Victoria, Macdonald (1956) recorded the highest densities (2,000 - 2,500 ind.m$^{-2}$) of both planktonic and mud-dwelling stages in deeper water particularly in 5 - 15 m while Okedi (1990) reported the highest density (38 ind.m$^{-2}$) in 8 m of water 500 m from the shoreline. Okedi (1990) recorded a mean density of 978 ind. m$^{-2}$ in 1.5 m of water near a papyrus shore. As the habitat was dominated by dead fibrous vegetable matter, he concluded that chironomids prefer a mud bottom. In contrast to this observation, no chironomids were found near *Eichhornia* edges and yet, in terms of bottom deposits and sediment characteristics (Tables 5,6,7,8), they are similar to papyrus habitats. Mbahinzireki (1994) did not consider bottom substrates nor statistical patterns but recorded 200 - 7,000 chironomid larvae ind.m$^{-2}$ between 5 and 30 m depths. These data sets are confusing. It appears that more specific taxa than previously used are involved in density and distribution patterns.

Substrate composition and larval migrations are major determinants in density distribution of Lake Victoria chironomids (Macdonald, 1956). This study has shown that in Lake Victoria, distance from the shore and vegetation are also important. For fish, a combination of the four factors may strongly influence habitat choice. The paucity of chironomids in *Eichhornia* and the relatively low densities in papyrus habitats may be related to wind and wave action (e.g Cooper and Knight, 1985) and, in *Eichhornia*, in addition to excessive sedimentation. Densities at stations 350 - 500 m away (Table 14) in 6 - 8 m of water (i.e where vegetation was not a factor) suggest that, provided sediment types are similar to those between 20 - 40 m from the shoreline, there will occur a similar pattern of abundance. Such areas (20 - 40 m and 350 - 500 m off) could in fact be the feeding grounds of fish. This is confirmed by Macdonald (1956) from examination of *Mormyrus* stomach contents and his description of the mud in bays: "it was very fine and flocculent and there was not a well-marked mud-sediment interface .... and was found to be composed of dead algae together with some living cells. In the main lake, it was much more firm and compact".

Some studies have shown the importance of sediment stability and vegetation development in supporting macrofauna (Cooper and Knight, 1985). However, habitat structural complexity (Crowder and Cooper, 1982), predation (Lodge *et al*. 1982) and greater colonisable area (Lodge, 1992; Brown and Lodge, 1993) have been reported to significantly contribute to distribution and abundance of benthic invertebrates. The present data therefore only partly illustrate the complexity and diversity of wetland habitats and of the benthic fauna in the study area.

Trichoptera showed a preference for sandy-clay substrates with the highest densities (800 - 1,350 ind.m$^{-2}$) between the edge and 20 m off *Typha*, *Phragmites* and *Vossia*. Fewer numbers (15; 6) were encountered in deeper (6 - 8 m) offshore sites (Table 21) in spite of similar sediment characteristics. It appears that eroding habitats with some detrital plant matter are essential features in habitat preference for this group and this could explain their paucity in both *Eichhornia* and papyrus habitats.

*Eichhornia* and papyrus habitats were the most preferred habitats especially for gastropods (Table 16) with the highest density (615 ind. m$^{-2}$) at the edge of the mats. In papyrus in June, there were 96 ind. m$^{-2}$ at the edge and 370 at 10 m off the edge. It is to be noted that the sampled *Eichhornia* mats were often up to 20 m wide, the edge limits corresponding to the edge- to 10 m zones in papyrus. In gastropods, abundance is significantly correlated with both macrophyte biomass (Tables 18 and 19) and other macrophytes characteristics. It is also likely that specific macrophyte characteristics such plant litter (Table 4) which were associated with both *Eichhornia* and papyrus favour gastropods. *Typha* and *Vossia* with considerable hydrological influences did not show similar gastropod development but the influence of *Eichhornia* would probably lead to their establishment in the habitats. Bivalves on the other hand were commonly distributed across habitats but were more abundant off *Vossia*, *Typha* and *Phragmites* and, their numbers increased with depth (Table 20). This may be a reflection of species diversity.

For higher trophic levels particularly fish, data on the benthic macrofauna of the investigated habitats have the following implications:
- Although chironomids may be a major food source for fish living close to papyrus edges, the group as a whole is well represented even at 400 m from the edge of vegetation. As sediment composition in this area (more or less coinciding with part of the area in previous studies) is uniform across all habitats, this could be the main chironomid habitat and an important feeding ground for insectivorous fish.
- In both papyrus and *Eichhornia*-dominated habitats, molluscs have an additional niche but their greatest abundance is at intermediate distances from the edge of the vegetation just as it is off *Phragmites* and *Vossia*.
- Habitats associated with sandy-clay substrates (*Vossia-Typha-Phragmites*) are richer in Trichoptera at intermediate distances from the vegetation fringe but as a group, the Trichoptera also shows a second similar pattern further away from the nearshore areas.

Overall, the results of this investigation have revealed patterns which distinguish the interface littoral habitats of Northern Lake Victoria apart from on one hand the interior of the swamps and, on the other the sub-littoral habitats of the lake. The investigation has also shown that there have been profound changes in the areal coverage of wetlands and woodland in the study area. These changes probably reflect the situation in the larger landscape of the lake. The changes are mostly due

to an increase in the population accompanied by changes in landuse as well as the previous rise in lake level brought about by exceptionally heavy rains in the period 1960/61. Some of the ecological changes in the lake are likely to be a result of influences from the watershed. Despite these changes, the study area has been shown to still contain intact wetland areas along the shores of the lake.

The wetland areas in the study area are associated with 5 plant communities: *C. papyrus, E. crassipes, V. cuspidata, T. domingensis* and *P. mauritianus* of which *C. papyrus* is the most dominant but *E. crassipes* has rapidly gained areal importance in some instances affecting the structure of the indigenous communities especially *Typha* and *Vossia*. As they occur at the interface in contact with the lake water, the plant communities' influence on water quality was estimated to extend to at least 80 m lakeward. In this zone, significant differences in depth profiles, bottom substrates, water quality and benthic macrofauna could be recognised among the different vegetation dominated habitats. Using these criteria, the habitats could be classified into 3 major habitat types: *Eichhornia-, C. papyrus-* and *Vossia-Typha-Phragmites*-dominated types. As it occurred most prominently off exposed papyrus coastlines and was in direct contact with a larger open water surface, *Eichhornia* may have created a different set of habitat type conditions from those in papyrus-dominated habitats.

All the studied habitats show significant seasonal and horizontal (spatial) differentiation especially with respect to nutrients and phytoplankton, and among vegetation types, some patterns were also significant. Initially, the patterns could be restricted to within the first 40 m from the edge of each vegetation type but a subsidiary pattern about 400 - 500 m off the vegetation fringes points to a zone where vegetation may not have much influence. Depending on the plant density and biomass at the shoreline, water carrying silt, nutrients and organic matter in the plant biomass will have varying impacts along horizontal gradients towards open water. In some habitats, this could easily be observed in a change in the colour of the water after exceptionally heavy showers and may have been reflected as well in higher conductivity. It seems that the pattern associated with such inflows is part of the "foul water" which drives fish out of the swamps referred to by Carter (1955). This differentiation is probably an important cue in determining the structure of fish populations, breeding and trophic characteristics. As the far off areas were uniform especially in sediment type, water quality and benthic macrofauna, they could be habitats of less fish diversity than the immediate interface.

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Appendix 1. Scores of individual species corresponding to cover abundance (R = Rare, Oc = Occasional, LF = Locally frequent, F = Frequent, LAb = Locally abundant, A = Abundant, LD = Locally Dominant and D = Dominant; for a determination of the procedure used to generate the scores, see Materials and Methods).

|  | R | OC | LF | F | LAb | A | LD | D |
|---|---|---|---|---|---|---|---|---|
| *Sesbania sesban/micrantha* | + | 1 | 2 | 3 | 4 | 5 | 5 | 5 |
| *Alchornea cordifolia* | + | 1 | 2 | 3 | 4 | 4 | 4 | 5 |
| *Cyperus papyrus* | + | 1 | 2 | 3 | 4 | 5 | 5 | 5 |
| *Phragmites mauritianus* | + | 1 | 2 | 3 | 4 | 4 | 4 | 5 |
| *Afromomum angustifolium* | + | 1 | 2 | 3 | 4 | 5 | 5 | 5 |
| *Loudetia phragmatoides* | + | 1 | 2 | 3 | 4 | 4 | 5 | 5 |
| *Hibiscus diversifolia* | + | + | + | 1 | 1 | 2 | 2 | 4 |
| *Hibiscus palmatus* | + | + | 1 | 2 | 2 | 3 | 3 | 4 |
| *Ipomoea/Vigna* | + | + | + | 1 | 1 | 2 | 2 | 3 |
| *Pluchea* sp. | + | + | + | 1 | 1 | 2 | 2 | 4 |
| *Vossia cuspidata* | + | + | 1 | 2 | 2 | 3 | 3 | 4 |
| *Typha domingensis* | + | 1 | 2 | 3 | 3 | 4 | 4 | 5 |
| *Polygonum* sp. | + | + | + | 1 | 1 | 2 | 2 | 3 |
| *Eichnochloa pyramidalis* | + | + | + | 1 | 1 | 2 | 2 | 3 |
| Ferns (*Dryopteris*) | + | + | 1 | 2 | 2 | 3 | 3 | 4 |
| *Cynodon dactylon* | + | + | 1 | 2 | 2 | 3 | 3 | 4 |
| *Pistia stratiotes* | + | + | + | + | 1 | 1 | 1 | 2 |
| *Nymphaea caerulea* | + | + | 1 | 2 | 2 | 2 | 3 | 3 |
| *Commelina benghalensis* | + | + | + | + | + | 1 | 1 | 2 |
| *Cyphostema* sp. | + | + | + | + | + | 1 | 1 | 2 |
| *Vallisneria spiralis* | + | + | + | + | + | + | + | 1 |
| *Eichhornia crassipes* | + | + | 1 | 2 | 2 | 3 | 3 | 4 |
| *Ceratophyllum* sp. | + | + | + | + | + | 1 | 1 | 2 |
| *Ficus valis* | + | 1 | 2 | 3 | 4 | 4 | 4 | 5 |
| *Cyperus articulatus* | + | + | + | 1 | 1 | 2 | 2 | 3 |
| *Cyperus latifolia* | + | + | + | 1 | 1 | 2 | 2 | 3 |
| *Cyperus rotundus* | + | + | + | 1 | 1 | 2 | 2 | 3 |
| *Fuirena pachyrrhiza* | + | + | + | 1 | 1 | 2 | 2 | 3 |

Appendix 2. Description of the sampling sites.

## A. EICHHORNIA SITES:
1. Kiryowa -(KE): between 00° 24.407'N: 033° 11.441E and 00° 24.459'N: 033° 11.459E, moderately exposed.
2. Masese - New-A (MEnewA): between 00° 26.413N: 033° 15.175E and 00° 26.398N:033° 15.143E, moderately sheltered.
3. Masese-New-B (MEnewB): between 00° 26.291N: 033° 15.065E and 00° 26.323N: 033 14.996E, exposed.
4. Kakira- (KE): between 00° 28.527N: 033° 17.052E: 00° 28.534N: 033° 17.017E, exposed.
5. Wanyange: 00° 27.687N: 033° 15.214E: 00° 27.657N: 033° 15.138E, exposed.

## B. PAPYRUS SITES:
1. Masese-Wanyange -(MWP):between 00° 26.547N: 033o 15.230E and 00° 26.493N: 033° 15.214E, sheltered.
2. Kirinya-Masese (KrMP):between 00° 25.474N: 033° 14.012E and 00° 25.426N 033° 14 030E, sheltered.
3. Kakira-New A (KPnewA):between 00° 27.431N: 033° 17.131E and 00° 27.490N:033° 17.204E, moderately sheltered.
4. Kakira-New B (KPnewB): between 00° 27.476N: 033° 17.163E and 00° 27.490N:033° 17.204E, moderately sheltered.
5. Wanyange Old (WP): 00° 27.704N: 033° 15.392E: 00° 27.690N: 033° 15.239E, moderately exposed.

## C. TYPHA SITES:
1. Kirinya-(KrT): between 00° 25.053N:033° 13.958E and 00° 25.159N:033° 13.939E, sheltered.
2. Rwabitooke-(RT): 00° 26.115N: 033° 15.422E: 00° 26.090N: 033° 15.444E, sheltered.

## D. PHRAGMITES SITES:
1. ULATI-(ULATI): between 00° 24.846N: 033° 13.113E and 00° 24.875N:033° 13.158E, sheltered.
2. Kisima - (KSP): between 00° 24.954N: 033° 16.174E and 00° 24.938N 033° 16.151E, strongly sheltered.

## E. VOSSIA SITES:
1. Kakira - (KV): between 00° 27.586N: 033° 17.586N: 00° 27.613N: 033° 17.270N, moderately sheltered.
2. Wanyange - (WV): between 00° 27.719N: 033° 15.472E: 00° 27.725N: 033° 15.388E, exposed.

## Appendix 3a. Physical and chemical characteristics (units are as in Materials and Methods) of the sampling sites. May 1995.

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | $NO_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus papyrus* | | | | | | | | | | |
| edge | 27.4 ± 0.5 | 111 ± 1 | 0.15 ± 0.02 | 8.0 ± 0.2 | 5.2 ± 0.6 | 0.93 ± 0.02 | 517 ± 23 | 5.6 ± 0.2 | 39.4 ± 0.9 | 6.7 ± 0.7 |
| 10-40 m off | 27.5 ± 0.1 | 112 ± 1 | 0.17 ± 0.01 | 8.1 ± 0.1 | 5.2 ± 0.2 | 0.92 ± 0.01 | 509 ± 21 | 6.2 ± 0.2 | 40.0 ± 0.6 | 7.3 ± 0.5 |
| open water | 27.4 ± 0.2 | 107 ± 0 | 0.14 ± 0.01 | 6.7 ± 1.7 | 6.1 ± 1.4 | 0.92 ± 0.01 | 463 ± 40 | 6.8 ± 0.7 | 52.1 ± 10.2 | 5.9 ± 0.6 |
| *Eichhornia crassipes* | | | | | | | | | | |
| 5 m from edge | 27.3 ± 0.2 | 107 ± 2 | 0.38 ± 0.09 | 7.6 ± 0.1 | 6.3 ± 0.4 | - | 505 ± 20 | 7.3 ± 0.7 | 66.0 ± 14.0 | 10.8 ± 4.4 |
| edge | 27.7 ± 0.1 | 104 ± 1 | 0.44 ± 0.11 | 7.7 ± 0.1 | 7.6 ± 0.4 | - | 441 ± 30 | 7.6 ± 1.1 | 36.5 ± 2.8 | 2.7 ± 0.4 |
| 10-40 m off | 27.7 ± 0.0 | 104 ± 1 | 0.15 ± 0.00 | 7.9 ± 0.1 | 7.9 ± 0.2 | 0.90 | 431 ± 19 | 6.9 ± 0.4 | 35.6 ± 2.4 | 2.3 ± 0.2 |
| open water | 27.7 ± 0.1 | 106 ± 2 | 0.52 ± 0.32 | 8.1 ± 0.3 | 8.5 ± 0.7 | 0.87 | 486 ± 47 | 5.4 ± 0.1 | 31.0 ± 6.3 | 2.1 ± 0.9 |

**Appendix 3b.** Physical and chemical characteristics (units are as in Materials and Methods) of the sampling sites. July 1995.

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO₃ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus papyrus* | | | | | | | | | | |
| edge | 24.9 ± 0.2 | 119 ±7 | 0.17 ± 0.00 | 7.5 ± 0.1 | 7.0 ± 0.2 | - | 48 ± 7 | 8.6 ±0.9 | 40.9 ± 4.8 | 0.8 ± 0.2 |
| 10-40 m off | 25.3 ± 0.1 | 119 ±4 | 0.17 ± 0.00 | 7.6 ± 0.1 | 7.5 ± 0.8 | - | 43 ± 3 | 8.3 ±0.5 | 36.9 ± 1.0 | 0.6 ± 0.2 |
| open water | 25.3 ± 0.3 | 104 | 0.18 ± 0.01 | 7.6 ± 0.4 | 7.6 ± 0.3 | - | 77 ± 25 | 7.9 ±1.2 | 35.1 ± 1.9 | 2.1 ± 1.8 |
| *Eichhornia crassipes* | | | | | | | | | | |
| 5 m from edge | 25.0 ± 0.1 | 119 ±7 | 0.19 ± 0.01 | 7.0 ± 0.1 | 5.8 ± 0.3 | - | 56 ± 6 | 10.8 ±0.8 | 89.1 ± 11.8 | 14.5 ± 2.3 |
| edge | 25.1 ± 0.1 | 119 ±7 | 0.19 ± 0.01 | 7.1 ± 0.1 | 6.5 ± 0.3 | - | 58 ± 4 | 6.5 ±0.7 | 40.7 ± 2.4 | 3.4 ± 0.1 |
| 10-40 m off | 25.2 ± 0.1 | 119 ±7 | 0.18 ± 0.01 | 7.4 ± 0.1 | 7.2 ± 0.2 | - | 51 ± 6 | 7.5 ±0.7 | 36.8 ± 1.2 | 1.2 ± 0.6 |
| open water | 25.2 ± 0.0 | 104 | 0.17 ± 0.01 | 7.5 | 7.3 ± 0.0 | - | 39 ± 5 | 7.4 ±0.7 | 41.4 ± 0.4 | 0.0 |
| *Vossia cuspidata* | | | | | | | | | | |
| edge | | . | | 7.9 | 6.5 | 0.90 | 179 | 8.1 | 59.3 | 1.3 |
| 10 m off | | 90 | | 8.2 | 6.8 | 0.85 | . | 3.3 | | 8.9 |
| 20 m off | | 90 | | 8.3 | 8.6 | 0.85 | 180 | 2.3 | 61.8 | 3.0 |
| 40 m off | | 90 | | 8.6 | 7.6 | 0.85 | 164 | 4.7 | 61.9 | 2.3 |
| open water | | 90 | | 8.9 | 9.5 | 0.90 | 89 | 4.5 | 69.9 | 4.0 |
| *Phragmites mauritianus* | | | | | | | | | | |
| edge | | - | | 7.2 | 8.8 | 0.90 | 78 | 11.1 | 75.4 | 31.6 |
| 10 m off | | - | | 7.3 | 9.4 | 0.85 | 67 | 8.1 | 68.2 | 18.8 |
| 20 m off | | - | | 6.0 | 9.2 | 0.85 | 47 | 8.3 | 70.1 | 24.0 |
| 40 m off | | 90 | | 7.5 | 8.7 | 0.88 | 40 | 7.4 | 70.6 | 19.7 |
| open water | | - | | 7.8 | 8.4 | 0.80 | 52 | 9.3 | 72.0 | 4.0 |
| *Typha domingensis* | | | | | | | | | | |
| edge | | 94 | | 7.6 | 7.1 | 0.90 | 160 | 1.6 | 88.9 | - |
| 10 m off | | 90 | | 7.6 | 7.3 | 0.93 | 170 | 0.9 | 72.6 | - |
| 20 m off | | 94 | | 7.6 | 7.6 | 0.95 | 98 | 0.5 | 59.8 | - |
| 40 m off | | 94 | | 7.5 | 7.6 | 0.93 | 98 | . | 57.2 | - |
| open water | | 92 | | 7.5 | 7.7 | 1.10 | 96 | 0.5 | 56.0 | - |

**Appendix 3c.** Physical and chemical characteristics (units are as in Materials and Methods) of the sampling sites. October 1995.

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO₃ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus papyrus* | | | | | | | | | | |
| edge | 27.1 ± 0.2 | 108 ± 1 | 0.10 ± 0.01 | 8.7 ± 0.1 | 7.5 ± 0.3 | 0.75 ± 0.01 | 266 ± 42 | 10.0 ± 1.2 | 51.2 ± 3.7 | 9.3 ± 0.8 |
| 10-40 m off | 27.1 ± 0.2 | 108 ± 1 | 0.07 ± 0.01 | 8.8 ± 0.1 | 8.2 ± 0.3 | 0.73 ± 0.01 | 234 ± 34 | 9.3 ± 0.8 | 43.0 ± 1.7 | 6.6 ± 0.3 |
| open water | 26.8 ± 0.2 | 108 ± 0 | 0.08 ± 0.01 | 8.9 ± 0.0 | 7.6 ± 0.2 | 0.77 | 228 ± 25 | 8.0 ± 0.7 | 45.5 ± 2.6 | 7.3 ± 0.4 |
| *Eichhornia crassipes* | | | | | | | | | | |
| 5 m from edge | 26.4 ± 0.3 | 107 ±1 | 0.14 ± 0.02 | 7.4 ± 0.1 | 4.4 ± 0.4 | 0.77 ± 0.00 | 283 ± 15 | 18.3 ± 2.3 | 85.8 ± 9.1 | 26.8 ± 2.4 |
| edge | 26.8 ± 0.2 | 107 ±1 | 0.13 ± 0.02 | 7.7 ± 0.1 | 5.4 ± 0.4 | 0.72 ± 0.00 | 158 ± 13 | 10.7 ± 1.8 | 52.9 ± 3.0 | 14.2 ± 2.5 |
| 10-40 m off | 26.8 ± 0.2 | 107 ±1 | 0.11 ± 0.02 | 8.2 ± 0.2 | 6.5 ± 0.3 | 0.73 ± 0.00 | 247 ± 11 | 8.5 ± 0.9 | 49.8 ± 1.9 | 8.9 ± 1.1 |
| open water | 27.5 ± 0.0 | 108 ±1 | 0.07 | 8.9 ± 0.1 | 8.2 ± 0.1 | - | 152 ± 4 | 8.1 ± 0.5 | 46.6 ± 2.0 | 10.2 ± 2.0 |
| *Vossia cuspidata* | | | | | | | | | | |
| edge | | 100 | | 8.3 ± 0.1 | 4.7 ± 0.4 | 0.86 ± 0.02 | 1160 ± 9 | 3.2 ± 0.6 | 54.1 ± 5.6 | 11.1 |
| 10 m off | | - | | 8.7 | 7.7 | | 343 | 5.9 | 120.2 | 4.4 |
| 20 m off | | - | | 9.2 | 6.8 | 0.87 | 314 | 2.9 | 102.1 | 3.3 |
| 40 m off | | - | | 9.0 | 7.1 | 0.86 | 310 | 2.0 | 105.1 | 1.6 |
| open water | | - | | 9.5 | 10.0 | 0.85 | 284 | 2.9 | 100.0 | 1.1 |
| *Phragmites mauritianus* | | | | | | | | | | |
| edge | | - | | 8.7 ± 0.2 | 5.4 ± 0.3 | 0.83 ± 0.02 | 736 ± 45 | 8.5 ± 1.4 | 63.0 ± 20.0 | 39.1 ± 7.3 |
| 10 m off | | - | | 8.0 | 5.6 | 0.89 | 508 | 3.8 | 107.9 | 7.8 |
| 20 m off | | - | | 8.5 | 6.6 | 0.85 | 492 | 2.5 | 98.1 | 4.6 |
| 40 m off | | - | | 8.0 | - | 0.85 | 461 | 4.2 | 121.0 | 6.2 |
| open water | | - | | 9.0 | 6.9 | 0.86 | 409 | 1.8 | 86.1 | 3.7 |
| *Typha domingensis* | | | | | | | | | | |
| edge | | - | | 8.5 ± 0.0 | 5.6 ± 0.1 | 0.65 | 966 ± 15 | - | 10.2 ± 0.1 | 69.8 ± 3.5 |
| 10 m off | | 95 | | 9.0 | 6.7 | 0.75 | 386 | 4.3 | 130.1 | 27.1 |
| 20 m off | | 99 | | 9.0 | 8.9 | 0.78 | 388 | 3.1 | 108.5 | 1.7 |
| 40 m off | | - | | 9.5 | - | 0.70 | 391 | 1.5 | 108.7 | 2.0 |
| open water | | 99 | | 9.5 | 8.2 | 0.66 | 355 | 0.8 | 158.7 | 1.0 |

**Appendix 3d.** Physical and chemical characteristics (units are as in Materials and Methods) of the sampling sites. February 1996.

| | Si | SRP | tot.-P | $NO_3$ |
|---|---|---|---|---|
| *Cyperus papyrus* | | | | |
| edge | 910 ± 23 | 5.8 ± 0.6 | 42.5 ± 5.7 | 12.7 ± 3.0 |
| 10-40 m off | 965 ± 19 | 4.0 ± 0.4 | 12.8 ± 1.8 | 5.5 ± 1.4 |
| open water | 999 ± 41 | 2.4 ± 0.4 | 41.4 ± 10.8 | 6.8 ± 1.2 |
| *Eichhornia crassipes* | | | | |
| 5 m from edge | 1034 ± 32 | 10.8 ± 0.8 | 26.5 ± 1.7 | 60.5 ± 4.9 |
| edge | 940 ± 31 | 6.5 ± 0.6 | 24.8 ± 1.7 | 50.8 ± 4.2 |
| 10-40 m off | 972 ± 37 | 5.8 ± 1.3 | 18.4 ± 2.1 | 32.9 ± 3.5 |
| open water | 890 | 1.5 | 14.9 | 3.0 |

Appendix 4.  Biomass (g DW.m$^{-2}$) of the six most common macrofauna taxa and their distribution patterns in the vegetation types studied (n.s = not sampled).

*Eichhornia crassipes* (n = 3)

| | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| Bivalvia | 7.8 | 0.6 | 5.0 | 19.2 | 10.7 | |
| Chironomidae | | | | | | |
| Gastropoda | 12.1 | 1.0 | 5.0 | 6.4 | 6.4 | 6.4 |
| Odonanta | 0.4 | | | 0.4 | | |
| Oligochaeta | | | 0.2 | 0.1 | | |
| Trichoptera | | | | 0.9 | 0.3 | 0.9 |

*Cyperus papyrus* (n = 3)

| | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| Bivalvia | | 5.7 | 9.9 | 0.7 | 1.4 | 2.7 |
| Chironomidae | | | 0.1 | | | |
| Gastropoda | | 5.0 | 19.2 | 12.1 | 14.9 | 6.4 |
| Odonanta | | | 0.4 | | | |
| Oligochaeta | | | | | | |
| Trichoptera | | 0.3 | | | | 0.2 |

*Typha domingensis* (n = 2)

| | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| Bivalvia | | 2.1 | 21.3 | 0.2 | 14.9 | n.s. |
| Chironomidae | | 0.2 | | | | n.s. |
| Gastropoda | | 2.1 | | | | n.s. |
| Odonanta | | | | | | n.s. |
| Oligochaeta | | | | 0.1 | 0.3 | n.s. |
| Trichoptera | | 0.9 | 0.9 | 0.3 | 1.2 | n.s. |

*Phragmites mauritianus* (n = 2)

| | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|
| Bivalvia | | 22.4 | 6.4 | 16.0 | 13.9 | 2.1 |
| Chironomidae | | 0.1 | 1.4 | 0.1 | 0.1 | |
| Gastropoda | | 6.4 | | 6.4 | 23.5 | 5.3 |
| Odonanta | | | | | | |
| Oligochaeta | | | 0.7 | 0.1 | 0.1 | 0.5 |
| Trichoptera | | 2.1 | 11.6 | 2.6 | 2.1 | 0.4 |

Appendix 4 (continued)

| *Vossia cuspidata* (n = 1) | | | | | |
|---|---|---|---|---|---|
| | - 5 m | edge | 10 m | 20 m | 40 m | open |
| Bivalvia | | | 32.5 | 53.3 | | n.s. |
| Chironomidae | | 1.8 | | 0.3 | 0.1 | n.s. |
| Gastropoda | | 4.3 | 8.5 | 4.3 | 2.1 | n.s. |
| Odonanta | | | | | 1.2 | n.s. |
| Oligochaeta | | | | | 0.2 | n.s. |
| Trichoptera | | 4.3 | 4.3 | 28.4 | 0.9 | n.s. |

OPEN WATER

| | 400 m offshore (n = 21) | 500 m offshore (n = 15) |
|---|---|---|
| Bivalvia | 5.4 | 4.1 |
| Chironomidae | 0.2 | 0.1 |
| Gastropoda | 16.9 | 11.4 |
| Odonanta | 0.2 | 0.4 |
| Oligochaeta | 0.1 | 0.1 |
| Trichoptera | 0.2 | 0.1 |

# Chapter 4

# Species composition and biomass of fish in the shallow (wetland) habitats of northern Lake Victoria, East Africa[*]

## ABSTRACT

*In situ* fish sampling techniques were used to determine species composition, relative abundance and biomass in shallow ( < 2.5m depth) habitats of the wetland-interface zone in Lake Victoria between 1994 and 1996. The dominant fringing plant species: *Cyperus papyrus*, *Vossia cuspidata*, *Typha domingensis*, *Phragmites mauritianus* and, a new wetland type, *Eichhornia crassipes* comprised the habitat types. Fish species composition and biomass in the habitats within 50 m to about 80 m from the shore appeared to be influenced by the type of dominant plant community at the lake's edge.

About 30 species of fish were identified from these habitats in contrast to 10 in the open deeper (4-8 m) water habitats which were more than 300 m away from the lake's edge. The haplochromine group contained many species which could not be identified but the insectivores were the most abundant trophic group in the taxon. Community structure in the investigated habitats was dominated by three stocked species (the Nile perch - *Lates niloticus*, the Nile tilapia - *Oreochromis niloticus* and *Tilapia zillii*) and three endemic species (*Brycinus jacksonii*, *Astatoreochromis alluaudi* and *Protopterus aethiopicus*), and the haplochromines. The 3 stocked species contributed at least 90% of the estimated numerical and biomass densities but their respective relative importance varied with habitat type and distance from the edge of the vegetation. The 5 vegetation-dominated habitats showed significantly different biomass patterns with respect to seasons.

## INTRODUCTION

In East Africa, Lake Victoria because of its fisheries, contributes much to the nutrition and welfare of the riparian human population in the lake's densely populated catchment (Fig. 1). Through explosive speciation (Greenwood, 1965), the lake previously contained at least 300 haplochromine cichlid species (van Oijen *et al.*, 1981) and up to 50 non-cichlid fish species (Lowe-McConnell, 1975), the majority of them cyprinids (Balirwa, 1984). Despite the high diversity, haplochromines were only locally important to fisheries (Kudhongania and Cordone, 1974).

Previously, the commercial fishery depended on a few endemic taxa such as *Oreochromis esculentus*, *O. variabilis* and *Labeo victorianus*. These were overfished and to boost the fisheries, several species were introduced into the lake in the 1950s (Lowe-McConnell, 1987; Welcomme, 1988). Among these were the Nile tilapia (*O. niloticus*), *T. zillii* and a large predator, the Nile perch (*L. niloticus*). These introductions have been associated with a decline in species diversity (e.g. Hughes, 1983; Barel *et al.*, 1985; Ogutu-Ohwayo, 1990; Witte *et al.*, 1992), but an increase in fish production (Fig. 2) with an estimated 1995 production of 182,513 tonnes and an overall export market of US$ 33 million (UFD Ann. Rep. 1994) from the Uganda part of the lake. These data mainly refer to commercial landings and may not reflect part of the catch which is directly utilised by the communities living close to the wetlands. In fact, little is known about the extent to which the shallow littoral areas contribute to the fishery potential.
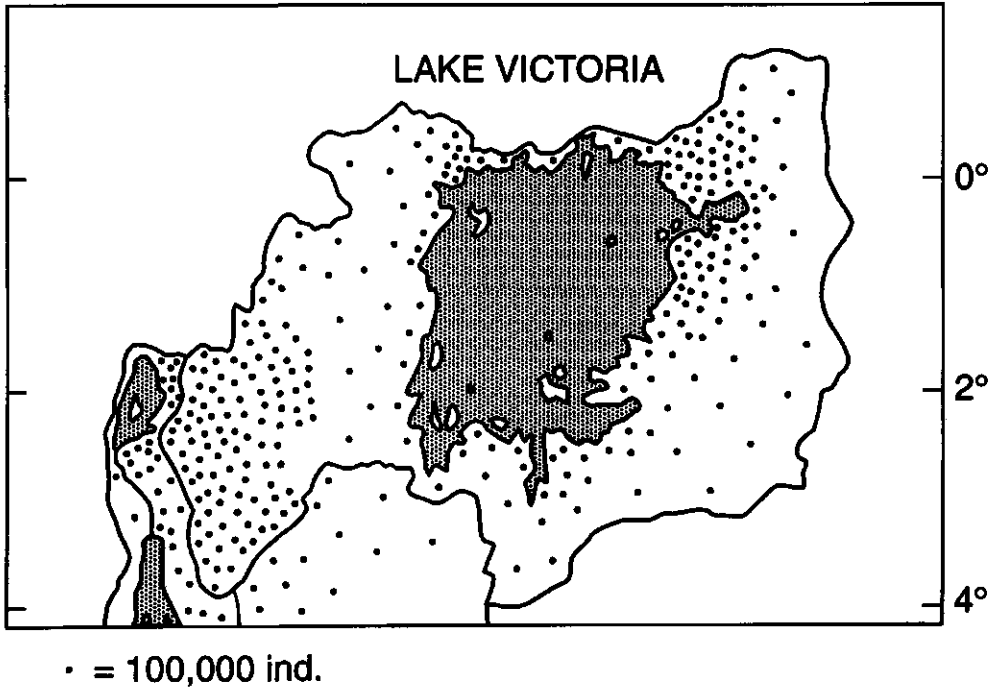
· = 100,000 ind.

Fig. 1.   Map of Lake Victoria showing population density in its catchment; 1 dot = 100,000 inhabitants (after Bootsma and Hecky, 1993).
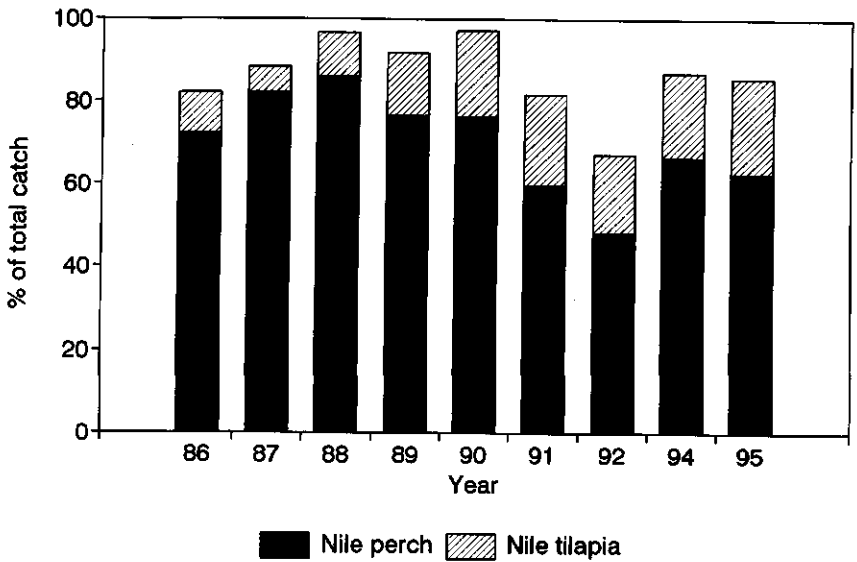


Fig. 2.   The contribution to commercial fish production by the Nile perch and Nile tilapia from Lake Victoria between 1986 - 1995.

In intensive studies conducted by The Haplochromis Survey Team (HEST), (e.g. Witte, 1981; van Oijen, 1982; Goudswaard, 1988; Witte *et al.*, 1992, 1995), the sub-littoral zone of Mwanza Gulf in the south of the lake was the main focus. Observations on distribution patterns among the haplochromine prey, and their subsequent rate and sequence of disappearance were attributed to their relative abundance, adult size and their habitat overlap as prey for the Nile perch. Additional causes of ecological impacts on the fish community have recently been suggested (Coulter *et al.*, 1986; Bugenyi and Balirwa, 1989), but have been less investigated. These include eutrophication (Hecky, 1993), habitat loss and wetland buffer degradation (Lowe-McConnell, 1993; 1994a, b; Balirwa, 1995). They have been manifested in algal blooms and changes in phytoplankton structure (Ochumba and Kibaara, 1989; Mugidde, 1992). The overall change in the ecology of the lake is depicted in Fig. 3.
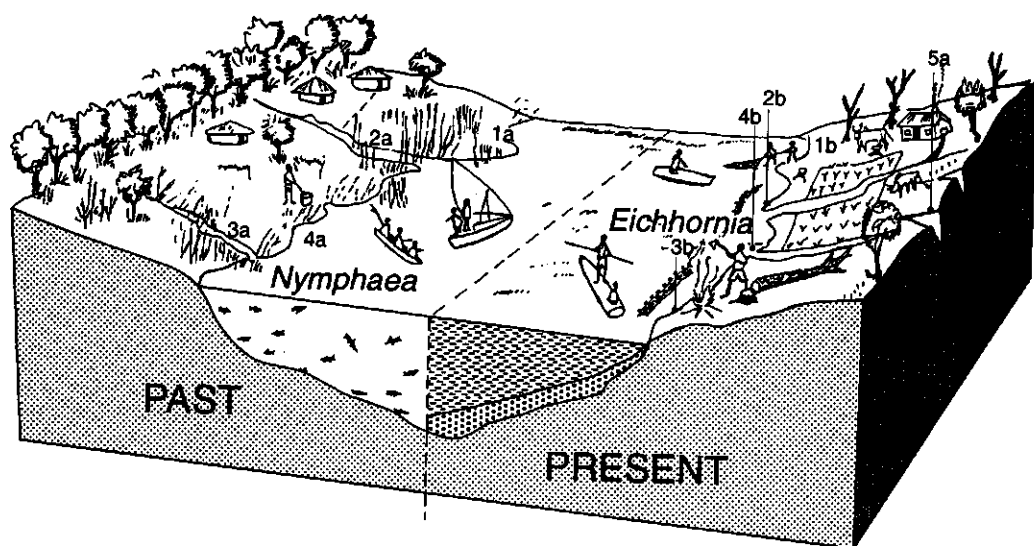


Fig. 3.     A schematic representation of a historic (up to 1950s) and present (after 1970s) state.

State A: historic. 1a. Shoreline previously covered by complex riparian vegetation, e.g. papyrus, *Vossia* (collectively known as swamp). 2a. Riverine - stream habitats utilised by potamodromous species; *Barbus*, *Labeo*, *Clarias*, *Schilbe* etc. and also sites of seasonal fisheries and grazing pastures. 3a. Smaller stream/swamp areas rich in rare species; *Ctenopoma*, *Protopteris*, *Mormyrids* etc. and used as subsistence fisheries. 4a. No influence of exotic species; *Nymphaea*, *Pistia*, *Ceratophyllum* and *Potamogeton* - dominant euhydrophytes. Nile perch and Nile tilapia of no significance to the fisheries. 5a. Natural allochthonous inputs particularly of the complex food webs. 6a. Low population density; interannual climatic seasonality more predictable.
State B: present. 1b. Fragmentation and deterioration of wetland buffers particularly near urban centres; influence of sewage. 2b. Drainage for agriculture due to climatic variability and population pressure; increase in silt loads. 3b. Same as in 2b; devegetation biomass by burning etc. 4b. Influence of exotic species (Nile perch, Nile tilapia, waterhyacinth). 5b. Anthropogenic inputs, e.g. sewage, silt, pollutants probably exceed background levels in some areas. 6b. Increase in human population and climatic variability.

A major shortcoming of most studies on Lake Victoria fisheries has been the lack of an ecosystem approach involving the wetland (littoral) zone which is assumed to be an important fishery area. Fish (1957) and Talling (1957, 1966, 1987) studied the influence of seasonality on deeper (in comparison to the wetland habitats) waters of the lake; the cycle of stratification and phytoplankton succession were emphasized in these studies. Welcomme (1966, 1969) investigated the biological and ecological effects of climatic changes on some fishes of the shallow marginal areas (lagoons, streams and rivers) but the principal variable was the abnormal rise in lake level following heavy rains of the 1960s. Kudhongania and Cordone (1974) established distribution patterns and biomass characteristics of major demersal fishes between the 5m depth zone and the deeper offshore zones; their study showed that depth had a major influence on both distribution and biomass with higher catch rates of the tilapias occurring in the shallow areas. However, the large spatial frame and absence of seasonal classification in the studies impose limitations on inferences about the ecological importance for fish of the littoral zone. We have to conclude that the immediate interface littoral zone which may experience some of the more subtle impacts of ecological change (Chapter 3), is not equally understood.

Studies of ecological communities in general (e.g Hall and Werner, 1977) consider that resource partitioning among fish in the littoral zone of freshwater lakes is related to food and habitats utilised. Pet (1995) suggested that resource partitioning among species and size classes within species in fish communities provides insight into spatial and temporal patterns of the fish and fishermen. Chick and McIvor (1994) explained patterns of abundance and fish composition on the basis of different submersed macrophyte beds in Lake Okeechobee but such beds are rare in Lake Victoria. In this lake, Balirwa (1990) showed that the time fishermen land their catch and its composition could be correlated with fishing grounds (Table 1) but it was not clear whether the pattern was correlated with vegetation habitats.

Table 1. Commercial catch data (4 - 24 Jan. 1990) and landing times for the main species (weight in kg from al boats) recorded at an isolated landing in Lake Victoria (data from Balirwa, 1990).

| Landing period: | 07.00 - 11.00h inshore | 11.00 - 14.00h offshore |
|---|---|---|
| *Oreochromis niloticus* | 4335 | - |
| *Lates niloticus* | 1900 | 11,127 |
| *Protopterus aethiopicus* | 20 | - |
| *Clarias gariepinus* | 8 | - |

Like in many tropical lakes, the littoral zone of Lake Victoria is possibly the most frequented part of the fishery. As the zone has a wetland dominated shoreline of mostly emergent species (Chapter 3), there is need for information regarding the structure and biomass of the fish communities there, especially in relation to the commercially important *O. niloticus*. At the smaller village scale, other species may also be important because it is the quantity and weight of fish caught which is most relevant for home consumption and recognition of the importance of the wetland zone. Hence, though some species may not be recorded in catch statistics (Balirwa, 1995), it is clear from the intensity and type of fishing techniques employed (gill nets, cast nets, angling, beach seines, traps, ensnaring in enclosures or actively driving fish into nets) (Balirwa, 1990) that the littoral zone supports substantial fishery resources and, could be an area of high fish diversity. Seehausen (1994, 1966a, 1996b) has shown that in Lake Victoria a high ecological and genetic diversity of fish is preserved in rocky littoral habitats, despite predation and fishing pressures. The wetland littoral zone may therefore also contain remnants of fish species which are assumed to have disappeared from the lake.

This study investigated species composition, the fish communities and biomass in interface habitats fringed by emergent swamp buffers. The rocky shores and sandy beaches are part of the littoral zone but are not considered in this study. The rocky shores are particularly difficult to sample with standard gear and are for the great part of the day exposed to strong wind and wave action; the sandy shores are mostly used as bases of human activity - boat landings, seining beaches, fish processing, etc and do not provide close to natural conditions.

An assessment of the relative importance for fish of interface habitats abutting *Cyperus papyrus* L. (also referred to in this paper as *Cyperus* or papyrus), *Vossia cuspidata* (Roxb.), *Eichhornia crassipes* (Mart.) Solms-Laub, *Typha domingensis* Pers. and *Phragmites mauritianus* Kunth communities, was made over a period of about 16 months between February 1994 and June 1996. All the habitats were simultaneously sampled for other ecological aspects such as seasonal and horizontal patterns in physico-chemical conditions, phytoplankton and macrofauna (Chapter 3) and the area sampled in this study closely fits on the pattern found in that paper.

As null hypotheses for the present study we stated that:

a) As the sampled habitats are all in shallow water, there should be no differences in fish species composition between the habitats and open water; hence it is also expected that fish abundance and biomass will only vary randomly rather than seasonally or with habitat type, and

b) There were be no significant differences in the response variables: fish numbers and biomass between and within habitats at zone 1 and zone 2 (see under Materials and Methods) and among the vegetation dominated habitats. Zone 1 represented habitats at the immediate interface i.e. from the edge of each

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vegetation type up to about 20 m off; zone 2 was the area from about 20 m off to about 70 m away from the edge of the vegetation.

To evaluate the hypothesis empirically, species composition, fish density (number of fish per hectare), biomass (kg. fresh weight per hectare) of each habitat type were compared in replicate shoreline habitats dominated by the five wetland plant species according to the above assumptions. Comparisons were also made for within and between fish species differences in relation to (a) and (b) above.

## MATERIALS AND METHODS

### The study habitats

Because of its immense size (c. 69,500km$^2$; maximum depth 80m, mean depth 40 m) and a diverse 3440 km shoreline (Beadle, 1981; Welcomme, 1966; Crul, 1995), Lake Victoria supports many ecological habitats which may contain different fish populations. Some of the habitats are characterised by the type of dominant plant community at the shore. The habitats investigated in this study are all in the northern part of Lake Victoria in Napoleon Gulf.

The shoreline in the study area is fringed by various plant species. The major fringing vegetation types were *C. papyrus, V. cuspidata, E. crassipes, T. domingensis* and *P. mauritianus* (here after referred to by the genera names) and these were used as test habitat identifiers. *Eichhornia* and papyrus-dominated habitats were the most common types, occupied deeper zones (2.7 - 3.3 m), and were characterised by a higher organic content of the sediments than the other three. *Typha, Vossia* and *Phragmites* zones were shallower (1.0 - 1.6 m), more gently sloping and generally more sandy (Chapter 3). The width of the zone was earlier determined by repeated soundings for Secchi transparency and total depth at 2 - 4 m distance intervals from the edge of the vegetation.

The littoral zone extended for about 50-80 m from the shore. At the limit of this zone the lake was between two and four metres deep and had a higher silt content in the sediments. Beyond this limit, the lake was deeper (4 - 8 m). A sampling unit comprised the littoral zone parallel to the shoreline off each dominant vegetation type, henceforth called "habitat". Within each of the habitats, two simultaneously sampled sub-units have been recognised: the first 20 m from the shore, and an area beyond 20 m to about 70 m away from the shoreline. The main physico-chemical and other features of the investigated habitats have been given in Chapter 3.

### Seasonality

The seasonal patterns were based on the rainfall-temperature regime. Fig. 4 shows the most important climatic elements (rainfall and temperature) during the study period. On examination of the data as well as the main hydrographic and limnological conditions for Lake Victoria (Fish, 1952, 1957; Akiyama *et al.*, 1977, Talling, 1957, 1966), the annual cycle was divided into four seasons according to 1994 rainfall-temperature and other, long-term, climatic data (Table 2). The long dry season (December - March 15), the main rainy season (March 16 - June), the

short dry but cool season (July - September 15), and the short rainy season (September 16 -November) were the main categories.

**Sampling sites and frequency**
16 sites were fished (Table 3) and were the same as had earlier been characterised for physico-chemical variables, phytoplankton, macrophytes and macrofauna (Chapter 3).
Each sampling unit was fished in the years 1994 till 1996 as to include the identified seasonal patterns (Table 4).

Table 2.    Characteristics of seasonality in the study area.

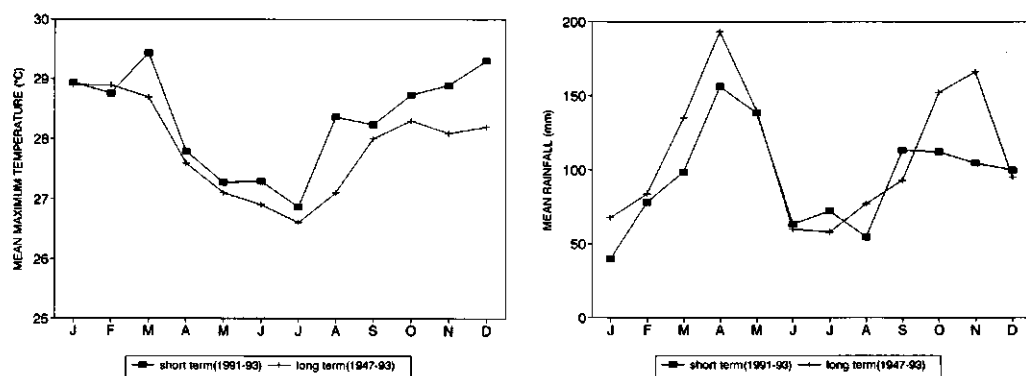| | Dec. - Mar 15 | Mar 16 -June | July -Sept 15 | Sept 16 -Nov |
|---|---|---|---|---|
| Mid-season: | Feb. | May | July | October |
| water level (m) | -0.015 | 0.162 | -0.064 | 0.066 |
| no. of days with rain | 6 | 16 | 6 | 13 |
| rain in mid month (mm) | 65.8 | 166.8 | 75.8 | 112.4 |
| mean minimum temp.($^\circ$C) | 17.7 | 16.8 | 15.7 | 16.6 |
| average maximum temp.($^\circ$C) | 30.4 | 26.6 | 26.1 | 27.3 |
| sunshine duration (h) | 7.2 | 6.1 | 5.5 | 7.6 |



Fig. 4.    Major climatic patterns in the study area during 1990/94. Left: monthly mean maximum temperature; right: monthly mean rainfall.

Table 3.     Distribution of sampling sites according to the dominant vegetation and sampling frequency in each habitat type.

|                   | Eichhornia | Cyperus | Typha | Vossia | Phragmites |
|-------------------|-----------|---------|-------|--------|------------|
| no of sites       | 6         | 5       | 2     | 1      | 2          |
| fishing frequency | 22        | 32      | 9     | 12     | 15         |

Table 4.     Number of fishing experiments per habitat type in each of the major seasons .

|              | Eichhornia | Cyperus | Typha | Vossia | Phragmites |
|--------------|-----------|---------|-------|--------|------------|
| Main dry     | 1         | 8       | 4     | 3      | 4          |
| Main rain    | 12        | 17      | 9     | 4      | 6          |
| Short dry    | 5         | 5       | 4     | 3      | 3          |
| Short rain   | 4         | 2       | 2     | 2      | 2          |
| no. of times | 22        | 32      | 19    | 12     | 15         |

main dry season = December - 15 Mar; main rain season = 16 Mar - June; short dry, but cool season = July - 15 September; short rain season = 16 September - November

Replication varied depending on weather and the number of sites to be covered in one particular season as well as the increasing influence and dynamic character of water hyacinth.

**Fish sampling**
Samples from several fishing techniques were used to determine species composition. The main method used in quantitative assessments is described below.

Main sampling methodology:
Data on fish composition and abundance were collected using a fleet of multi-ply, multi-mesh stretched gillnets (Fig. 5) with a 0.5 hanging ratio. Two nets of each mesh size were used. Panel length for each net was 45 m and 1.5 m in height. The nets could therefore fill the water column from bottom to surface in most cases. A fleet of nets was made up of 18 separate pieces. These were set in parallel as a block to occupy most of the sampling unit i.e equivalent to the width of the littoral zone. The nets were arranged in alternating mesh sizes, with the first 5"

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mesh net proximal to the vegetation (also called front position) followed by 1" (rear), 4.5" (front), 1.5" (rear) and so on till the last and 18th net of 5" (Fig. 5). An approximate distance of 1.0 - 2.5 m between adjacent net pairs was allowed depending on weather conditions. The type of setting was code-named "Block Fishing Experiments - Type I". To complement aspects of species composition, a subsidiary pattern (1"-1") also called **Block Fishing Type II** was used. As it had the smallest mesh size proximal to the vegetation, small fishes which could have been missed in the main set-up would be liable to capture by the "1-1" arrangement.

The inshore distance fished was determined by tying one end of a rope to shoreline vegetation and moving with the rest of the rope in a boat perpendicular to the whole set till the last net. The area of the sampling unit was taken as the product of the inshore distance fished and the standard length (45 m) of a net. As this area could vary with sampling conditions, the inshore distance had to be measured every time that nets were set. The entire fleet of nets was set between 17.30-18.00 hours and retrieved at 06.00 hours i.e left overnight. To provide a comparable indication of the biomass characteristics of other open water habitats, an offshore site about 500 m from the edge of papyrus in 6-8 m of water was identified and was fished over three nights in June 1996.
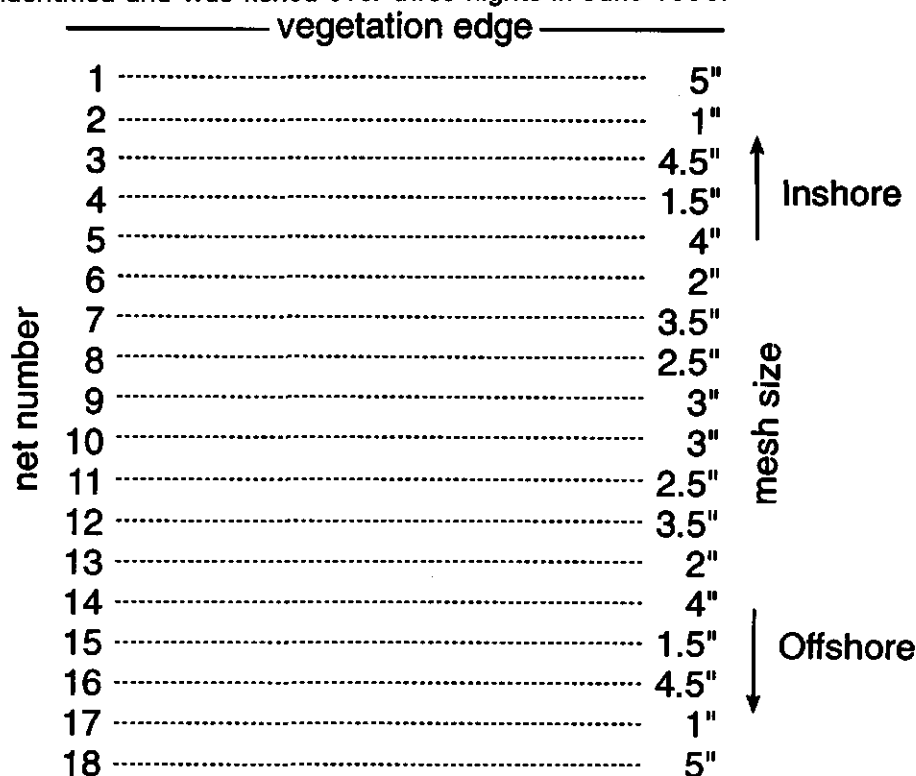


Fig. 5. Experimental set-up by Block Fishing Type I.

Commercial landing statistics have not been used, because these do not provide a true indication of species composition nor of biomass since the fishing is highly geared to market demands. As it allowed various assessments, the method used in these studies was considered the most useful for sampling the width of the littoral zone in association with the possible vegetation influences. Furthermore, the serial lay-out of mesh sizes was geared at capturing as many sizes of fish at each distance.

In order to obtain further insight into the importance of vegetation, sampling units of habitats have been categorised into sub-units (zone 1 or zone 2) on the basis of distance from the shore line. In Block fishing Type 1, one of the duplicate set of nets was fished in "zone 1", that is proximal to the vegetation, and extending from the lake edge to about 20 m offshore. The second set (from the 10th net of 3" mesh to the 18th 5" mesh) was fished in "zone 2", that is from 20 m to the edge of the littoral platform which could extend to 50, 70 or 80 m further offshore (Fig. 5). Given a fishing width of 45 m the area fished varied (mean 2840 ± 1870 S.D $m^2$, COV 60%). Accordingly all catch data have been calculated in terms of one hectare (10,000 $m^2$).

For ease of reference, data from observations of the entire sampling units are referred to as "overall" and those from the sub-units as "zone 1" or "zone 2" respectively.

Additional specimens were collected by high opening bottom trawl with MV Mputa (125HP). The dimensions of the trawl net were 276 meshes of 114 mm stretched with a head rope of 22 m. The length of the net was 22 m including a codend of 25 mm mesh. Trawling was usually conducted at a depth of about 2-4 m and at an approximate distance from the shore of 300-500 m. Occasionally, trawl paths cut across deeper areas.

To evaluate biomass as a function of habitat, pooled data from the five habitats were initially analyzed . The data generated by the innovative fishing technique subsequently allowed analysis of trends with respect to habitat type, seasonal patterns and within habitat fish composition by distance from the edge off each dominant vegetation at the shore. The dominant vegetation defined the habitat type as in Chapter 3.

### Identification of the species
The tilapias and all non-cichlid species were identified to species according to Greenwood (1966). Definitive  haplochromine taxonomy is extremely difficult because many species have not been scientifically described and also due to name changes and redesignation for some species. Owing to such difficulties, haplochromine fish were categorised into trophic groups (insectivores, piscivores, zooplanktivores, molluscivores and others) on the basis of morphological features (van Oijen et al. 1981; Witte and van Oijen, 1990). Following identification, fishes were weighed, measured and sexed.

**Data Analyses**

Species composition was determined for each habitat type as the number of different species recovered. Frequency of occurrence of a particular species was recorded as a percentage of the number of times the species turned up in the samples from the respective vegetation dominated habitats.

In general arithmetic means and standard errors were calculated; the effects of habitat on numbers and biomass, and comparisons among vegetation dominated habitats and within seasons were tested by ANOVA ($p < 0.05$) and unless stated, the level was maintained in all comparisons.

Raising factors were used to calculate fish density on a per hectare basis. Initially, a per hectare overall fish density (mean number and biomass kg.fresh weight) was calculated as a function of the shallow water region as a whole and without reference to specific vegetation types or possible seasonal influences. Subsequently, areas abutting to each of the dominant vegetation communities were used as distinct habitats. In calculation of the number of individuals and of the biomass per hectare for zone 1 and zone 2, the area was based on half that used in calculating the overall biomass. Seasonal patterns were based on the same classification of distinct periods used in the structural characterisation of the habitats (Chapter 3).

To test the main hypothesis, the following comparisons were made:

- Number of individuals and biomass with respect to differences between and within habitats.

- Number and biomass according to seasonal patterns for each habitat.

- Interaction effects between habitats and seasonal patterns on numbers and biomass.

Habitat (vegetation type), season and zone (zone 1 or zone 2) were used as factor levels in a stepwise comparison for their significance in relation to numbers, immature fishes and biomass.

## RESULTS

**Species composition and overall frequency in the habitats**

At least 23 fish taxa were encountered in the shallow wetland zone, about half of them belonging to non-cichlid genera. Cichlid genera were dominated by haplochromines but the previously rare endemic tilapiines (*O. esculentus* and *O. variabilis*) were also encountered. Cyprinids, particularly the smaller *Barbus* spp., were not encountered. The percent frequency of occurrence of individual species and of haplochromine trophic groups in the investigated habitats is presented in Tables 5 to 7.

Table 5.    Species percentage occurrence in shoreline interface habitats of Lake Victoria (Block-fishing: 5"-5").

|  | Eichhornia | Vossia | Typha | Cyperus | Phragmites |
|---|---|---|---|---|---|
| No. of fishings | 30 | 13 | 23 | 40 | 18 |
| 1. *L. niloticus* | 86 | 100 | 96 | 100 | 100 |
| 2. *O. niloticus* | 86 | 100 | 96 | 100 | 100 |
| 3. *O. leucostictus* | 17 | 62 | 39 | 18 | 44 |
| 4. *O. esculentus* | - | - | - | - | 6 |
| 5. *O. variabilis* | 7 | - | 9 | - | 22 |
| 6. *T. zillii* | 31 | 100 | 96 | 55 | 100 |
| 7. *Astatoreochromis* | 31 | - | 4 | 20 | 11 |
| 8. *Alestes (Brycinus)* | 83 | 77 | 91 | 88 | 94 |
| 9. *Protopterus* | 28 | 8 | 4 | 38 | 22 |
| 10. *Gnathonemus* | - | - | - | 3 | - |
| 11. *Mormyrus* | - | - | 26 | 3 | 28 |
| 11. *Clarias gar.* | - | - | - | - | - |
| 12. *C. alluaudi* | - | - | - | - | - |
| 13. *C. carsonii* | 3 | - | 4 | 5 | 33 |
| 14. *Bagrus docmac* | - | - | - | 3 | - |
| 15. *Afromastacemb.* | 3 | - | 9 | - | - |
| 16. *Synodontis* | 3 | - | 9 | - | 6 |
| 17. *Barbus* | - | - | - | - | 11 |
| 18. *Haplo. ins.* | 48 | 92 | 61 | 48 | 67 |
| 19. *Haplo. zoo.* | - | - | 4 | - | - |
| 20. *Haplo. pisc.* | 28 | 92 | 70 | 45 | 67 |
| 21. *Haplo. moll.* | - | - | - | - | 6 |
| 22. *Haplo. barab.* | - | - | 4 | - | - |
| 23. *Haplo. moll.* | - | - | - | - | - |
| 24. *H. lividus* | - | - | - | - | - |
| 25. *H. nubila* | - | 8 | 4 | 13 | - |
| 26. *other haplos* | - | - | 4 | 3 | - |
| 27. *Mercusenius* | - | - | - | -3 | 3 |
| No. of taxa | 13 | 10 | 18 | 15 | 17 |

*Claria gar.* = *C. gariepinus*, *Afromastacemb.* = *Afromastacembelus*, *Hap.* = *Haplochromis*, ins., zoo., pisc., moll., = insectivorous, zooplanktivorous, piscivorous, molluscivorous, respectively trophic groups; *Haplo barab.* = *H. barbarae*.

The highest number of taxa including several species (e.g *O. esculentus*, *Marcusenius grahami*, *Barbus altianalis* and *H. barbarae*) which did not occur in samples from the other habitats was from *Typha* and *Phragmites*-dominated habitats. *Eichhornia* and *Vossia*-dominated habitats had fewer taxa.

Table 6.  Species percentage occurrence in shoreline interface habitats of Lake Victoria (Block-fishing: 1"-1").

| | Eichhornia | Cyperus | | Eichhornia | Cyperus |
|---|---|---|---|---|---|
| No. of fishings | 4 | 5 | | | |
| 1. *L. niloticus* | 100 | 100 | 15. *Bagrus dogmac* | - | - |
| 2. *O. niloticus* | 100 | 100 | 16. *Afromastac.* | 20 | - |
| 3. *O. leucostictus* | - | - | 17. *Synodontis* | - | - |
| 4. *O. esculentus* | - | - | 18. *Barbus* | - | - |
| 5. *O. variabilis* | - | - | 19. *Haplo. ins.* | 80 | 75 |
| 6. *T. zillii* | 60 | 50 | 20. *Haplo. zoo.* | - | - |
| 7. *Astatoreochromis* | - | - | 21. *Haplo. pisc.* | 60 | 25 |
| 8. *Alestes (Brycinus)* | 100 | 100 | 22. *Haplo. moll.* | - | - |
| 9. *Protopterus* | 60 | 25 | 23. *Haplo. barab.* | - | - |
| 10. *Gnathonemus* | - | - | 24. *Haplo. moll.* | - | - |
| 11. *Mormyrus* | - | - | 25. *H. lividus* | - | - |
| 12. *Clarias gar.* | - | - | 26. *H. nubila* | - | - |
| 13. *C. alluadii* | - | - | 27. *other haplos* | 20 | - |
| 14. *C. carsonii* | 3 | - | 28. *Mercusenius* | - | - |
| | | | No. of taxa | 13 | 10 |

Of the introduced species, *Lates niloticus* and *Oreochromis niloticus* were associated with each other in all habitats (Table 5), and the 2 species occurred in most samples. In terms of species diversity, *Typha* and *Phragmites*-dominated habitats were the richest and, together with *Vossia*, the three habitats tended to have similar frequencies of occurrence for the species in the habitats. The endemic *O. variabilis* and *O. esculentus* were more associated with *Phragmites* sites than with any of the other habitats. Open water sites (Table 7) had the lowest diversity but the highest *T. zillii* frequency.

Among the haplochromines, insectivores and piscivores were present in all habitats but were most frequently encountered in *Vossia*, *Typha* and *Phragmites* dominated habitats. Of the other indigenous species, *Alestes (Brycinus) jacksonii*, *Astatoreochromis alluaudi*, *Protopterus aethiopicus*, *Aplochelichthys pumilus* and the small clariids were more frequent in samples from habitats abutting *Typha*, *Phragmites* and *C. papyrus* than in open water or *Eichhornia* dominated habitats.

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Table 7.     Species percentage occurrence by trawling in habitats about 300 m
             from the shoreline of Lake Victoria. Number of fishings is 22.

|  | perc. (%) |  | perc. (%) |
|---|---|---|---|
| 1. *L. niloticus* | 100 | 15. *Bagrus dogmac* | 18 |
| 2. *O. niloticus* | 96 | 16. *Afromastacemb.* | - |
| 3. *O. leucostictus* | 5 | 17. *Synodontis* | 41 |
| 4. *O. esculentus* | - | 18. *Barbus* | - |
| 5. *O. variabilis* | - | 19. *Haplo. ins.* | 27 |
| 6. *T. zillii* | 100 | 20. *Haplo. zoo.* | 5 |
| 7. *Astatoreochromis* | - | 21. *Haplo. pisc.* | 32 |
| 8. *Alestes (Brycinus)* | - | 22. *Haplo. moll.* | - |
| 9. *Protopterus* | - | 23. *Haplo. barab.* | - |
| 10. *Gnathonemus* | - | 24. *Haplo. moll.* | - |
| 11. *Mormyrus* | - | 25. *H. lividus* | - |
| 12. *Clarias gar.* | - | 26. *H. nubila* | - |
| 13. *C. alluadii* | - | 27. *other haplos* | 5 |
| 14. *C. carsonii* | - | 28. *Mercusenius* | - |
|  |  | No. of taxa | 10 |

**Analysis of block fishing technique and overall community abundance**
From 100 fishing nights, about 7000 specimens weighing 4700 kg were recovered
from the sampling units associated with vegetation. The mean catch per night in
frontal nets combined was $4.8 \pm 0.4$ kg. The catch from the rear set nets was
$6.1 \pm 0.8$ kg. There was no significant effect ($p > 0.05$) of the technique on the
quantity of fish caught in frontal or rear set nets. At the time of sampling, fish
could randomly be caught in either set of nets.

The mean number of specimens from the near shore sampling units was $130 \pm 13$.
This was equivalent to a mean weight of $46.7 \pm 4.0$ kg.ha$^{-1}$. There were no
significant differences in numbers or in biomass within sites of each vegetation
dominated habitat ($p > 0.05$). Taken as "overall" the data showed a range in
number (5-733) and in biomass (3-310 Kg) indicating a high level of variability both
between and within habitats.

The three offshore samples produced 0.8 kg in both front and rear nets. This was
significantly lower than the quantity from habitats within 70 m from the vegetation
edges. However, the offshore nets only covered a fraction of the water column and
therefore did not sample the entire space. Compared to the vegetation dominated
habitats, the offshore mean area (2250m$^{-2}$) produced a lower biomass equivalent
to $6.2 \pm 0.1$ kg.ha$^{-1}$.

## Overall patterns

The patterns shown by each habitat initially considered the shallow water region within about 70 m from the edge of each vegetation type.

## Relative abundance (numbers)

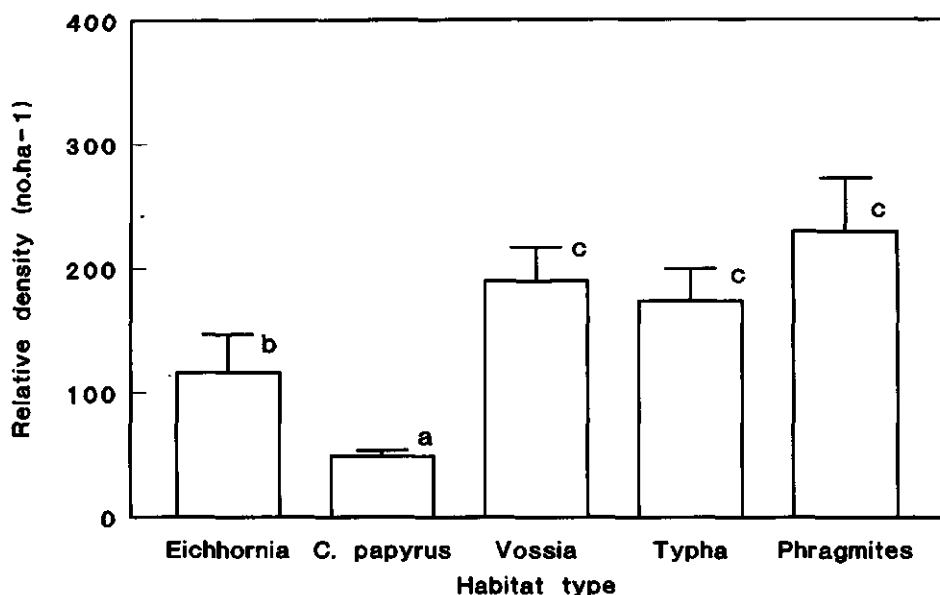Fig. 6 shows the relative abundance (mean number) of fish per hectare of each habitat.



Fig. 6.        Relative abundance (mean no.ha$^{-1}$ ± SE) in the various habitats. Data are pooled over distance from the edge of the vegetation up to about 70 m away from the vegetation. Means that are not significantly different share a common letter.

The following major patterns irrespective of distance from the edge of the vegetation or season of sampling are revealed from the data.

The *Phragmites* habitat had the highest number of fish but did not significantly differ ($p > 0.05$) from *Vossia* and *Typha*. The pattern shown by the three habitats (*Vossia, Typha and Phragmites*) was significantly different from that shown by papyrus and *Eichhornia*-dominated habitats.

Although the investigated habitats showed no significant differences in numbers between male and female fish, the differences in the number of immature fish among the habitat types (Fig. 7) were significant ($p < 0.05$).

The number of immature fishes in *Vossia* and *Phragmites* habitats was significantly higher than the number found in the other habitats.

**Individual species relative abundance**
Eight species were regularly encountered. The individual contribution to the mean numbers and percentage of their occurrence in each habitat is given in Table 8.
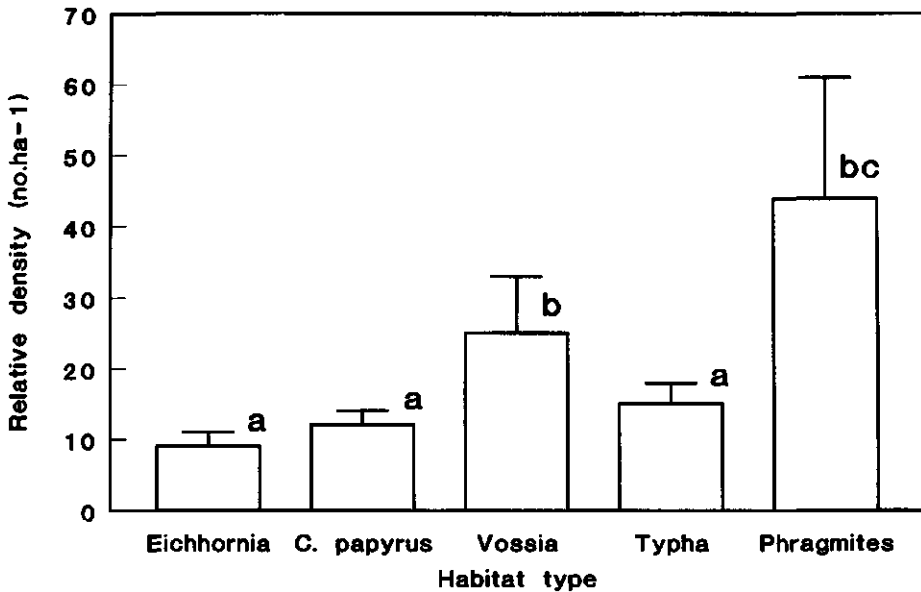


Fig. 7.  Immature fish distribution patterns according to habitat type (mean no. ha$^{-1}$ ± SE). Data are pooled over distance from the edge of the vegetation up to about 70 m away from the vegetation. Means that are not significantly different share a common letter.

Among the endemic species *Brycinus* were most abundant in *Eichhornia*-dominated habitats while haplochromine cichlids were more associated with *Vossia* and *Phragmites*. Three stocked species (*O. niloticus*, *L. niloticus* and *T. zillii*) were present in all habitats but most abundant in *Vossia*, *Phragmites* and *Typha* dominated habitats. Considered as percentages, the data in the table further indicate the frequency by which particular species could be caught. For example, though the mean total number of fishes from papyrus was low, *L. niloticus* was the most frequently caught species there. *O. niloticus* was caught in an increasing sequence from *Eichhornia* - papyrus - *Vossia* - *Typha* - *Phragmites*. The stocked species together could be caught 34 - 70% of the time from any of the habitats. The major species are analyzed further below.

Table 8.   The contribution to numerical abundance (mean no.ha⁻¹) and percentage occurrence of the more common species from the investigated habitats.

| | Eichhornia | | Cyperus | | Vossia | | Typha | | Phragmites | |
|---|---|---|---|---|---|---|---|---|---|---|
| | no. | % | no. | % | no. | % | no. | % | no. | % |
| Endemic spp. | | | | | | | | | | |
| *Brycinus* | 30 | 26 | 11 | 2 | 7 | 4 | 14 | 8 | 16 | 7 |
| *Astatoreochromis* | 8 | 7 | < 1 | < 1 | 2 | 1 | < 1 | < 1 | 1 | < 1 |
| *Haplochromis* | 7 | 6 | 8 | 16 | 78 | 41 | 38 | 22 | 44 | 19 |
| *Protopterus* | 1 | 1 | 1 | 2 | 1 | < 1 | < 1 | < 1 | < 1 | < 1 |
| Stocked spp. | | | | | | | | | | |
| *Lates niloticus* | 19 | 16 | 19 | 39 | 31 | 16 | 18 | 10 | 23 | 10 |
| *O. niloticus* | 18 | 16 | 9 | 18 | 38 | 20 | 59 | 34 | 82 | 35 |
| *T. zillii* | 2 | 2 | 2 | 4 | 17 | 9 | 40 | 23 | 63 | 27 |
| *O. leucostictus* | 2 | 2 | < 1 | < 1 | 1 | < 1 | 2 | 1 | 2 | 1 |
| Total no. | 87 | | 52 | | 175 | | 172 | | 232 | |
| No. of fishings | 22 | 32 | 12 | 19 | 15 | | | | | |

*Astatororeochromis = A. alluaudi, Brycinus = B. jacksonii, Haplochromis = includes all species and trophic groups as identified, Protopterus = P. aethiopicus*

**Biomass**
A comparison of the mean biomass from the five investigated habitats (Fig. 8) shows that papyrus had the lowest bomass in comparison to the other three habitats (*Eichhornia, Vossia, Typha* and *Phragmites*). *Eichhornia* showed the highest variability (%COV = 81, range = 4-210) in biomass characteristics which had also been observed in numbers (Fig. 6).

**Seasonal patterns in abundance**
Fish biomass varied (Fig. 9) according to the major seasonal patterns which were depicted in Fig. 4 and Table 2.

In all habitats generally, there was an increase in fish biomass from the main rainy period (March 16 - June, represented by May) to the short dry cool season (July - September 15, represented by July). In *Eichhornia* and *Vossia*, the increase appeared to be sustained through the short rainy season (represented by October) whereas in *Typha*, it decreased after the short dry cool season. Some of the seasonal patterns appeared to be dependent on sex or size (adult or immature fish). These are summarised for each habitat as follows.

*Eichhornia*-dominated habitats
The number of males remained about the same through the seasons but the densities of female and immature fishes were highest in the short dry cool season

(July - September 15). This was followed during the short rainy season (September 16 - November) by lower numbers of all categories though the biomass stayed high.

*C. papyrus*-dominated habitats:

The highest density of male fish occurred during the main dry season (December - March 15) while immature fishes reached peak abundance during the the short wet (September 16 - November) season. In general, both biomass and numbers were low during the the main rain season (March 16 - June period).

*Vossia*-dominated habitats:

The pattern of male fish during the study period showed a consistent increase from the main rain (March 15-June) season up to the end of November with the highest densities for all categories of fish occurring during this short rain (September16-November) season.

*Typha*-dominated habitats:

There appeared to be a general increase of all categories of fish from the main dry season especially from December till the short dry cool (July-September 15) season. The latter season had the largest density of each of the different categories of fish but this pattern was followed by a decrease in fish density during the short rain season (September 16 - November).

*Phragmites*-dominated habitats:

Male and female fish showed a similar pattern of abundance; the highest density for both occurred during the short dry cool season (July-September) and the short rain (September-November) season. Immature fishes were most abundant during the main rain season (March 15 - June) when both total biomass and adult fish numbers were low.
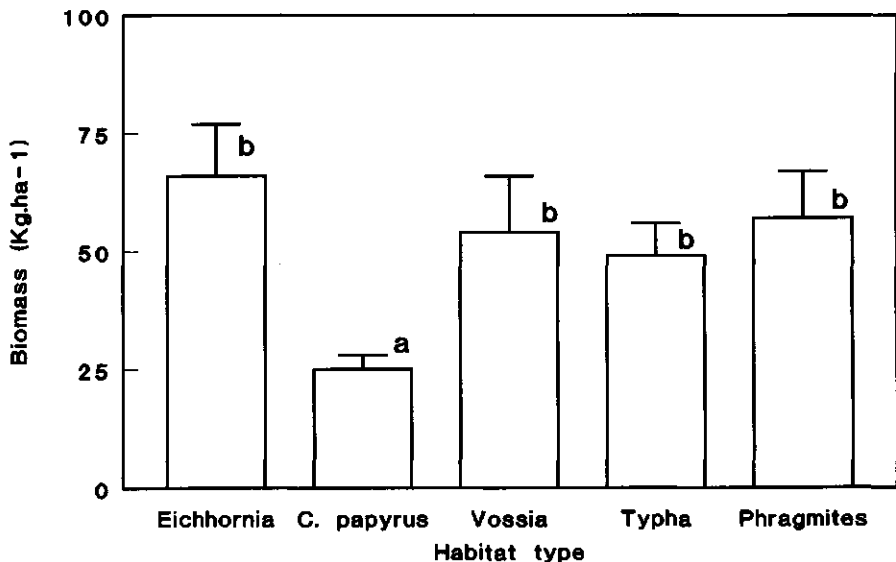


Fig. 8.    The fish biomass (kg.ha$^{-1}$ ± SE) in the littoral zone off the different investigated habitats. Data are treated as in Fig. 7.

**Zone 1 and zone 2**

Zone 1 and zone 2 were used to distinguish between possible spatial patterns associated with distance from the edge of vegetation within the investigated habitat types. To illustrate the significant abundance patterns with respect to distance from the edge of the vegetation, the mean individual taxa numbers (Table 9) and biomass in the investigated habitats are shown in Fig. 10 and 11. Compared to the open water biomass (6.2 ± 0.1 kg.ha-1), all zone 1 and zone 2 habitats had a higher biomass. Among habitats, *Typha*, *Phragmites* and *Eichhornia* showed significantly higher numbers in zone 1 than in zone 2 whereas *Vossia* did not.
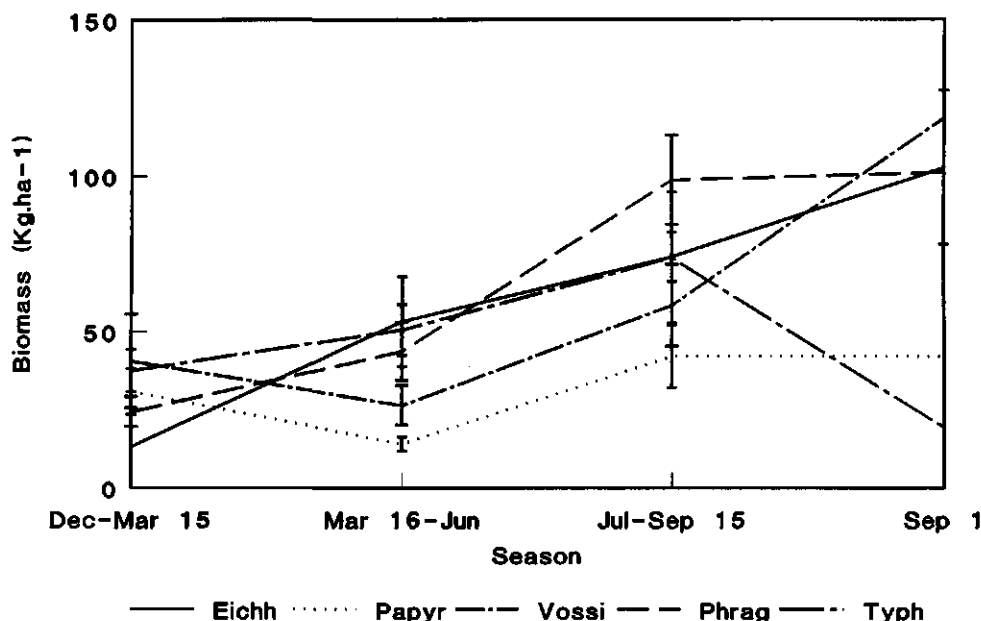


Fig. 9.     Changes in the pattern of biomass in each habitat according to season.

There was a higher but variable biomass (30-68 kg.ha$^{-1}$) in zone 1 (i.e. nearest to the vegetation at the edge) irrespective of vegetation type (Fig. 11). *Phragmites* dominated habitats had the highest zone 1 biomass (68 kg.ha$^{-1}$) and *C. papyrus* had the least (30 kg.ha$^{-1}$). *Vossia* had the largest biomass in zone 2 (53 kg.ha$^{-1}$) and papyrus had the least (14 kg.ha$^{-1}$). In Table 10, the relative importance of the biomass for individual species is given.

Table 9.   The numerical abundance of individual taxa from the investigated habitats.

| zone | Eichhornia 1 | 2 | C.papyrus 1 | 2 | Vossia 1 | 2 | Typha 1 | 2 | Phragmites 1 | 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| **Endemic spp.** | | | | | | | | | | |
| Brycinus | 18 ± 3 | 13 ± 3 | 4 ± 1 | 29 | 5 ± 2 | 2 ± 1 | 12 ± 6 | 1 ± 0 | 6 ± 3 | 11 ± 3 |
| Astator. | 7 ± 3 | <1 | <1 | <1 | 1 ± 0 | <1 | <1 | 0 | 1 ± 0 | <1 |
| Haploch. | 28 ± 8 | 8 ± 3 | 6 ± 0 | 1 ± 0 | 60 ± 5 | 27 ± 4 | 25 ± 3 | 13 ± 2 | 33 ± 3 | 12 ± 1 |
| Protopt. | 1 ± 1 | <1 | <1 | <1 | <1 | 1 ± 0 | <1 | 0 | <1 | 0 |
| O. vari. | <1 | 0 | <1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| O. escu. | <1 | <1 | <1 | <1 | 0 | 0 | <1 | 0 | <1 | 0 |
| Mormyri. | <1 | <1 | <1 | <1 | 0 | 0 | <1 | 0 | 0 | <1 |
| Clarias | 0 | 0 | 0 | <1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Afromas. | <1 | <1 | | | | | | | | |
| **Stocked spp.** | | | | | | | | | | |
| Lates | 35 ± 23 | 6 ± 2 | 9 ± 1 | 10 ± 2 | 18 ± 9 | 13 ± 4 | 8 ± 2 | 10 ± 2 | 7 ± 1 | 13 ± 4 |
| O. nilot. | 10 ± 3 | 6 ± 3 | 6 ± 2 | 2 ± 1 | 26 ± 9 | 30 ± 9 | 43 ± 16 | 17 ± 5 | 53 ± 19 | 34 ± 18 |
| O. leuco. | 2 ± 1 | <1 | <1 | 0 | 1 ± 0 | <1 | 2 ± 0 | <1 | 2 ± 1 | <1 |
| T. zillii | 2 ± 1 | <1 | 1 ± 0 | <1 | 10 ± 2 | 12 ± 3 | 32 ± 8 | 10 ± 3 | 49 ± 13 | 13 ± 4 |

Astator. = Astatoreochromis, Haploch. = Haplochromis, Protopt. = Protopterus, O. vari. = O. variabilis, O. escu. = O. esculentus, Mormyri. = Mormyrids, Afromas. = Afromastacembelus, O. nilot. = O. niloticus, O. leuco. = O. leucostictus
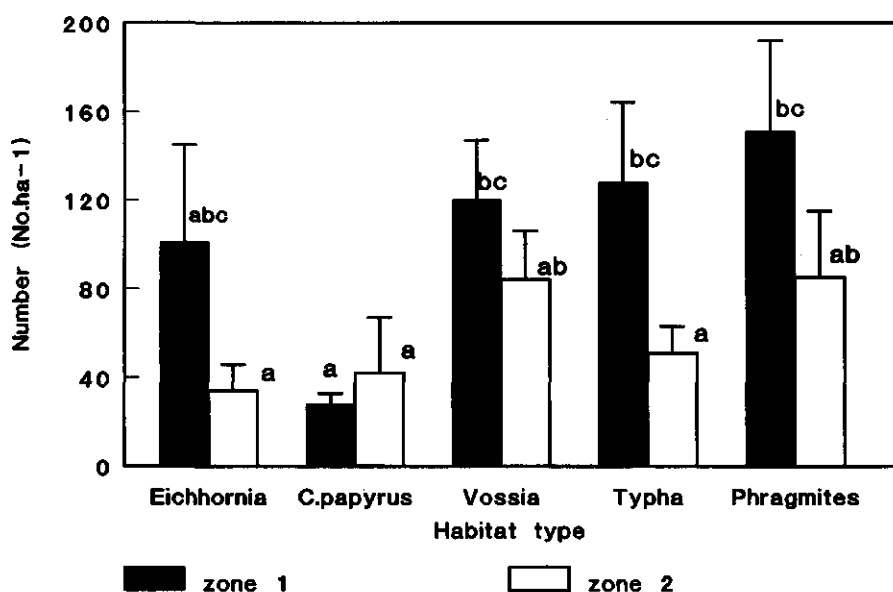


Fig. 10.   A comparison of the mean number (no.ha$^{-1}$ ± SE) of fish from the investigated habitats with respect to distance from the edge of each dominant vegetation. Zone 1 is the area nearest to the vegetation up to 20 m, zone 2 is further offshore, from 20 to about 70 m. Means that are not significantly different share a common letter (modified LSD test maintaining experimental error rate at 0.05).
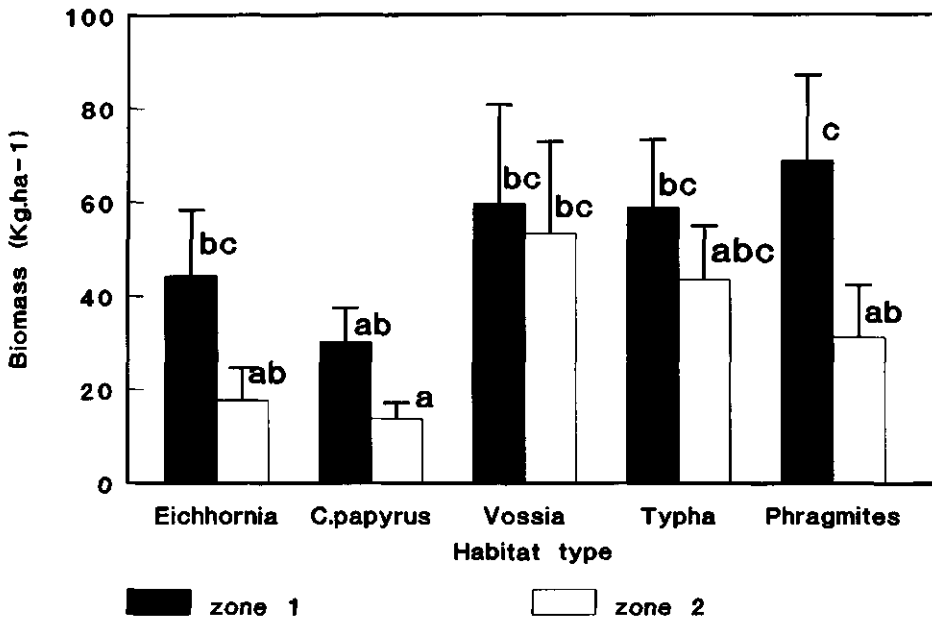
Fig. 11.    A comparison of the mean fish biomass (kg.ha$^{-1}$ $\pm$SE) from the investigated habitats with respect to distance from the edge of each dominant vegetation  Data are treated as in Fig. 10.

Six species contributed at least 70% of the biomass irrespective of zone. The species were *Brycinus jacksonii*, *Haplochromis* (as a group), *Astatoreochromis*, *O. niloticus*, *L. niloticus* and *T. zillii*. Their relative importance to community biomass varied among and within the habitats (Fig. 12).

**Eichhornia habitats**
*O. niloticus* contributed 50% to the biomass in zone 1 followed by *L. niloticus* (15%), and *Protopterus* (10%). Haplochromines, *Brycinus* and *Astatoreochromis* between them registered 20% of the biomass in zone 1. *O. niloticus* was again the most dominant component (44%) of the biomass in zone 2 but the indigenous species (*Brycinus*, *Astatoreochromis*, *Protopterus* and the haplochromines) accounted for 51% of the biomass.

**C.papyrus habitats**
There was a higher biomass of *O. niloticus* (66%) in zone 1 of papyrus than that in *Eichhornia* dominated habitats but *L. niloticus* biomass was more or less similar (14%) to that in papyrus zone 1. *L. niloticus* however contributed a higher proportion to zone 2 biomass (40%) in papyrus than in *Eichhornia*, but with *O. niloticus* (42%) still the biggest contributor. *Brycinus* and the other endemic species consequently had much less influence in the biomass picture of zone 2 as well.

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Table 10.   The biomass (kg.ha$^{-1}$ ± SE) of individual taxa from the investigated habitats.

| zone | Eichhornia 1 | 2 | Cyperus 1 | 2 | Vossia 1 | 2 | Typha 1 | 2 | Phragmites 1 | 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| **Endemic spp.** | | | | | | | | | | |
| Brycinus | 2.5 ± 0.6 | 2.7 ± 0.7 | 0.5 ± 0.1 | 1.2 ± 0.2 | 0.7 ± 0.3 | 0.4 ± 0.1 | 1.6 ± 1.1 | 0.4 ± 0.1 | 0.6 ± 0.2 | 0.2 ± 0. |
| Astator | 1.5 ± 0.6 | 0.1 ± 0.1 | 0.1 ± 0.0 | 0.0 | 0.2 ± 0.1 | 0.2 ± 0.1 | 0.0 | 0.0 | 0.3 ± 0.2 | 0.3 ± 0. |
| Haploch. | 4.1 ± 0.2 | 1.0 ± 0.1 | 1.2 ± 0.0 | 0.4 ± 0.0 | 12.7 ± 1.2 | 8.0 ± 1.2 | 6.2 ± 0.9 | 5.9 ± 0.3 | 6.9 ± 0.7 | 16.7 ± 3. |
| Protopt. | 4.5 ± 1.9 | 2.6 ± 1.7 | 2.4 ± 1.0 | 0.4 ± 0.2 | 0.4 ± 0.3 | 4.8 ± 3.1 | 0.5 ± 0.4 | 0.0 | 0.8 ± 0.3 | 2.1 ± 0. |
| O. vari. | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 ± 0.1 | 0.0 | 0.2 ± 0.0 | 2.4 ± 2. |
| O. escu. | 0.1 ± 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Mormyri. | 0.0 | 0.3 ± 0.2 | 0.1 ± 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 ± 0. |
| Clarias | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 ± 0.1 | 0. |
| Afromas. | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0. |
| Barbus | 0.0 | 0.0 | 0.0 | 0.1 ± 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 ± 0. |
| **Stocked spp.** | | | | | | | | | | |
| Lates | 6.8 ± 2.1 | 2.6 ± 1.0 | 4.3 ± 0.6 | 5.6 ± 1.1 | 8.1 ± 0.1 | 4.8 ± 1.9 | 3.3 ± 0.72 | 2.8 ± 0.6 | 3.2 ± 0.7 | 0.6 ± 0. |
| O. nilot. | 22.7 ± 11.2 | 7.7 ± 0.9 | 20.0 ± 1.6 | 5.8 ± 0.5 | 29.4 ± 3.6 | 27.7 ± 3.6 | 32.9 ± 2.7 | 27.8 ± 2.7 | 32.4 ± 3.2 | 4.0 ± 1. |
| O. leuco. | 0.9 ± 0.7 | 0.2 ± 0.1 | 0.1 ± 0.1 | 0.0 | 0.5 ± 0.3 | 0.2 ± 0.1 | 1.5 ± 0.5 | 0.3 ± 0.2 | 2.2 ± 0.5 | 1.8 ± 1. |
| T. zillii | 1.2 ± 0.6 | 0.3 ± 0.2 | 1.5 ± 0.5 | 0.1 ± 0.1 | 7.8 ± 1.8 | 7.3 ± 2.2 | 12.9 ± 2.5 | 6.5 ± 2.0 | 22.0 ± 5.6 | 0.3 ± 0. |

Astator. = Astatoreochromis, Haploch. = Haplochromis, Protopt. = Protopterus, O. vari. = O. variabilis, O. escu. = O. esculentus, Mormyri. =
Mormyrids, Afromas. = Afromastacembelus, O. nilot. = O. niloticus, O. leuco. = O. leucostictus
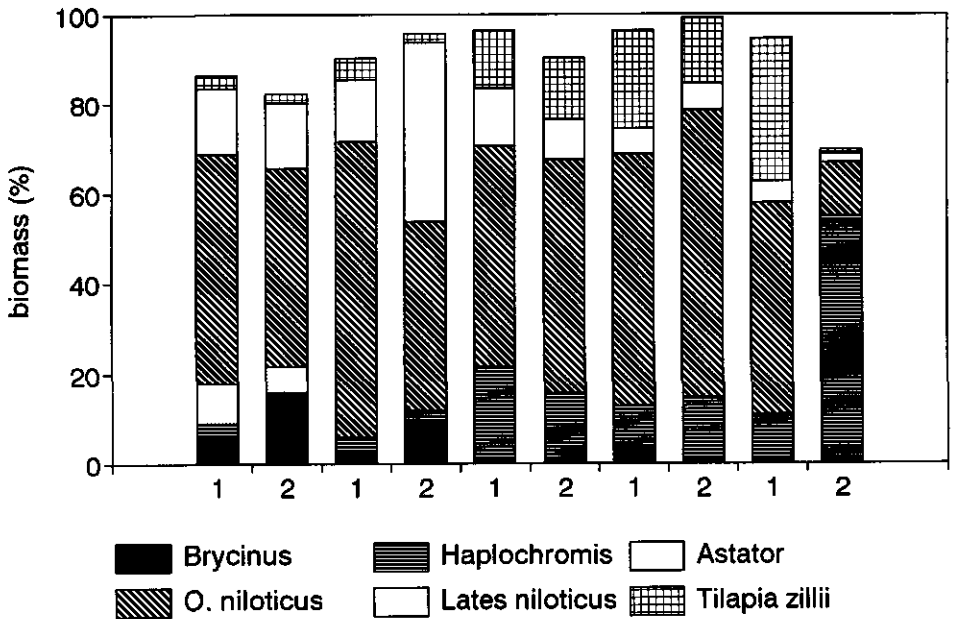


Fig. 12.   Percentage biomass of the more common species from the five vegetatio(n) dominated habitat types according to distance from the vegetation (zone 1 an(d) zone 2, see Fig. 10 and Materials and Methods).

**Phragmites-Vossia-Typha habitats.**
Areas immediately in contact with the vegetation in the investigated habitats i.e. zone 1 were dominated by *O. niloticus* where it contributed about 45 - 65% of total biomass. Zone 1 of the three habitats also showed the highest abundance of *T. zillii* and haplochromines. In zone 2, *Phragmites* was particularly different in that fish biomass was dominated by haplochromines.

**Influence of stocked species to zone 1 and zone 2 biomass**
From Fig. 12 the relative importance of the 3 stocked species (*O. niloticus, L. niloticus, T. zillii*) to the total biomass in the investigated habitats can be discerned.

The highest biomass of stocked species was from zone 1 of *Phragmites* and all areas in *Typha* and *C. papyrus*. A significant proportion of the biomass (15-30%) in *Vossia, Typha* and *Phragmites* was due to *T. zillii*. 80% of the biomass in zone 1 of papyrus was due to *O. niloticus* while *L. niloticus* had a maximum 40% contribution to the biomass in zone 2 of papyrus and only 2% off *Phragmites*.

**Multiple comparisons for significant factors and among species' patterns**
In stepwise multiple comparisons using ANOVA, the significance of various factor levels (habitat/vegetation type, zone, season) on the response variable (total numbers, biomass, number of immature fishes) was tested. When a factor level was significant, it was considered to influence the indicated variable (total number, number of immature fish, biomass or a particular species).

Table 11 presents the outcome from analysis of the significance of habitat, zone and season on fish numbers and biomass. The amount explained (percentage) of the sum of squares is given for the significant factors.

Table 11.    Significance of various factors to the number (mean total number) and biomass (kg fresh weight.ha$^{-1}$) of all the fishes in the investigated area (p = probability, SS = sum of squares).

| | Habitat p | % SS | Zone p | % SS | Season p | % SS |
|---|---|---|---|---|---|---|
| Total no. | 0.000$^*$ | 49 | 0.001$^*$ | 23 | 0.207$^{ns}$ | - |
| Biomass | 0.015$^*$ | 17 | 0.000$^*$ | 35 | 0.000$^*$ | 40 |

$^*$ = significant, $^{ns}$ = not significant.

The data show that habitat and therefore vegetation type at the edge was a significant factor for the two response variables (total number and biomass). Habitat could explain 49% of the number of fish and, at another factor level, 40% of the model could explain the significance of season for biomass.

In the next step, interaction between habitat (vegetation type) and zone (distance from the vegetation edge) was shown to be significant for only total biomass made up of all the species Table 12) but it explained only 25% of the model. To split the influence of different factors on each of the major species, factor level outcomes for the major species are given in Table 13a-c.

Table 12.   Three-way ANOVA for assessing the significance of interaction between habitat (vegetation type) and distance from edge of vegetation (distance) on number (mean no.ha$^{-1}$ of habitat) and biomass (mean fresh weight, kg.ha$^{-1}$ of habitat) of fish (levels of significance = p, % SS = sum of squares as % of total sum of squares explained by a factor).

| | Habitat | | Distance | | Interaction | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| Total no. | 0.000* | 66 | 0.001* | 22 | 0.207$^{ns}$ | - |
| Biomass | 0.000* | 41 | 0.000* | 34 | 0.000* | 25 |

* = significant, $^{ns}$ = not significant.

Habitat (vegetation type) was significant for total number in at least five species and all Nile tilapia of less than 25 cm in length. For *T. zillii*, all factors were significant.

Different species appeared to be influenced in different ways by the analyzed factors. For example, from Table 13a-c, it is shown that for *Astatoreochromis*, habitat and habitat * zone interaction were significant for total number but not so with regard to biomass or to the number of immature fishes. Season which was not significant with respect to numbers was a significant for biomass and immature *Lates niloticus*.

## DISCUSSION
### Species composition and diversity
The present fish populations of Lake Victoria and the commercial fishery in particular, are dominated by the stocked fishes - *Lates niloticus* (the Nile perch) and *Oreochromis niloticus* (the Nile tilapia), and the native cyprinid, *Rastrineobola argentea*. As fish introductions result into mostly undesirable effects such as reduced diversity of other species (Zaret and Paine, 1973), there is concern regarding those species that have been stocked into Lake Victoria. However, the frequent reference to effects of these species, particularly Nile perch, in the literature is based more on sampling of the open water including the sub-littoral zone than the interface habitats of the littoral zone. Recent evidence (Seehausen, 1996a, b) suggests that rocky littoral habitats contain assemblages of species which were not equally affected by Nile perch predation. The area investigated

Table 13. The significance of different factors (habitat, distance from the vegetation edge, season according to one of four seasons - see under Materials and Methods, and interaction between habitat and season) to individual species abundance (13a on numbers, 13b on biomass and 13c on number of immature fishes) of the more common species in the littoral vegetated habitats.

| | Habitat p | Distance p | Season p | Hab. * Lev. p |
|---|---|---|---|---|
| **a. Numbers** | | | | |
| *Brycinus* | 0.003$^{*}$ | 0.172$^{ns}$ | 0.104$^{ns}$ | 0.098$^{ns}$ |
| *Astatoreoc.* | 0.043$^{*}$ | 0.032$^{*}$ | 0.824$^{ns}$ | 0.045$^{*}$ |
| *Haplochrom.* | 0.112$^{ns}$ | 0.013$^{*}$ | 0.435$^{ns}$ | 0.740$^{ns}$ |
| *L. niloticus* | 0.762$^{ns}$ | 0.285$^{ns}$ | 0.906$^{ns}$ | 0.350$^{ns}$ |
| *O. nilotic* [1] | 0.163$^{ns}$ | 0.760$^{ns}$ | 0.414$^{ns}$ | 0.157$^{ns}$ |
| *O. nilotic.* [2] | 0.000$^{*}$ | 0.176$^{ns}$ | 0.026$^{*}$ | 0.585$^{ns}$ |
| *O. nilotic.* [3] | 0.000$^{*}$ | 0.098$^{ns}$ | 0.019$^{*}$ | 0.210$^{ns}$ |
| *O. nilotic.* [4] | 0.000$^{*}$ | 0.045$^{*}$ | 0.053$^{ns}$ | 0.300$^{ns}$ |
| *T. zillii* | 0.000$^{*}$ | 0.000$^{*}$ | 0.000$^{*}$ | 0.004$^{*}$ |
| **b. Biomass** | | | | |
| *Brycinus* | 0.000$^{*}$ | 0.579$^{ns}$ | 0.093$^{ns}$ | 0.137$^{ns}$ |
| *Astatoreoc.* | 0.054$^{ns}$ | 0.032$^{*}$ | 0.942$^{ns}$ | 0.070$^{ns}$ |
| *Haplochrom.* | 0.371$^{ns}$ | 0.548$^{ns}$ | 0.864$^{ns}$ | 0.594$^{ns}$ |
| *L. niloticus* | 0.071$^{ns}$ | 0.083$^{ns}$ | 0.012$^{*}$ | 0.560$^{ns}$ |
| *O. nilotic* [1] | 0.221$^{ns}$ | 0.336$^{ns}$ | 0.048$^{*}$ | 0.300$^{ns}$ |
| *O. nilotic.* [2] | 0.001$^{*}$ | 0.013$^{*}$ | 0.184$^{ns}$ | 0.006$^{*}$ |
| *O. nilotic.* [3] | 0.000$^{*}$ | 0.003$^{*}$ | 0.000$^{*}$ | 0.026$^{*}$ |
| *O. nilotic.* [4] | 0.037$^{*}$ | 0.004$^{*}$ | 0.001$^{*}$ | 0.146$^{ns}$ |
| *T. zillii* | 0.000$^{*}$ | 0.000$^{*}$ | 0.064$^{ns}$ | 0.000$^{*}$ |
| **c. Number of immature fishes** | | | | |
| *Brycinus* | - | - | - | - |
| *Astatoreoc.* | 0.256$^{ns}$ | 0.328$^{ns}$ | 0.782$^{ns}$ | 0.350$^{ns}$ |
| *Haplochrom.* | 0.553$^{ns}$ | 0.954$^{ns}$ | 0.060$^{*}$ | 0.310$^{ns}$ |
| *L.niloticus* | 0.226$^{ns}$ | 0.670$^{ns}$ | 0.000$^{*}$ | 0.095$^{ns}$ |
| *O. nilotic* [1] | - | - | - | - |
| *O. nilotic.* [2] | 0.005$^{*}$ | 0.990$^{ns}$ | 0.144$^{ns}$ | 0.998$^{ns}$ |
| *O. nilotic.* [3] | 0.182$^{ns}$ | 0.167$^{ns}$ | 0.102$^{ns}$ | 0.092$^{ns}$ |
| *O. nilotic.* [4] | 0.003$^{*}$ | 0.942$^{ns}$ | 0.186$^{ns}$ | 0.999$^{ns}$ |
| *T. zillii* | 0.030$^{*}$ | 0.085$^{ns}$ | 0.045$^{*}$ | 0.372$^{ns}$ |

*Astatoreoc.* = *Astatoreochromis*, *Haplochrom.* = *Haplochromis*, **1** = *O. niloticus* (>25 cm TL), **2** = *O. niloticus* (<15 cm TL), **3** = *O. niloticus* (15-25 cm TL), **4** = *O. niloticus* = (all length groups), TL = total length.

during the present study was regarded as representative of most of the threatened vegetated shoreline landscape in Lake Victoria. The primary interest were fish populations in habitats associated with the dominant wetland species (*Eichhornia crassipes*, *Cyperus papyrus*, *Vossia cuspidata*, *Typha domingensis* and *Phragmites mauritianus*) at the shoreline.

At least 30 fish species (Tables 6 - 8) were found in the shallow wetland zone of Lake Victoria during this study. This finding indicated that the area includes habitats in the lake with a higher species diversity than that found in open water sites. There could also be other habitat types in the lake such as in bays or indentations in the shoreline where species diversity and abundance may be different from the habitats which have frequently been sampled in the past. Among shoreline habitats which were not sampled are those associated with other vegetation types (see Chapter 3), rocky and sandy shores.

The presence among the haplochromines of virtually all trophic groups particularly the insectivores, molluscivores and piscivores in the represent study indicates that in total, species diversity of the investigated littoral compares quite well with the rocky shore studied by Seehausen (1994) even though it was not possible to identify all taxa in the trophic groups to species rank. In the study by Seehausen (1994), 50 "new" species were found, the majority belonging to only two trophic groups (algae scrapers and insectivores). This contrasts with the picture of predation associated with Nile perch. The reported predation-induced decline in species diversity (e.g. Hughes, 1986; Barel *et al.*, 1985; Ogutu-Ohwayo, 1990; Witte *et al.*, 1992), appears to have been greater in the sub-littoral and open water than in the vegetated littoral habitats. The higher structural diversity of shoreline habitats may account for the bigger number of trophic groups encountered despite the presence of *Lates*. The littoral zone therefore may contain many endemic species which previously were assumed to have disappeared through predation pressure.

Witte *et al.* (1992) noted that the rate and sequence of disappearance of haplochromine prey (of the sub-littoral zone) were dependent on habitat overlap with the predatory *L. niloticus*. In that study, the relatively low catch rates of Nile perch were cited as accounting for a higher number of surviving cichlids in the shallow area. In a related study, Chapman *et al.* (1996) showed that lagoon habitats and papyrus fringes provide a structural and chemical barrier to the lateral colonisation by *Lates* of such habitats but not some of the endemic species. But in this study, Nile perch were distributed in all habitats sampled, and their number and biomass were relatively high (Tables 6-11). In spite of the overlap, the habitats contained different species-frequency combinations of many of the haplochromine trophic groups and the Nile tilapia. It appears that the impact of predation by the size range of Nile perch found in these habitats may be more limited than in open water. The patterns of occurrence also strongly suggest selective preference by some species or species groups for particular vegetated habitat types in spite of the presence of a key predatory species, *L. niloticus*.

The diversity of the habitats (vegetation, depth, substrate types, etc) and, other physico-chemical conditions including seasonal and diurnal patterns (Chapter 3) offer a very wide choice for many species to coexist on the scale of the study area. In fact, beyond a certain level of predation, Nile perch in the presence of habitat structural diversity probably contributes to the surviving species diversity on a large spatial scale. However, some species especially among the cyprinids which previously were commonly reported (McConnell, 1975; Welcomme, 1969; Balirwa, 1984) were not encountered during this study. As they were associated more with lotic conditions, the species absence during this study may be related to a change in habitat conditions (e.g. drainage) which are detrimental to fish (McConnell, 1993, 1994) and for which Balirwa (1995) has attributed to population growth, land use change and wetland cover reduction (Chapter 4).

In comparison to open water sites (Table 8), species diversity was higher in all interface habitats (Tables 6 and 7) of which dominant vegetation was the main characteristic. This is a major indication of the ecological importance of shoreline vegetation as a factor in habitat selection by fish. The endemic tilapiines (*O. variabilis* and *O. esculentus*) were more associated with *Phragmites*-dominated habitats; the haplochromines, particularly the insectivores and piscivores, were more frequent in the *Vossia-Typha-Phragmites* series than in either *Eichhornia* or *C. papyrus*-dominated habitats. These patterns suggest similarities among the three sets of habitats (*Eichhornia, C. papyrus* and the *Vossia-Typha-Phragmites* series) which contribute to habitat selection by fish. The significant differences among habitat types along physico-chemical gradients and seasonal patterns revealed the habitats could be divided into the 3 major categories (Chapter 3). As a major feature of habitat, the type of vegetation which develops along geomorphologically determined features, is important in modifying the water quality in its vicinity for example by providing specific substrate for colonising macrofauna and for the fish specific combinations.

Due to vegetation type and depth, habitat structure may also be specified in gradients of abiotic and biotic factors along the horizontal axis (Chapter 3). The factors are coupled to the watershed (e.g nutrients like Si, $No_3$-N, P) and show strong seasonal and diurnal cycles (e.g water temperature, pH, algal cycles, etc). These patterns could further be mapped on the investigated habitat types and probably account for the three major categories of fish population habitats: *Eichhornia, C. papyrus* and the *Vossia-Typha-Phragmites* types. In Lake Victoria, a great variety of shores are present and, Welcomme (1966) noted that the shores differ in degree of exposure even on a diurnal basis. The shores range from wave beaten rocky or sand beaches to shallow, sheltered and papyrus lined bays. As vegetation clearly develops on diverse geomorphological patterns identified in an earlier study (Chapter 3), it is to be expected that apart from exposure, factors associated with the vegetated shores (e.g. depth, slope, bottom sediments) contribute to diversify habitat structure. Exposure in particular has various influences depending on shore type. This can be illustrated by papyrus shores.

*C. papyrus* lined shores are of two types: those which are more exposed to on-shore winds (seasonal and diurnal patterns, cf Welcomme, 1966) and, therefore are associated with an *Eichhornia* fringe of varying width, and those which are exposed to off-shore and along-shore winds and tend to be free of *Eichhornia*. In this study, papyrus lined shores without hyacinth were considered as the more typical papyrus habitats while those with hyacinth were regarded as a new habitat type. Since the presence and quantity of *Eichhornia* fringes seems to vary with the nature of the coastline with respect to wind directions (fetch), this classification may be artificial. Exposure may be the main factor accounting for within habitat variances which were generally larger in *Eichhornia* even though the fishing was carried out as much as possible under similar conditions. But organic matter from *Eichhornia* plants could also restructure the originally exposed conditions off this type of papyrus shoreline. However, because preceding conditions and the nature of fish populations are largely unknown, it is difficult to at all accurately point to the real quantitative species differences between these two types of papyrus lined shores. At this point, it has to be mentioned that just like in the other habitats, sampling in *Eichhornia* habitats was from the edge rather than deep inside of the mats. By its lake ward extension, *Eichhornia* creates entirely different conditions some distance from the actual edge of papyrus in habitats it has colonised.

A high degree of habitat structural complexity involving vegetation, depths and sediment types as shown by some studies (e.g Hall and Werner, 1977; Crowder and Cooper, 1982) is probably responsible for the diversity and abundance of fish in the investigated littoral habitats but on the scale of Lake Victoria, exposure of shores also contributes. It is likely that without the influence of *Eichhornia*, patterns of distribution and abundance in this habitat type could be different from what is presently observed.

### Relative abundance (Fish density)
In general, the closer to the vegetation, the higher was the biomass of all fish (Fig. 10, 11; Tables 12, 13). Among the more important factors which contribute to the overall abundance of fish in the very shallow habitats is the high littoral zoobenthic biomass even though their horizontal patterns were not well differentiated (Chapter 3). Treated as a single community, the littoral zoobenthos may serve as an index of the potential productivity of a lake for fish (Rasmussen, 1988) but the heterogenous patterns associated with the different habitats in the study area may account for differences in relative abundance.

From data on fish abundance (both numbers and biomass), significant differences were observed with respect to shallow water and open water. Even depth alone without considering whether or not a habitat type is associated with vegetation or any other factor influences numbers and biomass. The hypothesis that shallow and deep water habitats may randomly have the same density or biomass of fish can be rejected. If depth is a factor and vegetation has no influence, it would be expected that the different habitat types would show the same patterns in number and biomass of fish. As they do not, we can reject the hypothesis that there are

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no differences between habitat types with regard to number and biomass of fish. Species distribution and abundance are probably linked to a depth and production gradient (Gascon and Legget, 1977). Although fish abundance systematically varies with depth, the production gradient in Lake Victoria probably extends beyond the limits of the investigated area. This is shown by bathyo-spatial distribution and biomass patterns from 5m to deeper areas from an earlier survey of those areas (Kudhongania and Cordone, 1974). With an increase in Nile perch densities and other ecological changes, a similar survey would be required to verify the present patterns in deeper water.

To evaluate the significance of vegetation as an identifier of habitat type requires that fish be investigated as close to the vegetation as possible. Applied to the investigated area, a further distinction was made between wetland habitats at the very edges of vegetation (referred to as zone 1) and those some distance away (zone 2) but still within the littoral zone. The corresponding values of fish abundance were 30-70 kg.ha$^{-1}$ for zone 1 and 14-53 kg.ha$^{-1}$ for zone 2 (Fig. 10 and 11). Within these ranges, the type of dominant wetland vegetation at the interface determines the biomass. The series *Vossia-Typha-Phragmites* may be considered as falling in the more productive ranges from the edge of the vegetation up to the open water sites. This could be due to a higher invertebrate biomass associated with those habitats in comparison to either *Eichhornia* or papyrus dominated habitats. Within these ranges, habitat factors already discussed will determine biomass differences between species according to the most suitable habitat types. While for example the abundance of small fishes in *Typha* and *Vossia* is probably due to a large macrofauna density and diversity, and diurnal changes in pH, temperature, etc, extremes in these physico-chemical conditions (Chapter 3) could be beneficial to some fish species in *Eichhornia* or papyrus. This confirms the alternative hypothesis that vegetation type has a significant effect on fish abundance.

### Seasonal patterns in fish abundance

Fish biomass (Fig. 9) and abundance (numbers) varied with season. There appeared to be a lag in increase of the biomass after the rainy season. Some of the changes in fish parameters occurring after May (i.e towards the end of the main rain season) could indicate resumption of post-breeding activity which has often been associated with rainy seasons (McConnell, 1975; Welcomme, 1966; 1969). The different patterns shown by immature fishes with respect habitat type suggest differences in timing of breeding cycles and spatial use of habitat types. In Table 13a-c a per species analysis of significant factors associated with habitat, distance from vegetation (zone) and season, provides an indication of the dynamics of the more common species and how they utilise vegetated habitats. For example, both biomass and numbers of *L. niloticus* were correlated with season but this was not a significant factor for immature *O. niloticus*. In this species, habitat (vegetation) and interaction with distance from the vegetation were the significant factors for immature fishes. Small tilapia immature fishes seek the shelter of shoreline vegetation which may serve as refuge from predators or from wind which may

mask the influence of seasonality. This is confirmed from observations made by Welcomme (1964) who associated this preference with extremes in physical conditions of temperature and pH (see also Chapter 3). The very small juvenile tilapia may also be missed by the sampling technique. Seasonality in *O. niloticus* was significant for total biomass and the 15-25 cm size class which suggests differential use of habitat conditions. In *T. zillii*, all factors (habitat, distance from vegetation, season) and their interaction were significant. In general however, it appears that habitat suitability in time and space largely depends on resource availability as shown by several studies (e.g Gascon and Legget, 1977; Pierce *et al*. 1994).

Studies of fish populations are generally limited by equipment and methods that should ideally provide representative samples of the populations being investigated. Although gill nets may not capture all species of fish with the same efficiency, alternative methods e.g. seining or electro-fishing become inefficient in diverse habitats in large water bodies such as the investigated area. The use of catch per net (c.p.n) has frequently been used in fish production studies. However, it has the disadvantage is that it requires a very large effort and commercial catch data are ususally the main source of information. By combining different mesh sizes as evaluated by Jensen (1986) the bias towards particular length classes of the species liable to gill-net capture in well defined habitats was considerably reduced by the methods used in this study. The data on relative density therefore provide a real indication of the fish yield in an area without any reference data. Given the difficulties of sampling the diverse wetland habitats and the increasing influence of the water hyacinth, this is hardly surprising. From the estimates carried out, the fish yield of the shallow wetland zone in Lake Victoria was $46.7 \pm 4.0 kg.ha^{-1}$ in comparison to $6.2 \pm 0.1$ $kg.ha^{-1}$ for offshore habitats. This could be an underestimate of the annual yield but falls in the range of 40-60 $kg.ha^{-1}$ given by Welcomme (1979) for floodplain fisheries. The range of $25 \pm 3\text{-}66 \pm 11$ $kg.ha^{-1}$ accounts for the diversity of shoreline type, but different species will show different responses. This has been shown in assessments for significant differences among habitat types and within habitats with respect to distance from the vegetation. Also seasonal patterns were confirmed for biomass, numbers and differences between species and was suggested as a form of resource partitioning among species and size classes within species in fish communities (Pet and Piet, 1995). These patterns may also account for the spatial and temporal distribution patterns of the fish and fishermen.

Data on fish biomass as discussed so far should be regarded as estimates of yield indices rather than actual yield. If some of the various components of biomass were randomly to be distributed in the entire sampling unit, the fishing arrangement depicted in Figure 4 would capture only a fraction of what is present. In addition, no account of possible day-night differences in distribution patterns were taken into account. To increase the efficiency of capture for all possible sizes of all the species would require either a total removal method or that the range of mesh sizes employed be separately set uniformly throughout the sampling unit for each fishing

exercise at various times. Hence, the nine different mesh sizes would have to be set separately in a block formation of 18 nets. There would be far too many iterations as to render the exercise practical. This could be avoided by use of a raising factor and the calculated biomass would probably be much higher than figures obtained in this study. The range would vary with habitat and with distance from the edge of each vegetation as before as well as with time of day.

Changes which may have affected the littoral zone fish fauna is partly associated with habitat degradation in its various forms (e.g Coulter *et al*. 1986; Hecky, 1993; Lowe-McConnell, 1993; Balirwa, 1995). Another source of changes which is currently being evaluated are the impacts of predation following the Nile perch upsurge (e.g. Witte *et al*. 1995; Goudswaard and Witte, 1997). Therefore, understanding the full extent of the present fish diversity partly depends on the efficiency of sampling the littoral habitats. Hence, although it was not possible to sample the full range (e.g the rocky and sandy beaches) of shoreline habitats during this study, the work of Seehausen (1994, 1996) provides more evidence that there are more species in the rocky littoral zone of the lake than previously assumed from gross assessments of faunal changes in the lake. In some recent studies with electro-fishing gear for instance, Willoughby *et al*. (1992) were unable to show the presence of some species such as *Brycinus jacksonii*, *Afromastecembelus victoriae*, the smaller mormyrids and clariids. Their frequency of occurrence during this study could be described as high (70-95% for *Brycinus*). It seems therefore that apart from technique, or not sampling some of the habitats associated with vegetation, previous studies may have been limited by not sampling in all seasons among other factors.

In view of the rapid changes taking place in the wetland littoral zone (e.g. wetland drainage, urban influences, the increasing importance of the water hyacinth, etc) any study carried out in most parts of the shoreline interface at present is likely to reflect transitional conditions. Of particular concern are two threats: the use of swamp buffers as waste water treatment areas or their drainage, and the increasing infestation of the littoral zone with *Eichhornia crassipes*. The impact of waste water on the interface ecology in swamp treatment areas is not fully understood but the study by Kansiime *et al*. (1994) indicates that the effects of waste water are manifested in a width of the littoral zone equivalent to the entire area investigated in this study. The effects of water hyacinth are not fully understood because of the dynamic character of the weed. In some of the physico-chemical aspects such as SRP, tot-P, Chl-a, conductivity and dissolved oxygen, habitats associated with water hyacinth and those associated with papyrus appeared to be similar and yet significant differences in fish populations especially in biomass were observed. The observed differences could result from differences in the degree of exposure to winds which contribute to the generally more unstable conditions characteristic of *Eichhornia*. Therefore, results do not necessarily suggest that infestations with *Eichhornia* significantly fish production. It has to be considered that:
(a) There are two types of papyrus habitats in which preceding conditions regarding fish populations are unknown. Along the more exposed previously papyrus-

dominated (but currently *Eichhornia* infested) shores fish biomass and other population characteristics were probably different from the second type of papyrus habitat which tends to be free of *Eichhornia* infestation.

(b) The habitats sampled are at the edges rather than the interior of the *Eichhornia* mats which were shown by Willoughby *et al.* (1992) to have less fish diversity and biomass than the non-infested papyrus beds; it is by fishing in the interior of mats that their study could not show some species such as *Brycinus*, *Afromastacembelus* and mormyrids, and in which less fish diversity and biomass could be expected; the edges and narrow strips of hyacinth mats coupled to wind patterns may show different effects of hyacinth from those in heavy infestations.

(c) Conditions at the edge of *Eichhornia* are affected by wind and are therefore dynamic, but elsewhere, fish other than those which can utilise atmospheric oxygen (e.g *Protopterus* and *Clarias* and were common in hyacinth habitats) rarely penetrate the interior of the mats. Those that do probably do so to seek shelter during storms. Densely packed mats are unlikely to support fish densities as were observed from the fringes.

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# Chapter 5

# Patterns in the abundance and size structure of *Oreochromis niloticus* LINNÉ (The Nile tilapia) among different vegetation-dominated habitats of the littoral zone in northern Lake Victoria (Uganda)[*]

## ABSTRACT
Fish density (no.individuals and biomass, kg. fresh weight. ha⁻¹), size class and seasonal patterns in *Oreochromis niloticus* (the Nile tilapia) were investigated by quantitative sampling among macrophyte dominated interface habitats of the shoreline in northern Lake Victoria between 1994 and 1996. The dominant macrophyte species which defined these habitats were *Cyperus papyrus*, *Vossia cuspidata*, *Eichhornia crassipes*, *Typha domingensis* and *Phragmites mauritianus*. Fish abundance varied significantly among habitats. Numerical abundance ranged from $9 \pm 2$ ind.ha⁻¹ in *C. papyrus* dominated habitats to $82 \pm 27$ ind.ha⁻¹ in habitats off *Phragmites*. The mean total biomass of *O. niloticus* varied between 15.3 and 32.5 kg.ha⁻¹ corresponding to 45-60 % of the biomass of all the fish. Numerical abundance was not correlated with biomass. There were significant ($p < 0.05$) size related differences in habitat use by fish. In comparison to other habitats, *C. papyrus* and *Eichhornia* dominated habitats had significantly lower individual counts of large ($> 25.0$ cm) *O. niloticus* fish but even between these two, *Eichhornia* dominated habitats had a higher numerical and biomass density. *Phragmites* and a sandy habitat similar in bottom type to *Vossia* and *Typha* habitats were more important for small ($< 15.0$ cm) and juvenile fish. These patterns appeared to vary with distance from the vegetation edge and with season.

## INTRODUCTION
Generally fishes are not evenly distributed throughout a water body. Lake Victoria in East Africa with its diverse shoreline (Welcomme, 1966a), and shallow mean depth (40 m), is a typical example. The more shallow littoral habitats of lakes tend to be more productive than open water (Hall and Werner, 1977; Pierce *et al.*, 1994; Randall *et al.* 1995). Habitat selection in fish can also be narrow as well as wide and may vary among size or age classes (e.g. Rossier *et al.* 1996). In Chapter 4, data consistently showed that Lake Victoria fish density (numbers and biomass), was significantly higher towards the edge of vegetation than further away from the shore. Although the vegetated littoral habitats have been shown to be populated by fishes for breeding or feeding purposes and as refuge from predators (Werner *et al.* 1977; Chick and McIvor, 1994), there are hardly any comparable data on size related patterns of abundance of *Oreochromis niloticus* among the different habitats of Lake Victoria especially the shoreline wetlands which are assumed to be important for the species. The previous research (McConnell, 1958; Fryer, 1961; Fryer and Iles, 1972; Kudhongania and Cordone, 1974) tended to assume the littoral zone as a homogeneous landscape of ecological importance to the endemic tilapia (*O. esculentus* and *O. variabilis*). These tilapias were overfished and the predominant commercially important species from these habitats appears to be the now stocked *O. niloticus*. The Nile tilapia therefore provides a practical choice for study not least because of the deterioration in shoreline wetlands (Lowe-McConnell, 1993, 1994a, 1994b; Balirwa, 1995) but, also, as a stocked species,

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because of its apparent success in the lake (Balirwa, 1992) especially in relation to the shoreline wetland habitats.

Several studies on *O. niloticus* in African lakes where it is endemic, suggest that shallow areas are important in the biology of the species. In Lakes Albert and Rudolf (Turkana), Lowe-McConnell (1957, 1958) observed that *O. niloticus* are found only around the edges of the lakes; in Lake Edward, the species was found well away from the shore while in Lake George, it was found all over the lake but was less common near papyrus-fringed shorelines. The distribution of *O. niloticus* within lakes seems to vary with ecological conditions. In Lake Victoria, Lowe-McConnell's studies considered that the endemic tilapias move from zone to zone because of the shallow depth and uniform conditions. These studies did not consider the Nile tilapia which had just been introduced into the lake nor the subsequent changes associated with species introductions. Following species stockings in Lake Victoria, Welcomme (1964) associated the presence of young Nile tilapia along gradient beaches with the species' considerable resistance to high temperatures. The fishes were also thought to move progressively offshore with increase in size (Welcomme, 1966b). It seems from these studies that the peak in reproduction associated with the rainy seasons (Lowe-McConnell, 1975; 1987) was thought to be related to the appearance of small fishes in shallow lagoons. This pattern probably accounts for the presence of large fishes nearer to the shore. A study of the spatial distribution patterns of the *O. niloticus* commercial fishery in Lake Victoria by Balirwa (1990) indicated that fish of $25 \pm 10$ cm total length were more often caught in the vegetated littoral zone while the bigger fishes of over 35 cm were more common off hard bottoms towards deeper water. In general, the depth ranges encountered in these studies were wide. Nile tilapia of all sizes have been caught in various habitats ranging from the shallow to the deep and open areas of the lake. The above picture therefore does not clearly point to the assumed importance of the wetland zone in the ecology of the Nile tilapia as it is difficult to assess with any certainty whether or not the reported patterns and which factors are significant. Also, it is difficult to assess whether patterns reported from other lakes and habitats hold for Lake Victoria.

Spatial and temporal (seasonal and diurnal) variations have been demonstrated in physico-chemical and biotic conditions among shoreline habitat types (Chapter 3). These are shallow habitats mostly less than 3 m. Vegetation type and seasonality were found to be significant factors in fish diversity and overall fish biomass (Chapter 4). Nile tilapia could therefore be one of the species which responds to seasonal patterns by selecting feeding or breeding areas. Apart from feeding and breeding, many fish species in Lake Victoria exhibit ontogenetic changes in habitat preference (Corbet, 1961). These shifts may be due to patterns in the hydrological regime (e.g. water level) and their influence on habitat suitability. The change in physico-chemical and biotic factors among different vegetated habitats (see Chapter 3) distinguished between habitats where different size classes of the Nile tilapia occur before and after the juvenile fishes appear (if they do) along gradient beaches (Welcomme, 1964).

This study investigates the relative abundance of the Nile tilapia with respect to different size classes, and seasonal use by the species of fringing interface habitats in the northern Lake Victoria. These interface habitats were dominated by *Cyperus papyrus* L., *Vossia cuspidata* (Roxb.) Griff., *Eichhornia crassipes* (Mart.) Solms, *Typha domingensis* Pers. and *Phragmites mauritianus* Kunth. plant communities hereafter referenced respectively by the generic name of the main macrophyte. A major aim of the study was to find out whether the total biomass of *O. niloticus* in the different habitats shows seasonal trends. The study was carried out over a period of about 28 months between February 1994 and June 1996 to include the four major characteristic seasons: the main dry season (December - March 15), the main rainy season (March 16 - June), the short dry but cool season (July - September 15) and the short rainy season (September 16 - November). All the habitats investigated were simultaneously sampled for other ecological aspects such as seasonal and horizontal patterns in physico-chemical conditions, phytoplankton, macrofauna and fish populations (Chapter 3 and 4).

In order to verify whether or not fish abundance and size structure of the Nile tilapia showed any relation to habitats associated with shoreline vegetation, a zero hypothesis ($H_0$) was formulated thus:

Abundance and size structure in *O. niloticus* of Lake Victoria vary independently of wetland habitat type or season and distance from the shore.

## MATERIALS AND METHODS

**The study habitats**

The size-related spatial and temporal distribution patterns for the Nile tilapia were recorded in the Jinja area in the northern part of Lake Victoria. The sampled habitats were associated with plant communities at the edge of the lake. The dominant plant species were: *Cyperus papyrus, Vossia cuspidata, Eichhornia crassipes, Typha domingensis* and *Phragmites mauritianus* and these were used to define the various interface habitat types. The location and limnological features of the investigated habitats are outlined in Chapter 3 and 4.

The area sampled off the vegetated shore in each habitat remained within the littoral zone. It extended from the shore, where it was less than one metre deep, for about 50-80 m towards the open, deeper water. At the limit of this zone the lake was between two and four metres deep. Within each of the habitats, two simultaneously sampled sub-units have been recognised: the first 20 m from the shore, and an area beyond 20 m to about 70 m away from the shoreline.

**Fish data**

Data on abundance, size structure and distribution were collected using gillnets set over night. There were 9 different mesh sizes: 22, 33, 37, 50, 60, 76, 90, 115 and 125 mm stretched mesh. Because the habitats were shallow, nets could occupy the entire water column. In a preliminary phase, it was found that a combination

of mesh sizes from the smallest to the 125 mm mesh could capture most sizes of fish except the smallest. Two nets of each mesh were used making a total of 18 nets. The whole fleet of nets could occupy most of the width of the littoral zone, with the first net set parallel to and adjacent to the vegetation fringe. The rest of the nets were respectively arranged in the manner described in Chapter 4.

Despite the use of electro-fishing apparatus, the smallest fish were not easily caught in the vegetated habitats even though large shoals were often seen in clearer areas along the shores. As literature data indicate that juvenile *O. niloticus* utilise sandy beaches for part of the life cycle (Lowe-McConnell, 1958; Welcomme, 1964, 1965), it was decided to sample one such habitat with a 5.0 mm mesh seine net over a period of three months (April - June, 1993) during preliminary assessments. The seine was deployed from a small boat in a semi-circle extending from the shoreline, and enclosing an area of about 30 $m^2$. Depth at the shore was about 50 cm sloping to about 1.5 m at the deepest end. The seine net was pulled to the shore from both ends. Sampling of the sandy habitat was done between 0900 and 1300 h when shoals of juvenile fishes seemed to regularly appear. As the area became increasingly disturbed due to human occupancy, it was not possible to sample through all seasons. The vegetated habitats were regularly sampled between February 1994 and June 1996. The distribution of the fishing effort per season in each habitat type was given in Chapter 4.

All the fish caught or sub-samples were counted and the total length (TL) measured to the nearest 5 mm. After all fish had been measured and weighed, specimens of the Nile tilapia were sorted out and counted. Individuals were weighed to 0.1 g and subsequently sexed. The gonad condition was recorded using Nikolsky's scheme (1963). Some smaller specimens could not be sexed accurately and were assumed to be immature.

The Nile tilapia of Lake Victoria shows first signs of maturity at about 25 cm and fishes below 15.0 cm are generally immature (Balirwa, 1992b). Therefore, the length range of all fishes was separated into three size classes: 0-15 cm, 15.1-25.0 cm, > 25.0 cm. However, even among large fishes, a certain proportion may still be immature depending on several environmental factors (McConnell, 1958; 1975) and it may be useful to assess changes in size structure by both size class and maturity categories. The mean biomass and number for each size class and sex per hectare of habitat was based on the area occupied by the set-up of the fleet of nets.

As in the previous assessments of fish populations (Chapter 4), the overall fish density (mean number and biomass (kg.fresh weight. $ha^{-1}$) was calculated as a function of the shallow water region as a whole and without reference to specific vegetation types or possible seasonal influences. Subsequently, areas abutting to each of the dominant vegetation communities were used as distinct habitats. In addition, the width of the littoral zone could be subdivided into two areas: the shallowest part nearest to the vegetation up to about 20 m away i.e. "zone 1" and

the part that extended to the limit of the littoral zone about 50 m, 70 m or 80 m away i.e. "zone 2". Where statistically applicable, these levels are also referred to as zone 1 and zone 2 respectively. In calculation of the number of individuals and of the biomass per hectare for zone 1 and zone 2, the area was based on half that used in calculating the overall biomass. Seasonal patterns were based on the same classification of distinct periods used in the structural characterisation of the habitats (Chapter 4 and 5).

### Statistical analyses

The use of a combination of nine different mesh sizes was considered efficient to capture a representative size range of fish (Jensen, 1986) and has been used to analyze abundance patterns in various tropical fishes (Pet and Piet, 1993). Therefore, gill net catch data were used without correction for fishing effort or gear selectivity. Arithmetic means and standard errors were calculated for the response variables. The area fished in each habitat and the replicate samplings varied widely (mean = $2840 \pm 1870$ m$^2$, n = 100). Catch data were therefore calculated in terms of one hectare (10,000 m$^2$). To evaluate the influence of vegetation (habitat type), distance from the shore (i.e. zone) and season, analyses were based on the littoral zone when split into two zones. The significance of factor levels: habitat (type of dominant vegetation at the shore), zone (distance from the vegetation at the shore), season, interaction effects and comparisons among habitats were tested by ANOVA ($p < 0.05$), and unless stated, the significance level was maintained in all comparisons. Analyses were done with the SPSS software on non-transformed data except where variances were not homogeneous. The explained model variance (Sum of Squares) was partitioned into the component contributions of those factor levels which were significant. Only probability levels (p) of the various factors and the percentage of explained variance due to such a factor are reported.

## RESULTS

### Juvenile fishes off sandy habitats

Between 365 and 887 juvenile fishes were caught per sampling date during the period. As the sampling represented the total from the repetitive removal from the same area of about 30 m$^2$, the cumulative totals in the sampling period could be calculated in terms of numbers per square metre or per hectare i.e (12 - 30 ind. m$^{-2}$ or 120,000 - 300,000 ind.ha$^{-1}$). The length frequency characteristics of the very small fishes which could not be caught in gill nets, and were found off sandy habitats is given in Table 1. The fishes were most abundant in clear very shallow water (10 - 50 cm deep) between 09.00 and 13.00 h after which they disappeared. The table shows that fishes between 1.0 and 3.0 cm total length were the most abundant and frequent at this site.

### Fish abundance in the shallow water region

An evaluation of the shallow water region combining all the vegetation dominated habitat types showed significant differences in the discerned categories of specimens. From the main fishing set up, 3476 specimens weighing 2500 kg fresh

weight were caught from 100 fishing runs. Without the use of size class categories, the distribution of the number and weight of *O. niloticus* caught are given in Table 2.

Table 1.    Length frequency distribution of juvenile Nile tilapia from a sandy habitat in the study area.

| Size class | Percentage frequency in each class | | |
|---|---|---|---|
| (cm, TL) | April | May | June |
| 0-1.0 | 14 | 13 | 0 |
| 1.1-2.0 | 63 | 60 | 28 |
| 2.1-3.0 | 21 | 16 | 70 |
| 3.1-4.0 | 1 | 9 | 2 |
| 4.1-5.0 | 1 | 1 | 0 |
| 5.1-6.0 | 0 | 1 | 0 |
| n (number examined) | 515 | 365 | 887 |

Table 2.    The distribution of components from combined catch data ($\pm$ SE) in the investigated vegetated habitats.

| | Male | Female | Immature | Total |
|---|---|---|---|---|
| Number | 2105 | 892 | 479 | 3476 |
| Weight (kg) | 1471 | 985 | 44 | 2500 |
| No.ha$^{-1}$ | 21 $\pm$ 4 | 9 $\pm$ 1 | 5 $\pm$ 3 | 35 $\pm$ 6 |
| Wt. kg.ha$^{-1}$ | 14.7 $\pm$ 1.5 | 9.9 $\pm$ 1.3 | 0.4 $\pm$ 0.2 | 25.0 $\pm$ 2.4 |
| Mean ind. wt (kg) | 0.1 | 1.10 | 0.09 | 0.72 |

The number and cumulative weight of male fish was considerably higher than that of females. With regard to immature fishes, the sandy habitat had more smaller juvenile fishes than the vegetated habitats although the sampling methods were strictly not comparable.

**Fish abundance according to habitat types**
Fish density as mean total number per hectare varied according to the type of habitat (Fig. 1). By comparing overall data of the shallow water zone (Table 2) with that of individual habitat types (Fig. 1), differences ($p < 0.05$) can be seen between the entire shallow region and the *Vossia-Typha-Phragmites* dominated habitats. The highest number of fishes came from *Phragmites* and *Typha* while the lowest was from *Eichhornia* and *C. papyrus* dominated habitats.

Other population characteristics (the number of male, female and immature fish) are given in Table 3. In general, all size classes (excluding the category shown in Table 1) were represented; the smallest fish were about 6.0 - 7.0 cm and the largest specimens were about 40 cm.
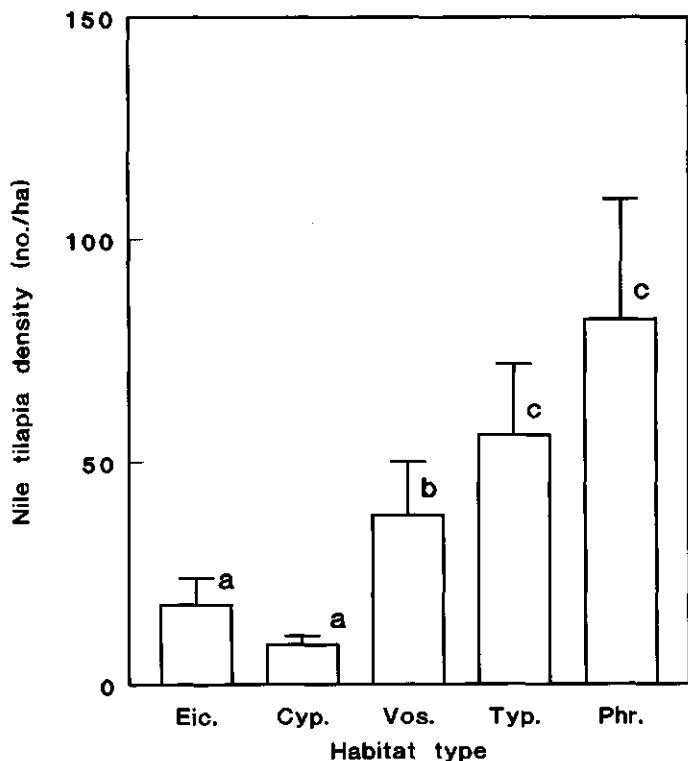


Fig. 1.  Density of the Nile tilapia (no.ha$^{-1}$) in the littoral zone as a whole off different wetland vegetation types. Data are pooled over season and distance from the edge of vegetation to about 70 m away from the vegetation. Means that are not significantly different share a common letter (modified LSD test maintaining experimental error rate at 0.05), vertical bars represent 1 SE.

A $X^2$ test revealed a disproportionately higher number of males than females in the *Vossia*, *Typha* and *Phragmites* habitat types in comparison to the sex ratio in *Eichhornia* and *C. papyrus* dominated habitats (Table 3). *Phragmites* habitats had the highest number of immature fishes while the other habitats had more or less the same pattern for immature fish.

The mean biomass (kg. ha$^{-1}$, fresh weight) of the Nile tilapia (male, female and immature) from each of the investigated habitats and the biomass of all fish are given in Table 4.

Between 45% and 60% of the biomass of all fish from the investigated habitats was made up by the Nile tilapia. The biomass according to habitat type are shown in figure 2.

Table 3.    Numerical abundance (no. ind. ha$^{-1}$, ± 1 SE) of the Nile tilapia by sex and immature categories (imm.) in the different vegetation dominated habitat types of the littoral zone; tests for significant differences between male and female numbers are by $X^2$ at p = 0.05.

|  | Eichhornia | Cyperus | Vossia | Typha | Phragmites |
|---|---|---|---|---|---|
| No. samples | 22 | 31 | 12 | 20 | 15 |
| No. male | 12 ± 5 | 5 ± 1 | 26 ± 9 | 37 ± 12 | 42 ± 10 |
| No. female | 5 ± 1 | 3 ± 1 | 11 ± 4 | 18 ± 6 | 12 ± 4 |
| $X^2$ | 2.882$^{ns}$ | 0.50$^{ns}$ | 6.082$^{*}$ | 6.564$^{*}$ | 16.666$^{*}$ |
| No. imm. | 1 | <1 | 1 | 1 | 28 ± 16 |
| No. exam. | 391 | 273 | 455 | 1125 | 1232 |

* = significant, ns = not significant

Table 4.    The mean biomass (kg.ha$^{-1}$ ± SE) of the Nile tilapia from the investigated habitats (biomass of all fish is given in the first row).

|  | Eichhornia | Cyperus | Vossia | Typha | Phragmites |
|---|---|---|---|---|---|
| No. samples | 22 | 31 | 12 | 20 | 15 |
| All fish | 66 ± 11 | 25 ± 3 | 54 ± 12 | 49 ± 7 | 57 ± 10 |
| Nile tilapia |  |  |  |  |  |
| % of all fish | 49.2 | 61.2 | 45.6 | 60.6 | 49.3 |
| Bio. male | 19.1 ± 4.1 | 8.9 ± 1.8 | 13.5 ± 4.4 | 17.0 ± 3.4 | 18.2 ± 4.1 |
| Bio. female | 13.4 ± 3.8 | 6.4 ± 1.3 | 11.1 ± 4.6 | 12.6±2.9 | 7.2 ± 1.6 |
| Bio. imm. | 0.1 | 0.0 | 0.1 | 0.1 | 2.6 ± 1.6 |

The highest biomass of Nile tilapia was from *Eichhornia*-dominated habitats made up of comparatively large fishes. *Vossia*, *Typha* and *Phragmites* had the same total biomass patterns but immature fishes were most abundant in *Phragmites*-dominated habitats.
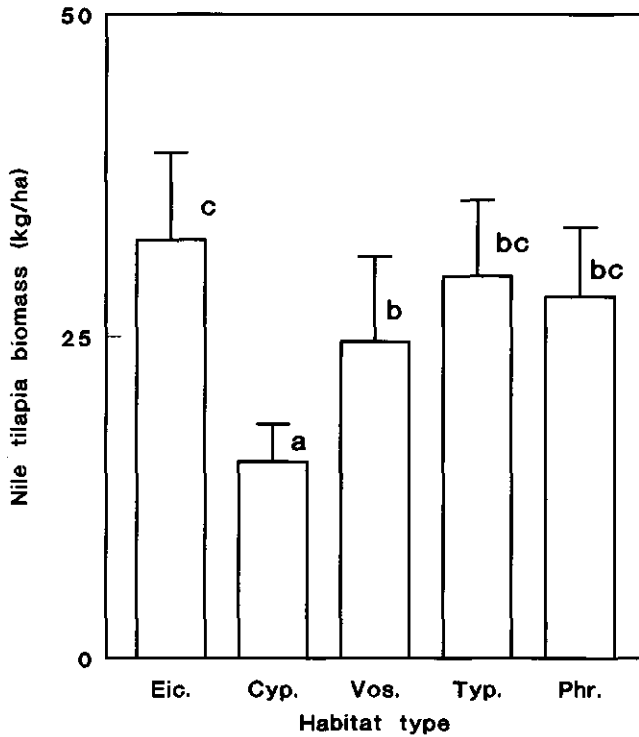
Fig. 2.  The mean biomass (kg.ha$^{-1}$) of the Nile tilapia in the littoral zone off different wetland vegetation types. Data are treated as in Fig. 1, vertical bars represent 1 SE.

**Seasonal patterns**
The biomass of the Nile tilapia varied with season and was at maximum in the short rainy season (September 16 - November) (Fig. 3).
Within habitat seasonal biomass patterns exhibited some differences (not shown): In the papyrus and *Vossia* dominated habitats the long rainy season (March 16 - June period) had the least biomass (17 ± 6.2 and 6.8 ± 3.1 kg.ha$^{-1}$ respectively). In *Typha* habitats, a low biomass was found during the dry seasons (December - March 15) (15.7 ± 3.4 kg.ha$^{-1}$) and (July - September 15) (16.2 ± 4.2 kg.ha$^{-1}$).

**Within habitat and among size class abundance patterns**
To evaluate the significance of factor levels: habitat (type of dominant vegetation at the shore), distance from the vegetation at the shore, season and interaction effects on the biomass (per size class) and density (numbers) among habitats, results of the three factor ANOVA ($p < 0.05$) are given below (Table 5).
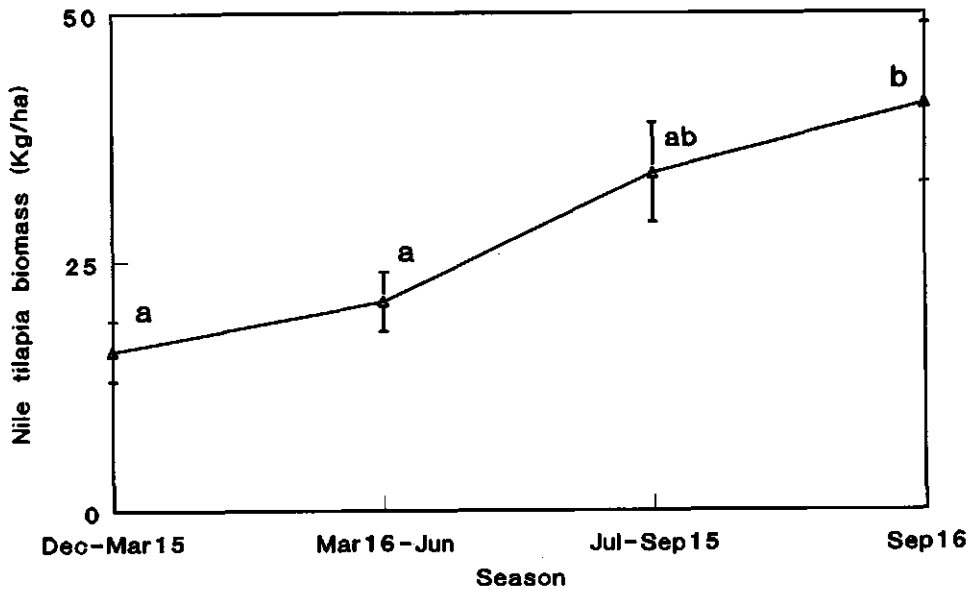
Fig. 3.    Seasonal patterns in the biomass of the Nile tilapia (vertical bars are
           SE, means that are not significantly different share the same letter).

In Table 5, habitat type which was established as corresponding to dominant
vegetation, zone which is distance from the edge of vegetation and season are
analyzed for their significance. The data show that the type of vegetation is
significant for the Nile tilapia for all sizes. When individual sizes were considered
vegetation (habitat) type no longer remained significant for number in large fish
implying that large fish could be found in any of the habitats. Fish density (no.ha$^{-1}$)
for length up to 25 cm were significantly influenced by vegetation (habitat) type.
When separate effects of vegetation (habitat type), distance from the shore within
the littoral or season were compared (Table 5), generally vegetation (habitat type)
explained most of the variation but did not have significant effect on numerical
density or biomass of large fish ( > 25 cm). Distance from the vegetation was
significant for total biomass and numbers in large fish. Immature fish were present
only in the two size classes (0 - 15.0; 15.1 - 25.0 cm) and their density varied
significantly among habitat (vegetation types). A significant effect of season was
related to seasonal variation in abundance of the total number of small fishes ( <
25 cm). A two factor-ANOVA to test the effects of interactions between either of
the factors pooled showed basically similar results (Table 6).

Table 5.    Three-way ANOVA for assessing the significance of different factors (vegetation as habitat type, distance (as zone 1 and zone 2) from the shore and season with February, May, July and October as midpoints) on Nile tilapia abundance (total numbers ($no.ha^{-1}$); no. immature fish ($no.ha^{-1}$); and biomass ($kg\ FW.ha^{-1}$) per size class attributed to the factors (Levels of significance = p, %SS = sum of squares as % of the total SS explained by a factor (other species' influence on the level of significance by the factors is suppressed, cf. Table 13, Ch. 4).

| | vegetation | | distance | | season | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| a. All sizes | | | | | | |
| Tot. nos. | 0.000* | 76 | 0.035* | 7 | 0.016* | 17 |
| No. imm. | 0.001* | 86 | 0.095ns | - | 0.144ns | - |
| tot. biom. | 0.002* | 40 | 0.004* | 19 | 0.001* | 39 |
| b. >25 cm | | | | | | |
| Tot. nos. | 0.210ns | - | 0.021* | 43 | 0.657ns | - |
| tot. biom. | 0.429ns | - | 0.011* | 35 | 0.033* | 48 |
| c. 15.1-25.0 cm | | | | | | |
| Tot. nos. | 0.000* | 77 | 0.077ns | - | 0.005* | 23 |
| No. imm. | 0.098ns | - | 0.188ns | - | 0.180ns | - |
| tot. biom. | 0.000* | 62 | 0.107ns | - | 0.000* | 39 |
| d. 0-15.0 cm | | | | | | |
| Tot. nos. | 0.000* | 75 | 0.197ns | - | 0.033* | 25 |
| No. imm. | 0.001* | 87 | 0.924ns | - | 0.121 | - |
| tot. biom. | 0.000* | 79 | 0.339ns | - | 0.015* | 21 |

* = significant, ns = not significant

In all size classes of *O. niloticus*, interaction between vegetation (habitat type) and season was significant for total biomass, and explained between 50 and 70% of the variance. There was no significant effect on distribution pattern between habitats regarding distance from shore for small fish (< 25 cm). However, between vegetation (habitat type) and distance interaction was significant for only large fishes above 25 cm. Apart from the smallest fish (<15 cm), fish abundance (numbers) with respect to habitat was independent of season.

Table 6.    Two-way ANOVA for assessing the significance of interaction
between the factors (habitat type as vegetation and season; habitat
type and zone as distance) following procedures and conditions as in
Table 4.

| | vegetation * season | | vegetation * distance | |
|---|---|---|---|---|
| | p | % SS | p | % SS |
| a. All sizes: | | | | |
| Tot. nos. | 0.278[ns] | - | 0.273[ns] | - |
| No. imm. | 0.016[*] | 40 | 0.434[ns] | - |
| tot. biom. | 0.012[*] | 51 | 0.999[ns] | - |
| b. >25cm: | | | | |
| Tot. nos. | 0.184[ns] | - | 0.002[*] | 59 |
| tot. biom. | 0.038[*] | 63 | 0.015[*] | 57 |
| c. 15.1-25.0cm: | | | | |
| Tot. nos. | 0.120[ns] | - | 0.176[ns] | - |
| No. imm. | 0.002[*] | 29 | 0.515[ns] | - |
| tot. biom. | 0.001[*] | 69 | 0.082[ns] | - |
| d. 0-15.0cm: | | | | |
| Tot. nos. | 0.038[*] | 39 | 0.536[ns] | - |
| No. imm. | 0.050[*] | 30 | 0.517[ns] | - |
| tot. biom. | 0.004[*] | 52 | 1.000[ns] | - |

* = significant, ns = not significant

Within size class patterns of the Nile tilapia biomass as percentages of the total
biomass of all species (Table 7) varied among habitats and with distance from the
shore.

Table 7.    Spatial patterns (zone 1 = nearer to the vegetation and zone 2 = further away from the vegetation i.e according to distance from the vegetation edge towards the open water) in the biomass of the Nile tilapia (kg. ha$^{-1}$) by % size class of the total biomass in each of the two zones off each of the investigated habitats.

|                    | Eichhornia | Cyperus | Vossia | Typha | Phragmites |
|--------------------|-----------|---------|--------|-------|------------|
| size class         | Percentages of the total biomass | | | | |
| ZONE 1:            |           |         |        |       |            |
| > 25 cm            | 75        | 73      | 43     | 29    | 19         |
| 15.1 - 25.0 cm     | 24        | 26      | 50     | 62    | 58         |
| < 15.0 cm          | 1         | 1       | 7      | 9     | 22         |
| tot. biomass       | 22.73     | 19.97   | 29.39  | 32.85 | 32.39      |
|                    |           |         |        |       |            |
| ZONE 2:            |           |         |        |       |            |
| > 25 cm            | 43        | 73      | 28     | 54    | 67         |
| 15.1 - 25.0 cm     | 48        | 24      | 62     | 43    | 17         |
| < 15.0 cm          | 8         | 3       | 10     | 3     | 16         |
| tot. biomass       | 7.74      | 5.76    | 27.69  | 27.76 | 3.95       |
|                    |           |         |        |       |            |
| No. samples        | 22        | 32      | 12     | 20    | 15         |

In general, there was a higher biomass of *O. niloticus* in areas of habitats closer to the vegetation (Zone 1 i.e within 20 m of the shoreline) than further away towards open water (Zone 2 i.e 20 to 70 m way from the shoreline) confirming patterns seen in Tables 5 and 6. In these patterns, *Vossia*, *Typha* and *Phragmites* had a higher biomass than what occurred in either *Eichhornia* or papyrus habitats. The *Vossia*, *Typha* and *Phragmites* dominated habitats in zone 1 were important in the biomass of the two smaller size classes.

**Seasonal patterns in abundance within habitats**
In zone 1 (the area nearest to the vegetation), the Nile tilapia between 15 and 25 cm showed significant seasonal patterns in biomass. Biomass in this size range was highest during the short rainy season (September - October) for the entire shallow area as a whole. A similar pattern was shown by fish density irrespective of size in areas further away from the vegetation (i.e zone 2). The smallest fishes less than 15 cm increased in biomass in areas further away from the vegetation (Zone 2) after June i.e over the short dry period (July - September) into the short wet season (September - October).
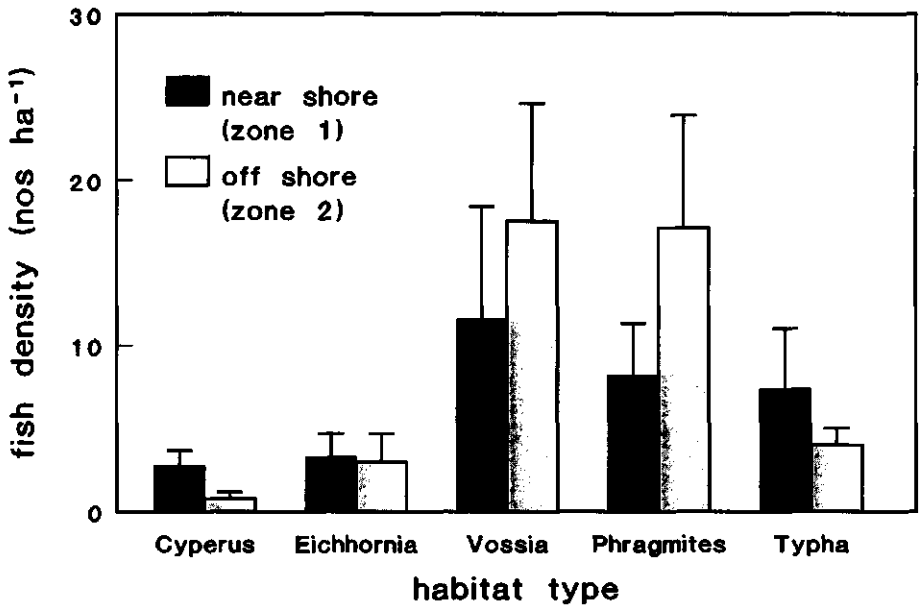
Fig. 4.    Nile tilapia density (no. ind. ha⁻¹) patterns during the short dry cool (July-September 15) season.

Data were inadequate to give an impression of the full range of seasonal variations. However, size class abundance patterns among and within habitats (Fig. 4) showed significant distance differences in numerical abundance of the Nile tilapia during the short dry cool season (July - September). *C. papyrus* and *Typha*-dominated habitats had more fish nearer to the vegetation (zone 1) than offshore (zone 2) in this period, while *Vossia* or *Phragmites* in the same period had more fish in zone 2. In the same period, *Eichhornia* habitats did not show significant effects on fish abundance according to distance from the edge of vegetation.

## DISCUSSION

The biomass of *O. niloticus* in the shallow water region averaged $25.0 \pm 2.4$ kg.ha⁻¹ (Table 2) and the mean total biomass of the species varied two-fold among individual habitats (15.3 - 32.5 kg.ha⁻¹, Fig. 1). The observed patterns support the alternative hypothesis that the abundance of the Nile tilapia varies with the type of habitat at the shore. Across the different habitats, the biomass of the species made up 45-60% of the total biomass of all fish. Therefore, in addition to its dominance, the results also suggest that vegetated littoral habitats may be important in the ecology of *O. niloticus*. In addition, the results confirm observations on the previously assumed importance of the shallow areas of lakes for the tilapias in general (Lowe-McConnell, 1958, 1971; Fryer and Iles, 1972; Kudhongania and Cordone, 1974). The patterns of distribution and abundance of *O. niloticus* in the

study area probably extend to other parts of Lake Victoria where vegetation type is the main habitat characteristic. These patterns are consistent with observations made on the distribution of the species in Lake George (Burgis *et al.* 1973) and with what has been observed for some fishes in other lakes irrespective of climatic zone (e.g Hall and Werner, 1977; Pierce *et al.*, 1994; Rossier *et al.*, 1996). However, apart from vegetation and depth, distance from the shore and seasonality within climatic zones could also play significant roles in the structuring of fish populations. Seasonality for example may be coupled to temperature and basin factors through hydrological regimes.

While the biomass and abundance of the Nile tilapia were strongly influenced by vegetation (habitat) type, patterns within the species varied with season (Fig. 3), and with distance from the edge of the vegetation (Tables 4 and 5) according to size (age) categories. The presence of large numbers of juvenile fish and their size frequency distribution off sandy areas (Table 1), and relatively higher densities in *Vossia* and *Phragmites*-dominated habitats indicates the importance of habitat type for small ( < 15 cm) and juvenile fish. Together with *Typha*, the three habitat types were similar in physico-chemical features such as depth and slope profiles, silica content and macrofauna characteristics (Chapter 3). These conditions may be favourable to the young stages of the species, in particular the diurnally varying physico-chemical conditions (temperature) along the beaches observed by (Welcomme, 1964). In that study, it was shown that predatory fish were kept away from the high temperatures which the young tilapia tolerate better. In addition, the sandy substrate in shallow water characteristic of these habitats may also serve to increase visibility and facilitate escape responses in young tilapia. Apart from such physical conditions in these habitats, high densities of macrofauna observed in these habitats (Chapter 3) may be an additional benefit to the small fishes. The relatively low immature fish densities observed in these habitats in the main experimental set-up may be due to inadequate sampling (e.g. sampling when the fishes were not active), as shown by the appearance of juvenile fish only between 0900 and 1300 h in contrast to the overnight fishing and, to the use of big meshes. Therefore, the size structure of juvenile fishes (Table 1) and the reciprocal relationship between numerical density and biomass (Fig. 1 and Fig. 2) indicate that habitat use by *O. niloticus* depends on life history stage and differs for different size classes, a phenomenon also observed in reservoirs (Pet and Piet, 1993). The skewed sex ratio in some of the habitats and presence of large female fish (cf. Tables 3 and 4) also point to differential habitat occupancy which may point to segregation of the sexes soon after fertilisation in the female (Lowe-McConnell, 1958). The presence of large fish in *Cyperus* and *Eichhornia*-dominated habitats may also be explained by the observation that Nile tilapia move into deeper water further offshore as they grow (Lowe-McConnell, 1958, Welcomme, 1964). The two deeper habitat types (Chapter 3) probably represent transitional depths before the lateral movements further away from the shallow shoreline. The shallow littoral zone in the study area could therefore be considered as a mosaic landscape as defined by Chick and McIvor (1994) comprising of microhabitats for which *O. niloticus*, although a stocked species, is well adapted. The fact that Nile tilapia

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have been found in other areas such as deep parts and at rocky shores (Witte *et al.* 1995; Seehausen, 1996) shows that there are other micro-habitats in the lake and that Nile tilapia is well adapts to varied temporal and spatial conditions.

In comparison to numerical density, fish biomass in papyrus and *Eichhornia*-dominated habitats was considerably high and was made up of large fish. But *Eichhornia* had about twice the density and biomass of fish that occurred in *C. papyrus*-dominated habitats. Such a pattern sheds more light on differential use of shoreline habitats according to size (age) class of fish, but leaves questions regarding habitat structural differences between these two habitats, and their influence on the Nile tilapia. In Chapter 3, it was shown that these two habitats are primarely fringed by *C. papyrus* as the dominant vegetation at the shore, and that *Eichhornia* is a recent feature whose presence was used to distinguish between the two habitat types. The investigated *Eichhornia*-infested (often more than 20 m in width) habitats were further distinguished from pure papyrus habitats by exposure to on-shore winds, and depth among other factors. There are thus two types of papyrus shores in the study area: the *Eichhornia*-free *C. papyrus* fringe and the wind-exposed *Eichhornia*-infested papyrus fringe. Comparative information on the influence of *Eichhornia* on fish populations of the otherwise wind-exposed, previously *Eichhornia* free habitats is lacking (in this study, fishing experiments were conducted from the edge rather than within *Eichhornia* mats). Although a major structural difference between the two papyrus shores appears to be related to wind exposure (fetch), the present results do not provide a clear picture of what the pattern would have been closer to the shore in absence of *Eichhornia* in the infested *C. papyrus* habitats. However, it may be inferred from results of electro-fishing (Willoughby *et al.* 1992) that physical obstruction and extreme physico-chemical conditions (e.g. low dissolved oxygen, plant debris under the mats) are unlikely to support many fish other than those which can utilise atmospheric oxygen (e.g. *Protopterus aethiopicus* which was in fact common in *Eichhornia*-dominated habitats, see Chapter 4). The biomass recorded from *Eichhornia*-infested habitats during this study is therefore probably less than it would be under different conditions. Furthermore, the very edge of mats provide other biotic and abiotic conditions (water quality and invertebrates) atypical of pure *C. papyrus*-fringed habitats (Chapter 3). These relatively hyacinth-free papyrus-dominated habitats had a comparatively low numerical fish density and biomass. This may be the type of papyrus habitat referred to in Lakes Edward and George by Lowe-McConnell (1957, 1958) and, in Lake Victoria by Beadle (1974) as not supporting large populations of *O. niloticus*. Being less exposed to the strong on-shore winds, this type of habitat is characteristic of bays and other indentations in the shoreline which are associated with a different kind of along-shore diurnally changing winds (Welcomme, 1966a). A combination of the two wind patterns seem to be responsible for the wind-blown accumulation of extensive hyacinth mats in the more protected gulfs, bays and indentations which are characteristic of areas sheltered from strong on-shore winds in the lake (Twongo and Balirwa, 1996).

Coupled to the influence of the type of dominant vegetation at shore, the diversity of habitats in the littoral zone of Lake Victoria which is also related to differences in physico-chemical factors (Chapter 3), it appears that distribution in the Nile tilapia is both wide and dynamic. The species seems to shift habitat with size (age), time of day and season. For example, size specific shifts are probably related to shelter for young fishes but their appearance on sandy beaches could be due to seeking for food and predator avoidance. Seasonal shifts among adults could be influenced by inflows from the catchment during rain seasons but may also be related to seeking suitable spawning substrate. Carter (1955) associated the increase in catch by fishermen to what he called "foul water from the swamps which drives fish further away from the shore". Depending on the width, biomass and density of the macrophytes on one hand, and the intensity of the rains on the other, the timing of the rain and the duration that run off takes to penetrate the swamp barriers determines when fish are driven away from the very edges of the vegetation. In rivers and small water bodies with a small drainage, this takes a short time. As was shown in Fig. 3, there appears to be a lag phase between the onset of the main rain season (March - June) and the maximum in biomass which occurs later (September - October). This could indicate a prolonged activity of fish during and after reproduction but both adult and juvenile Nile tilapia have also been at rocky shores (Seehausen, 1996) and in deeper water far away from vegetation (pers. obs).

On the basis of the patterns shown by the Nile tilapia in the study area, four general trends seem to govern the dynamic use of the littoral zone. They are:

1)  The *Vossia-Typha-Phragmites* and sandy habitats are the richest in terms of total numbers, number of immature fishes and they have a higher male : female ratio. The habitats also provide physico-chemical conditions (temperature and firm substrate) which are suitable for the protection of young stages of the Nile tilapia.

2)  The exposed originally *C. papyrus* but presently *Eichhornia* infested type of habitat has the highest biomass made up of mostly large fish. Being deeper, the two seem to be the transition habitats as the Nile tilapia progressively moves further offshore as it grows.

3)  The relatively hyacinth-free (sheltered from on-shore wind) papyrus habitats support low fish abundance (numbers and biomass), are prone to hyacinth invasion particularly in bays, and are probably utilised on a shorter-term scale than could be discerned from the results.

4)  The utilisation of littoral zone habitats by the Nile tilapia varies according to size (age) of fish and season, but these patterns are superimposed on diurnally varying activity.

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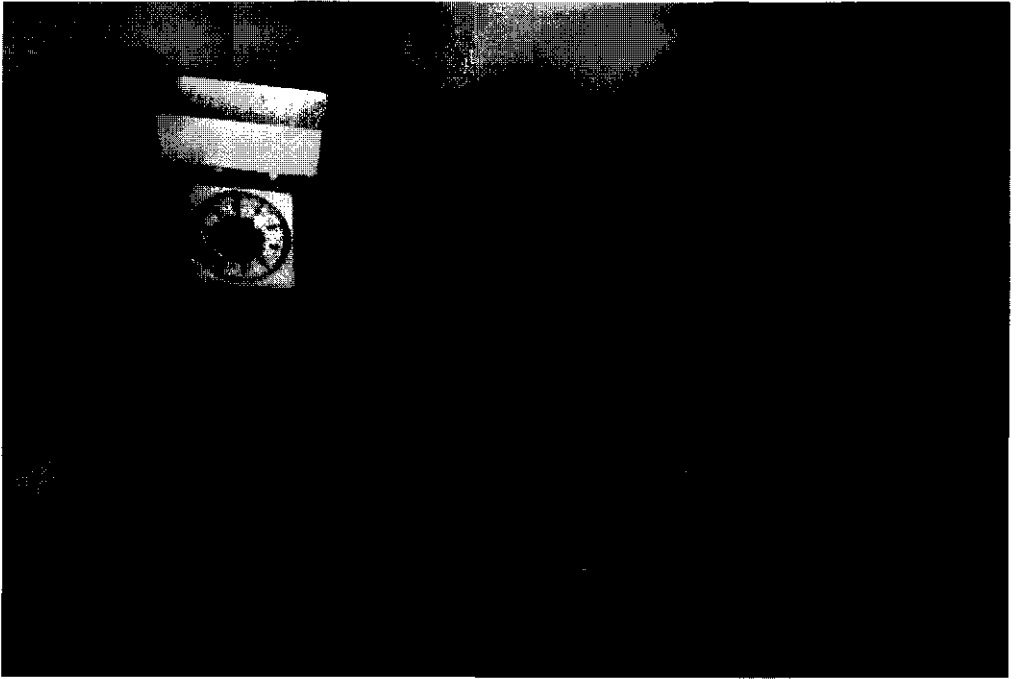
# Chapter 6

# Reproductive biology of the Nile tilapia, *Oreochromis niloticus* LINNÉ in some East African lakes with emphasis on littoral habitats in northern Lake Victoria (Uganda)[*]

## ABSTRACT

Size at first maturity, sex ratio, fecundity, gonadal somatic indices, condition and patterns of seasonal gonadal development were studied in the Nile tilapia (*Oreochromis niloticus*) from littoral habitats in Lakes Victoria, Albert, and Kyoga in East Africa between 1989 and 1996. Substantial inter-lake variation in size at first maturity, fecundity and sex ratio were observed. The 50 % size at first maturity in pooled samples of Lake Victoria fish was 18 cm and 24 cm for males and females respectively. In Lake Kyoga it was 23 cm and 26 cm. These sizes appeared to be influenced by habitat type in Lake Victoria fish but were still different from sizes (30 cm and 32 cm for males and females respectively) at first spawning. A 1:1 sex ratio was approached in the general littoral zone population of Lake Victoria Nile tilapia but the ratio varied according to habitat and with season. *Cyperus papyrus* and *Eichhornia crassipes*-dominated habitats had a higher proportion of males most of the year but females were more abundant in other types of vegetated littorals. Absolute fecundity varied widely (602 - 4818 ± 1262 ripe eggs. female[-1]) within lakes, according to season and size classes but followed the relationship: Abs fec. = $0.92TL^{2.25}$. However, no significant ($p > 0.05$) seasonal differences in fecundity could be detected. Both Lake Victoria and Kyoga fish had a significantly higher ($p < 0.05$) mean absolute fecundity (number of ripe eggs.female[-1] irrespective of size class) than Lake Albert fish ($3723 \pm 147$, $3277 \pm 244$ and $1992 \pm 233$ eggs.female[-1], respectively). These patterns were paralleled by significant differences in fish condition among lakes and may be due to genetic and dietary differences. The gonadal somatic index in Lake Victoria fish reached a peak in April and declined up to October suggesting two maxima in continuous breeding. This pattern indicated that peak spawning probably occurs sometime after the onset of the main rain seasons, which was confirmed by a similar pattern in gonad states of mature and spent fishes. A major environmental factor influencing peak reproduction in the Nile tilapia appeared to be the cyclic bi-annual increase in the water level, and its physical and biological effects in the littoral habitats.

## INTRODUCTION

Knowledge of the reproductive biology of fishes is essential in prediction of population stability and fluctuations (Ricker, 1971) and may therefore be used in fisheries management such as application of closed fishing grounds or seasons. For fishes like *Oreochromis niloticus* LINNÉ (the Nile tilapia) in Lake Victoria, this knowledge is particularly relevant because of the species' dependency on specific littoral habitats according to size class and season (Chapter 4 and 5). The same knowledge in combination with other measures, could be applied to water quality management such as through biomanipulation of target species (e.g. van Donk and Gulati, 1989; Gulati *et al.*, 1990; Hosper, 1997). Aspects of reproduction have been investigated in the Nile tilapia in East African lakes in the past (Lowe-McConnell, 1955, 1958) partly because of the species ecological dominance and commercial importance. Recent data are generally lacking, however. Reproduction in the species has also been investigated following species transfers (stockings)

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[*]This chapter is based on a manuscript by J.S. Balirwa.

and environmental changes (lake level rise) such as in Lake Victoria (Welcomme, 1964, 1966) or lake level decline such as in Lake Turkana (Stewart, 1988; Kolding, 1993). In the case of Lake Victoria, these studies were conducted before the Nile tilapia had firmly established itself in the lake and before the subtle changes in the lake's wetland landscape had manifested (Chapter 2 and 3). Reproduction in the Nile tilapia is also of interest because of the widespread use of the species in aquaculture (Fineman-Kalio, 1988) and its dominance in shallow littoral habitats (Chapter 5). For these reasons, studying the reproductive biology of the Nile tilapia is valuable in assessing the effects of environmental impacts on aquatic organisms and of the response and effects of introduced fish in new environments.

Environmental factors such as temperature, dissolved oxygen, pH, water level, salinity, food resources and trophic status of a water body are known to influence maturation, egg production and spawning success in fish (e.g. Lowe-MConnell, 1958, 1975; Fryer and Iles, 1972; Fineman-Kalio, 1988; Stewart, 1988; Hartman and Quosso, 1993; Kolding, 1993). These factors in addition to size- specific mortality (Kolding, 1993) which may also include predation and fishing, could explain many aspects of tilapia dynamics. The success of the Nile tilapia in the new environments has been attributed to various other factors. These include hybridization with endemic species (Welcomme, 1964, 1967; Moreau *et al.* 1988), competitive advantage for spawning grounds (Welcomme, 1967; Fryer and Iles, 1972; Lowe-McConnell, 1975; Ogutu-Ohwayo and Hecky, 1991), wide habitat tolerance (Twongo, 1992) and higher fecundity than endemic tilapiines (Lungayia, 1994). In as far as reproduction is concerned, these studies were either undertaken before the Nile tilapia had become fully established in the new habitats or were limited by inadequate sampling across habitats and seasons. Additionally, previous work such as by Welcomme (1964a, b, 1966) was concerned with the young stages of the species and their habitat preferences following climatic changes in the lake basin, but before other environmental changes associated with species extinction (Witte *et al.* 1992, 1995), eutrophication (Hecky, 1993), changes in the shoreline landscape (Balirwa, 1995) and the phenomenal increase in fish production of the Nile tilapia (Kudhongania *et al.* 1992). We have to conclude that the little available information on the reproductive biology of the Nile tilapia particularly in Lake Victoria may not fully describe the present patterns. This study therefore investigated the size at first maturity, sex ratio, fecundity, condition factor and the seasonal cycle of gonadal development in the Nile tilapia from inshore habitats of northern Lake Victoria. The same habitats were investigated for climatic patterns (seasonality), structural (macrophytes) and physico-chemical (e.g. nutrients, pH, temperature, conductivity) features and seasonal patterns in use of shoreline habitats by the Nile tilapia (Chapter 3 and 5). Additional data on fecundity in *O. niloticus* were collected from Lakes Albert and Kyoga during an earlier phase of study between 1989 and 1991.

## MATERIALS AND METHODS

### *Oreochromis niloticus*

*O. niloticus* is a mouth-brooding cichlid of the tilapiine group of fin fishes. It is widely distributed in many parts of the world either naturally or introduced (Lowe-McConnell, 1958; Trewavas, 1983). The species together with other tilapiines (*O. leucostictus, T. zillii* and *T. rendalli*) all of which occur in parts of the Great Lakes of Africa were introduced into Lakes Victoria and Kyoga (Fig. 1) during the 1950's and 1960's (Welcomme, 1964, 1966, 1981; Lowe-McConnell, 1975, Balirwa, 1992).
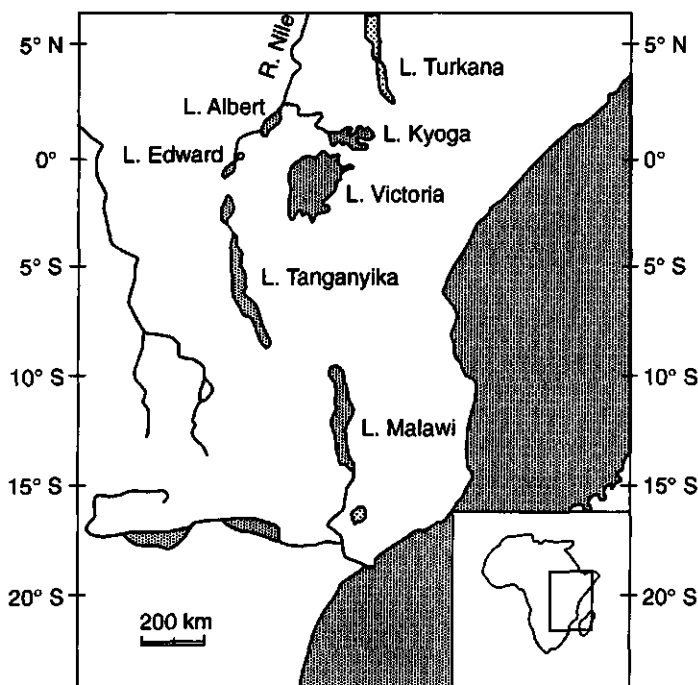


Fig. 1.       The area of the Great Lakes of Africa including the study lakes: Victoria, Albert and Kyoga.

The principal source for the Nile tilapia stockings was Lake Albert but in general, several sources of seed and mixtures of tilapias were involved in these stockings (Welcomme, 1981; Trewavas, 1983). In both Lakes Victoria and Kyoga, *O. niloticus* is firmly established. In these new habitats, it is associated with the other stocked species and, among the endemic tilapiines, with *O. esculentus* and *O. variabilis* but little is known about aspects of its reproductive biology. The species has replaced the native once commercially important tilapiines (*O. esculentus* and *O. variabilis*) which were overfished from inshore habitats (Beauchamp, 1956; Mann, 1969; Fryer and Iles, 1972).

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**Habitats and sample collection**
The investigations were carried out in Lakes Victoria, Albert and Kyoga (Fig. 1). In Lake Victoria where more systematic sampling was conducted, specimens were collected from vegetated littoral habitats and other shallow areas by gill nets and trawls as described in Chapter 4 and 5. The littoral habitats sampled by gill nets were in shallow water (0.5 - 2.0 m deep) and, were fringed by wetland vegetation dominated by stretches of *Cyperus papyrus* L.(papyrus), *Phragmites mauritianus* Kunth (reeds), *Typha domingensis* Pers. (cattail), *Vossia cuspidata* (Roxb.) Griff. (hippo grass) and *Eichhornia crassipes* (Mart.) Solms-Laub. (water hyacinth). Below, generic names are used to refer to these plant species or the habitats they were associated with. These vegetation-dominated habitats showed significant seasonal and horizontal (spatial) differentiation especially with respect to nutrients and phytoplankton and could be distinguished from those about 400 - 500 m off the vegetation fringes (Chapter 3). These other littoral habitats further offshore were 2.5 m to 4.0 m deep and were sampled by trawls. In Lakes Albert and Kyoga, Nile tilapia specimens were collected from similar habitats at boat landings from fishermen operating gill nets and beach seines in inshore areas which were no more than 4 m deep. It was considered that habitats within 500 m of the vegetation fringe comprised the littoral zone and experience the most direct seasonal climatic influences described in Chapter 3.

**Analyses**
Following collection, the total length to the nearest cm and weight to the nearest g of each specimen were recorded. The abdominal cavity was cut open, and sex and stages of gonad development were determined. The main aspects examined are described below.

Gonad states
The state of maturity (gonad state) was assessed according to the classification in Ricker (1971) which was modified to apply to Nile tilapia's approximate similarity to that scheme. The following maturity states were recognized:

*Stages I and II: Immature (Inactive)*. Young individuals mostly less than 15 cm in total length which may not have yet engaged in reproduction (cf. Chapter 4 and 5); gonads are of very small size and ribbon-like. Eggs are not distinguishable to the naked eye. In males, gonads are thinner and more elongate in comparison to the flat-shaped and more stout female gonads. Stage III and above were as much as possible determined according to the size categories identified in Chapter 5.

*Stage III: Mature (Ripening; inactive-active)*. Eggs are distinguishable to the naked eye as early scattered dots in the ovary; testes appear as longish pale rose ribbons; a very rapid increase in gonad weight and size is apparent from a large sample of individuals in this stage. This also represents the size attained at first maturity.

*Stage IV: Maturity and Recycling females (active ripe)*. Sexual products appear ripe but are not extruded when pressure by index finger is applied on the belly. Eggs are orange-reddish and clearly visible but smaller oocytes in various stages of development are also characteristic. In some females, mature eggs appear to be disintegrating within the ovary, a stage referred to as recycling; no equivalent situation is observed in the males. Testes are a cream colour with distinct blood vessels along the ribbons.

*Stage V: (Ripe)*. Sexual products are extruded in response to light pressure on the belly; ovaries fill most of the ventral visceral cavity; majority of eggs are round and yellow to orange. Testes are white and appear heavy with milt.

*Stage VI: Spawning (ripe-running)*. Sexual products are extruded more or less involuntarily with the slightest pressure on the belly; milt oozes freely.

*Stage VII: Spent condition*. Sexual products have been discharged; female gonads have the appearance of deflated purplish sacs and may contain a few left over eggs. Some individuals may have eggs in their buccal cavities (mouth-brooding state); males rarely show an easily recognisable spent condition.

## Size at first maturity, first spawning and sex ratio

Stage III was used to determine the size at first maturity according to Beverton and Holt (1957). By plotting percentage maturity against length, the length at which 50 % of the individuals (in sequential size classes) between 10 cm and 40 cm first exhibit maturity was determined for male and female fish from Lakes Victoria and Kyoga. In order to compare size at first maturity with literature data, the smallest sizes of mature fishes from different lakes according to habitat type was noted.

The size at first spawning for Lake Victoria fish was determined from specimens which were in the first phase of stage V or VI. Such specimens were distinguished from those which had passed through the first spawning by a distinct absence of broken-down oocytes typical of recycling females. Sex ratio was determined from specimens of at least 25 cm total length. In Lake Victoria, sex ratio was investigated separately for different vegetated habitats as well as for the general population. Sex distribution according to habitat and season was based on specimens in stage IV (active ripe fish) and above.

## Fecundity

Examination of mature female *O. niloticus* revealed that from stage IV onwards, specimens contained a high but variable frequency of small developing oocytes in comparison to the ripe ones. Usually there were at least three groups of small oocytes in different stages of development but these could easily be distinguished by eye from the mixture of oocytes. Therefore, only mature oocytes from gonads of ripe females (stages V and VI) were used in fecundity estimates.

Following determination of development stage, gonads of ripe females were carefully dissected out from individual fish and preserved in 5 % formalin solution for at least three weeks before further examination. After this period, the two gonads from individual specimens were soaked in water for about 1 h, mopped dry with blotting paper, separated and weighed. Sections of known weight from each gonad were teased to separate the eggs. Counts of eggs in each individual sample weight of gonad were made using a hand tally. The number and weight of ripe eggs obtained from each section of the gonad was used as a proportion of the total number of eggs in each part of the gonad and the total number of ripe eggs (absolute fecundity) was obtained from the sum of eggs in each gonad as in Ricker (1971). Relative fecundity per gram weight or length of fish was based on fresh weight and length. The number of eggs in mouth brooding females were counted in the few cases encountered. Regression analyses were carried out to find the relationship between fecundity and fish length and weight. The Gonadal Somatic Index (GSI) was calculated for females as:

$$GSI = \frac{Weight\ of\ ovaries}{weight\ of\ fish\ -\ weight\ of\ ovaries} X100$$

Breeding cycle
Gillnet data were pooled with trawl information to assess the percent frequency of breeding (maturity states V and VI) and spent (state VII) male and female individuals in each month. The percentages were then transformed and used as $Log_{10}(X+1)$. The mean condition factors (also known as Fulton's coefficient of condition, K) for the ready to spawn fishes in different seasons for the different stocks were calculated from the formula $K = W/L^3$, W = fresh weight (g), and L = total length (cm) as in Ricker (1971).

**Environmental data**
Meteorological information (rainfall and temperature) covering the period 1970-1994 was obtained from the central meteorological office in Kampala. Mean monthly data for the Jinja station were used to relate seasonal gonadal development to climatic (rainfall and temperature) influences. The seasons were based on the climatic regime in the northern part of Lake Victoria. Four characteristic seasonal patterns were recognized: December - March (dry season), March - June (main wet season), July - September (short dry season), September - November (short wet season). These seasons are influenced by seasonal fluctuations in rainfall and evaporation. Hence, the lake level shows two peaks - a maximum lake level between May and June, and a secondary peak about December following the two periods with more rain in the year. Surface water temperatures of Lake Victoria are lowest (24-26°C) during July and August/September (Chapter 3) which also corresponds to the period of strong winds.

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Data analyses on fecundity, condition, GSI, and comparisons among lakes were analyzed by regression and ANOVA ($p < 0.05$) after checking for homogeneity of variances and possible transformations. A Bonferroni corrected (experimentwise error rate) significance level of 0.05 was maintained in all comparisons. In cases where ANOVA requirements were not met (maturation size, sex differences), ratios and percentages were used to discern possible differences.

## RESULTS

### Size at first maturity

*Vossia, Typha* and *Phragmites* dominated habitats were associated with the smallest male and female mature Nile tilapia but fishes from the more open littoral habitats of all lakes were larger.

Fishes from *Eichhornia* and *Cyperus* dominated habitats were of intermediate sizes (Table 1).

Table 1.  The ranges of the smallest sizes of mature fish from the various habitats associated with dominant vegetation and other littoral areas in Lakes Victoria, Albert and Kyoga.

|  | depth (m) | size (cm) of smallest ripe male | size (cm) of smallest ripe female |
|---|---|---|---|
| Lake Victoria | 2.5 - 4.0 | 17.5 | 21.0 |
| *Cyperus* | 0.5 - 2.0 | 10.3 | 21 |
| *Eichhornia* | 0.5 - 2.0 | 10.5 | 17.3 |
| *Vossia* | 0.5 - 2.0 | 11.1 | 12.1 |
| *Typha* | 0.5 - 2.0 | 9.4 | 12.2 |
| *Phragmites* | 0.5 - 2.0 | 11.6 | 9.4 |
| Lake Albert | 2.5 - 4.0 | 19.6 | 20.0 |
| Lake Kyoga | 2.5 - 4.0 | 18.5 | 20.8 |

### Size at first maturity in Lakes Victoria, Kyoga and Albert

The length at which 50 % of the fish first exhibited maturity varied across lakes. In Lake Victoria, it was 18 cm and 24 cm in male and female fish respectively (Fig. 2a and 2b).

100 % maturity is achieved at about 30 cm and 32 cm in male and female fish respectively data which corresponded to data on the size of fish at first spawning (Fig. 3a and 3b).
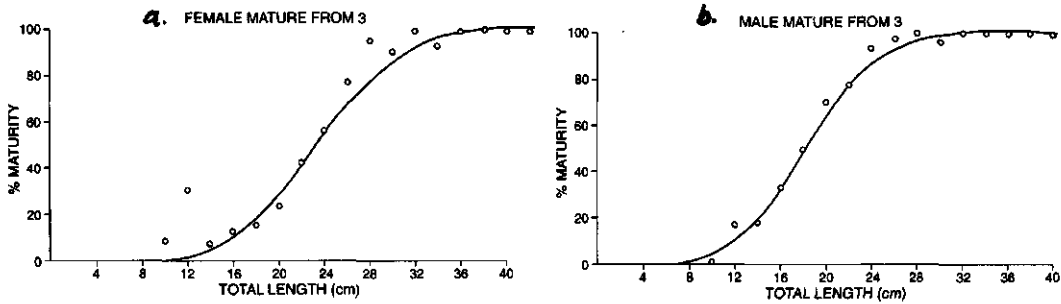
Fig. 2.    Size at first maturity in female (a) and male (b) *O. niloticus* (pooled from all sampled habitats) in Lake Victoria.
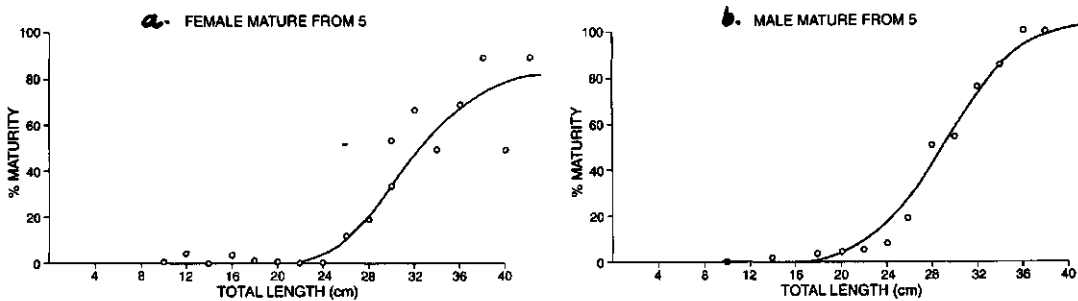


Fig. 3.    Size at first spawning in female (a) and male (b) *O. niloticus* (pooled from all sampled habitats) in Lake Victoria.

In Lake Kyoga, size at first maturity (not shown) was about 23 cm and 26 cm for male and female fish respectively. In the less sampled Lake Albert, maturation size was estimated at 20 cm and 23 cm in male and female fish respectively.

**Sex ratio in Lake Victoria Nile tilapia**
From pooled catches irrespective of habitat type and time of year (sample size = 997 specimens), a sex ratio of 1:1 was found for fish above 25 cm in total length (Appendix 1). The sex ratio varied according to habitat (Fig. 4) and showed various patterns and apparent differential use of habitats by males and females according to season.
The greatest variation from the 1:1 ratio was pronounced in the *Vossia*, *Typha* and *Phragmites* dominated habitats. A close examination of maturation sizes in vegetated habitats (Table 1) shows that male dominated habitats were characterized by larger sizes of maturation. In *C. papyrus* and *Eichhornia* dominated habitats, there were more males through most of the year while *Vossia*, *Typha* and *Phragmites* dominated habitats tended to have more females. In all the littorals, the short dry but cool season (July - September) had a higher proportion of male fish.
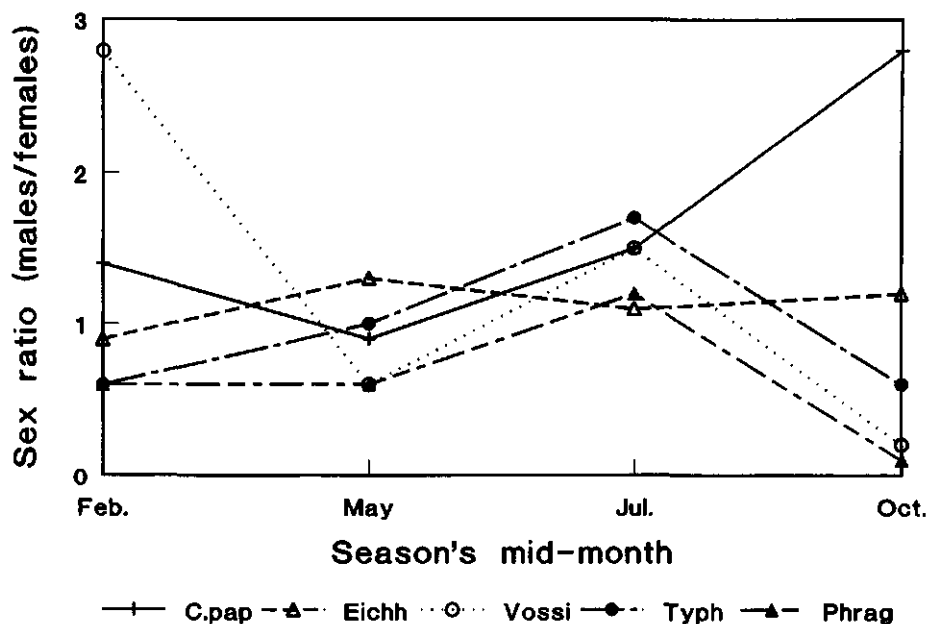
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Fig. 4.    Sex ratios in the Nile tilapia (>25 cm TL) of Lake Victoria according
to vegetation dominated habitat type (a = *Cyperus*, b = *Eichhornia*,
c = *Vossia*, d = *Typha*, d = *Phragmites*) and season (indicated by
mid month: Feb = long dry season; May = long rainy season; July
= short dry cool season; Oct. = short rainy season).

## Fecundity in Lakes Victoria, Albert and Kyoga
Absolute fecundity was positively correlated with size (Table 2).

Table 2.    Fitted regression parameters (a = slope, b = exponent) describing the
relationship between absolute fecundity and size according to the
expression AbsFec. = $aX^b$ where AbsFec = absolute fecundity, X =
weight (g), (mean ± SE) for the three investigated lakes.

|  | a | b | F | $r^2$ | df | p |
|---|---|---|---|---|---|---|
| All lakes | 21.8 ± 8.8 | 0.71 ± 0.06 | 896 | 0.53 | 159 | <0.001 |
| Lake Victoria | 27.8 ± 14.9 | 0.68 ± 0.07 | 626 | 0.53 | 112 | <0.001 |
| Lake Albert | 2.5 ± 2.8 | 1.02 ± 0.16 | 104 | 0.61 | 20 | <0.001 |
| Lake Kyoga | 40 ± 40.6 | 0.63 ± 0.14 | 173 | 0.47 | 23 | <0.001 |

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As fecundity was determined in ready to spawn fishes, regressions were made without a forced zero intercept. No significant differences ($p > 0.05$) were observed between linear and non-linear curves (F-tests of differences in residuals, Vermaat and Hootsmans, 1994) with respect to the best fit, and curves of different lakes were not significantly different ($p > 0.31$). Following literature convention (Ricker, 1971), a general non-linear curve showing the relationship between absolute fecundity and size (total length cm) of pooled data on all ripe female fish from the three lakes is given in Figure 5.
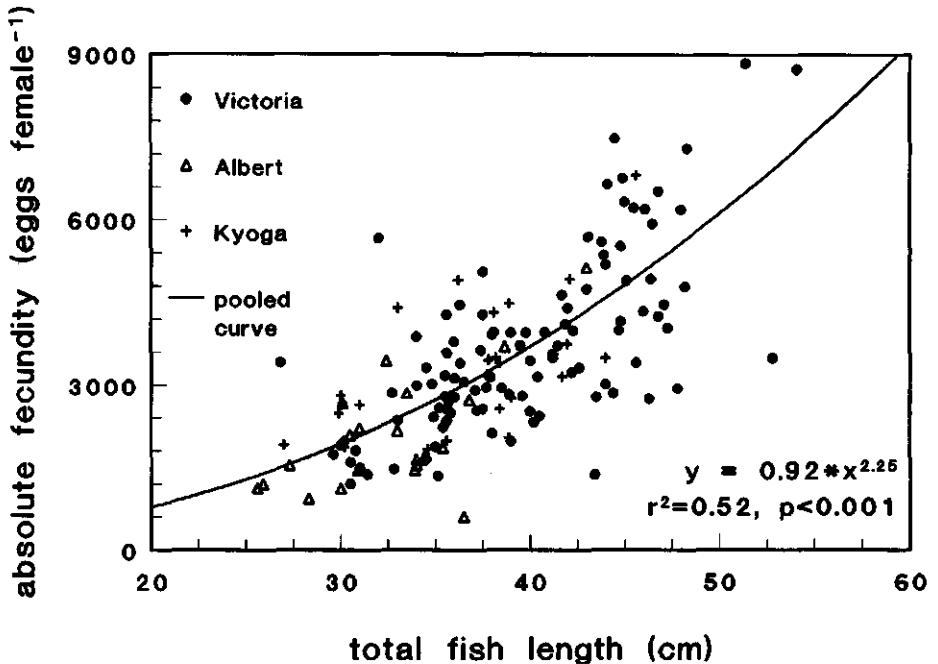


$$y = 0.92 * x^{2.25}$$
$$r^2 = 0.52, \quad p < 0.001$$

Fig. 5. The relationship between absolute fecundity (number of ripe eggs.female$^{-1}$) in the Nile tilapia and its total length (cm).

Appendix 2 gives various parameters associated with reproduction in the Nile tilapia from the three lakes. A remarkable contrast was observed between weight- and length-specific absolute fecundity. Generally, smaller fish (25 - 35 cm) had fewer eggs but seemed to be more fecund when weight (Abs fec.g$^{-1}$) was considered. Apparently weight-specific fecundity (Abs fec.g$^{-1}$) was more conservative than fecundity per length, indicating that plasticity in fecundity was more length-dependent over the life cycle (also see Table 4 below: Abs fec.g$^{-1}$).

Significant differences ($p < 0.05$) in absolute fecundity, fecundity per length and condition (K) among lakes were observed. Seasonal variation was only significant in the condition index (K), and explained as much of the variance as did differences between lakes. No significant seasonal differences in fecundity ($p > 0.38$) or GSI ($p > 0.18$) were detected (Table 3).

Table 3.    Two-way ANOVA for assessing the significance of different factors
(Lakes: Victoria, Albert and Kyoga, with February, May, July and
October as midpoints; and interaction for lake and season) on
fecundity (mean total numbers, fecundity per gram weight and
fecundity per cm length; GSI as Gonado-somatic index and K as
condition factor) in ripe female fishes (levels of significance = p, SS
= sum of squares, % SS = factor SS /explained * 100, a measure
of variation explained by that factor; a significant factor =  p <
0.05).

|  | lake | | season | | interaction | |
| --- | --- | --- | --- | --- | --- | --- |
|  | p | % SS | p | % SS | p | % SS |
| TL(g) | 0.000* | 81 | 0.794ns | - | 0.677ns | - |
| AbsFec. | 0.013* | 60 | 0.694ns | - | 0.984ns | - |
| Fec.g-1 | 0.471ns | - | 0.387ns | - | 0.424ns | - |
| Fec.cm-1 | 0.016* | 78 | 0.661ns | - | 0.980ns | - |
| GSI | 0.232ns | - | 0.180ns | - | 0.538ns | - |
| K | 0.012* | 44 | 0.037* | 44 | 0.669ns | - |

* = significant, ns = not significant

Analysis of pooled fecundity according to size and condition of fish across lakes
(Table 4) showed that the two were significantly higher in both Lakes Victoria and
Kyoga fish. Lake Victoria fish had the highest absolute fecundity ($3732 \pm 147$ ripe
eggs. female$^{-1}$) (Lake Kyoga, $3277 \pm 244$ ripe eggs. female$^{-1}$) in comparison to fish
from Lake Albert ($1992 \pm 233$ ripe eggs. female$^{-1}$). Despite the larger specimens and
therefore higher fecundity in Lake Victoria fish, there was still a significant
difference ($p < 0.05$) in the absolute fecundity of fish of comparable size (Table 4)
between Lakes Kyoga and Albert. The same pattern was evident for fecundity per
unit length. Fecundity per gram showed no significant differences among lakes.

Apart from significant differences in fish condition among lakes (Table 4), the
condition of ready to spawn fishes (i.e of size at first spawning and above as in Fig.
3) of comparable lengths varied according to season (Table 5).

Lake Victoria and Kyoga fish had a better condition than Lake Albert fish of
comparable length during the long dry season (December to March). The condition
of the fishes in all lakes was generally lower from June to November. The gonadal
somatic index (GSI) of ripe female fish was not correlated with season and no
significant differences in GSI were found across lakes (Table 4). However, when
all ovarian products were used to infer breeding periods in Lake Victoria fish, the
monthly GSI showed monthly trends (Fig. 6) which appeared to correspond to
seasonal patterns. The GSI was at maximum soon after the beginning of the main
rainy season (March 15 - June) after which it reduced to a minimum from the end

of June, through the short dry but cool season and increased again (from about October) after the start of the second rains (September 16 - November).

Table 4.    Mean ( ± SE) absolute fecundity (tot. no. ripe of eggs.female$^{-1}$, Fec.g-1, Fec.cm-1), fish length (TL, cm), fresh weight (WT, g) of *Oreochromis niloticus* in the three sampled lakes: Victoria, Albert and Kyoga. Replication was 114, 22 and 25 specimens respectively; lake means that share a common letter are not significantly different (modified LSD test maintaining an EER at 0.05); for calculation of condition factor (K) and GSI, see materials and methods.

| | Victoria | | | Albert | | | Kyoga | | | p |
|---|---|---|---|---|---|---|---|---|---|---|
| TL (cm) | 39.7 | ± | 0.5b | 32.8 | ± | 0.9a | 36.4 | ± | 1.1a | 0.000 |
| WT (g) | 1404 | ± | 565b | 713 | ± | 67a | 1087 | ± | 90a | 0.001 |
| AbsFec. | 3723 | ± | 147b | 1992 | ± | 233a | 3277 | ± | 244b | 0.000 |
| Fec.g$^{-1}$ | 2.9 | ± | 0.1a | 2.9 | ± | 0.2a | 3.2 | ± | 0.2a | 0.611 |
| Fec.cm$^{-1}$ | 91.4 | ± | 3.0b | 60 | ± | 5.8a | 89 | ± | 5.2b | 0.001 |
| GSI | 0.02 | ± | 0.00a | 0.02 | ± | 0.00a | 0.03 | ± | 0.01a | 0.169 |
| K | 2.12 | ± | 0.03b | 1.95 | ± | 0.07a | 2.15 | ± | 0.05ab | 0.027 |

Table 5.    The mean condition factors (K, see Table 4) in ready-to-spawn fishes from Lakes Victoria, Kyoga and Albert according to season (as in Table 2).

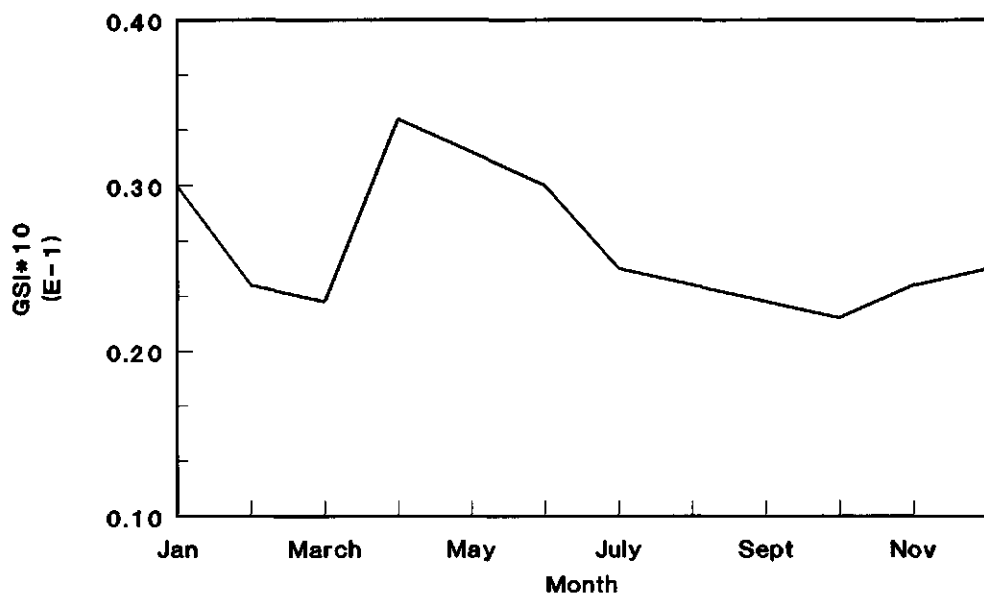| | Victoria | Kyoga | Albert |
|---|---|---|---|
| Dec. - Mar. | 2.20 | 2.27 | 2.10 |
| Mar. - June | 2.17 | 2.28 | 2.15 |
| July. - Sep. | 2.13 | 2.10 | 2.04 |
| Sep. - Nov. | 2.02 | 2.19 | 1.95 |
| n | 46 | 21 | 18 |
| size range (cm) | 30-40 | 30-40 | 30-40 |

Fig. 6.      Monthly changes in the gonado-somatic index (GSI) in female Nile
             tilapia (> 25 cm length) from Lake Victoria.

**Seasonal cycle of gonad development in Lake Victoria fish**
Considerable variation was discerned in the monthly pattern of ripeness in male and
female fish although breeding (as indicated by gonad states V and VI) continued
throughout the year (Fig. 7). The pattern shown by ripe fish during the rainy season
to the beginning of the short dry season (in April-July) corresponded to an increase
in spent fish.

The percentage of ripe male fish fell from 80 % in April (i.e. beginning of the rainy
season) to 40 % by June (Fig. 6). A similar but less systematic pattern was shown
by female ripe fish, and both male and female ripe fish had a secondary minimum
of ripe individuals after the second short rainy season (September 16 - November).
Two mouth-brooding specimens from Lake Victoria were encountered in November
during the preliminary phase of this study. They measured 39.0 and 42.5 cm TL
and, carried 1122 and 1105 eggs.brood[-1] respectively. An additional two mouth-
brooding fish were encountered in December and March during the main study. A
41.5 cm long (1500 g, designated Stage VII) fish had 474 eggs in the brood; the
specimen caught in March of 47.1 cm in length (2140 g, determined as stage IV -
 see M & M) had 264 eggs in the brood. From fecundity data (App. 2; Table 4) it
was apparent that not all ripe eggs were spawned at once, and neither were all
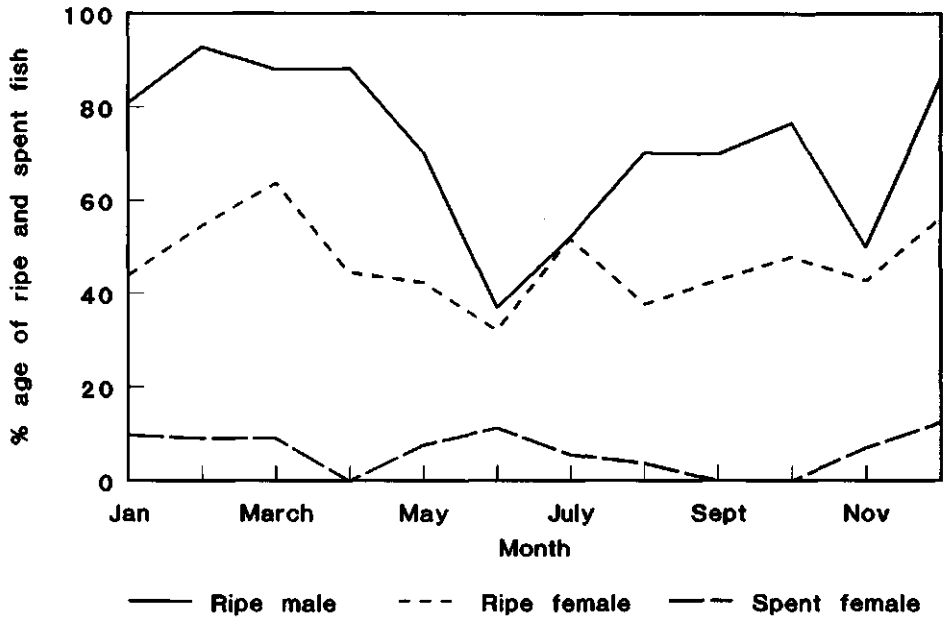spawned eggs taken up for mouth-brooding.

Fig. 7.    Monthly ripeness (Gonad states V and VI) and the spent condition
(Gonad state VII) in Lake Victoria fish.

## DISCUSSION

A survey of the literature on reproductive biology of *O. niloticus* reveals a less clear
understanding of the populations in Lakes Victoria and Kyoga where the species
was introduced, in comparison to the research effort on the species in other lakes
particularly Lake Turkana (e.g Lowe-McConnell, 1958; Stewart, 1988; Kolding,
1992, 1993) and other lakes where the species is endemic. Of all the tilapias
introduced into Lakes Victoria and Kyoga in the 1950s and 1960s, *O. niloticus* is
at present the most successful in terms of abundance and commercial importance
in the two lakes. In Lake Victoria, the species was the main tilapiine comprising not
less than 60 % of all tilapias, and at least 45 % of the total biomass of all fish in
littoral habitats between 1992 and 1996 (Chapter 4 and 5). Though strongly
represented in littoral habitats, Nile tilapia have a much wider distribution in Lake
Victoria. Both sub-adults and juveniles have frequently been encountered at rocky
shores (Seehausen, 1996), in deeper habitats in open water, and in rivers. The
species reproductive and survival strategies in the new habitats might therefore
either be similar or even superior to those in populations from Lakes Albert or
Turkana where the species is endemic. Though no recent figures are available, a
large part of the commercial catch from inshore areas of Lake Turkana is also made
up of the Nile tilapia (Stewart, 1988; Kolding, 1992, 1993).

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## Maturation and spawning size

Size (as total length and therefore age) at first maturity for respectively male and female fish from Lake Victoria was 18 cm and 24 cm, and, 23 cm and 26 cm in Lake Kyoga fish. Lake Albert fish had smaller maturation sizes. These data compare well with what has been observed in habitats (Lakes Albert, Baringo and Turkana) where the species is endemic (Lowe-McConnell, 1958; Okorie, 1975; Kolding, 1993) and suggest that *O. niloticus* has successfully adapted to the new environments. According to Kolding (1993), fish in those size ranges would be within the first year of growth. However, the observed variations in size at maturation (Table 1) during this study or the stunted but mature forms of 10 - 17 cm in Lake Albert lagoons (Lowe-McConnell, 1958) or 14 - 16 cm in Lake Ziway (Abebe and Getachew, 1992) could be due to habitat-specific environmental factors such as space and food availability. A high length at maturity may be associated with efficient utilization of carbon from available food resources and rapid growth (Harbott, 1975). The phenomenon of stunting in crowded conditions such as in fish ponds or dams is well known and physico-chemical data have been cited in some studies on reproduction. Electrical conductivity ($K_{20}$) is closely correlated with total ionic concentration and alkalinity (Talling and Talling, 1965). Lowe-McConnell (1958) attributed the stunted growth in fish of lagoons to extremely alkaline conditions (pH 9.2, conductivity 7200 $\mu$S.cm$^{-1}$ and alkalinity 43000 ppm $CaCO_3$). In Lake Baringo, with size at first maturity of between 16 and 17 cm, Okorie (1975) reported a conductivity of 600 $\mu$S.cm$^{-1}$ while the Lake Turkana values were 3500 $\mu$S.cm$^{-1}$ (362-744 $\mu$S.cm$^{-1}$ for Ferguson's Gulf), with a pH of 9.3 (Kolding, 1992, 1993). These saline conditions were not encountered in physico-chemical assessments of Lake Victoria's vegetation-dominated habitats (e.g. mean pH ranged between 7.1 and 8.9, conductivity was below 120 $\mu$S.cm$^{-1}$, alkalinity < 1.0 meq.l$^{-1}$) in spite of intensive sampling (Chapter 3). In another study, Fineman-Kalio (1988) observed that *O. niloticus* (average weight, 80 g) cultured in brackish water ponds were unable to reproduce at salinities above 30 ppt. However, in nature such as in Lake Victoria which is regarded as being dilute (Beadle, 1981), fish of that weight would be about 14 - 17 cm in length. This is below the size at first maturity (18 - 24 cm) or the effective size at first spawning (>30 cm) observed in specimens from the open water, and yet small mature sizes were associated with vegetation-dominated habitats (Table 1). It appears that apart from the reported influence of the above factors, other factors may be involved as well. Pullin and McConnell (1982) suggested that optimal oxygen and temperature were important in the switch from growth to reproduction although no data were specified. Diurnal and seasonal variations in physico-chemical factors of the Lake Victoria habitats were more pronounced in inshore than further away in the more open water (Chapter 3). Therefore, it appears that early maturation may primarily be associated with the physical habitat, in particular the relative instability of the water environment in shallow habitats. For example, fluctuations in water level of such habitats may lead to space constraints or to extreme conditions resulting from variations in physico-chemical factors (especially oxygen and temperature). It could also lead to over-crowding by various species of the littoral habitats. In Lake Turkana, a decrease in maturation size of *O. niloticus* in the shallow marginal areas

was thought to be caused by predation (by birds, crocodiles and man), "unstable" conditions compared to the main lake (e.g. through isolation and desiccation leading to deoxygenation and high temperatures) all resulting into high mortality rates (Kolding, 1993).

Two major conclusions can be made with respect to maturation size and spawning in *O. niloticus*. Fish in Lakes Victoria and Kyoga (the new environments) seem to grow larger, reach sexual maturity later and probably experience first spawning at larger sizes than fish from Lake Albert. This phenomenon which may be explained by the species' growth plasticity has been observed in various environments (Lowe-McConnell, 1955, 1958; Kolding, 1993) of varying chemical composition. Early maturation seems to be related more to water levels in shallow habitats. Additionally, vegetated shoreline habitats are probably occupied by a part of the population which may be vulnerable to early mortality (e.g predation, and seasonal water level changes) in open water, and in which individuals mature at an early size. In addition to being prone to high mortality (including that due to fishing cf Lowe-McConnell, 1975), early maturation in this part of the population could be due to the relatively more unpredictable conditions in the shallow vegetation-dominated habitats. Under these conditions, although fish may mature at a small size, they probably do not ripen until a greater length (size at first spawning) i.e when they are able to move to open water. In contrast, another part of the population stays in the more open water (where oxygen and temperature are more uniform over time, (cf. Pullin and Lowe-McConnell, 1982) and grows to a larger size but still utilises the shallow littoral habitats during breeding periods, with fish moving out to open water as they grow. Apart from its riverine origin, isolated populations of the Nile tilapia may also exist at rocky shores (Seehausen, 1996) or in more open water where reproduction is probably influenced more by density-dependent mortality. Being of riverine origin, the Nile tilapia's distribution pattern discussed above, and its apparent preference for littoral habitats (Chapter 4 and 5) in spite of their temporal unpredictability may indicate that the species has not fully adapted its reproductive phase to lacustrine conditions as previously discussed for some non-cichlid species in Lake Victoria (Corbet, 1961; Balirwa, 1984).

**Fecundity**
Fecundity and successful spawning are two of the host of factors which are responsible for the expansion of animal populations and their eventual establishment in newly acquired habitats (Marthur and Ramsey, 1974). Comparing absolute fecundity or fecundity per length across lakes makes it clear that Lakes Victoria and Kyoga fish were significantly more fecund than those in Lake Albert (Table 4, App. 2). Fish from Lake Victoria were also generally larger. These differences may be due to environmental variability (e.g space, food quality and quantity) and/or genetic differences between the different populations resulting from previous stockings. The two are probably among some of the more important factors for the apparent success of the Nile tilapia in the new environments, in spite of the apparent variation in the number of fertilised eggs that can be brooded after any single spawning.

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Populations living in environments imposing high density-independent (D.I) mortality (*r*-strategists) are selectively favoured to allocate a greater proportion of resources to reproductive activities at the cost of their capabilities to propagate under crowded conditions, and conversely, populations living in environments imposing high density-dependent (D.D) regulation (*K*-strategists) will be selectively favoured to allocate a greater proportion of resources to non-reproductive activities, at the cost of their capabilities to propagate under conditions of high D.I. mortality (Gadgil and Solbrig, 1972).

Predictable lacustrine environments are normally associated with density-dependent mortalities and highly specialised reproductive habits within the *K* selected end of the *r-K*-continuum (Kolding, 1993) even though several traits may covary with mortality and fecundity, and, may not necessarily be ordered along a single continuum (Stearns, 1992). However, for fish, several factors including water level changes, trophic status and species changes may lead to unpredictable conditions. Lake Victoria and to some extent Lake Kyoga are considered to have experienced ecological changes associated with species introductions (e.g. Witte *et al.* 1992, 1995), water level changes (Welcomme, 1966), eutrophication (Hecky, 1993) and changes in the shoreline landscape (Lowe-McConnell, 1994a, b; Balirwa, 1995, also see Chapter 3). These changes probably indicate that the two lake sets are relatively less stable than lakes in which *O. niloticus* is endemic. Furthermore, the two lakes are of more recent origin than either Lakes Albert or Turkana (Beadle, 1981), and Nile tilapia is even more recent in them (Lakes Victoria and Kyoga) and its populations may still be expanding in the new environments. Due to these factors, egg production by Nile tilapia in Lakes Victoria and Kyoga probably falls towards the *r*-end of the continuum (cf no. of fertilised eggs.brood$^{-1}$), while their mouth-brooding and protection-for-the young strategies are as in other species of *Oreochromis K*-selected.

Eutrophication which is associated with a deterioration in water quality of a water body (e.g algal blooms, disappearance of submerged macrophytes) may not fully account for the observed high fecundities in the Nile tilapia. In the whitefish, *Coregonus lavaretus*, high fecundity was associated with oligotrophic conditions (Hartman and Quoss, 1993). This indicates that fecundity in fish may or may not be positively correlated with the trophic state of a water body. In general, populations of *O. niloticus* in poor condition mature at much smaller sizes (Lowe-McConnell, 1982). In some previous studies of *Oreochromis* and other tilapiine populations, apart from drastic environmental changes, a decrease in the condition and/or earlier maturity have been mentioned (Stewart, 1988; Abebe and Getachew, 1992). In the present study, both maturation size and condition (Fig. 2, Tables 4 and 5) were higher in both Lake Victoria and Kyoga fish than in Lake Albert. In Lake Victoria fish, the condition had improved from K = 1.94 in 1964 (Welcomme, 1965) to K = 2.02 - 2.28 obtained during this study (Table 5) and maturation size was higher. In comparison, data from Lowe-McConnell (1958) gave condition factors of 2.1 for Lake Turkana and 2.04 for Lake George fish, and a maturation size of 22 cm for Lake George quoted by Harbott (1975). Getachew and Abebe

(1992) reported condition factors of 1.89 for Lake Ziway, and 2.03 for Lake Awasa. In several of these studies, condition and low maturation sizes were associated with food particularly its quality. Therefore, it appears that high fecundities and larger maturation sizes in fish of Lakes Victoria and Kyoga may be related to faster growth rates as a result of a higher nutritional status of the lakes. This could result from changes in the fish community composition of the two lakes (Witte *et al.* 1992, 1995) and, in turn could be associated with a reduction in competition for food resources, an increase in food (invertebrates) availability and subsequent improvement in condition and reproductive potential. This idea is consistent with the suggestion that nutrition is important in determining size and age of first spawning (Nikolsky, 1963). In addition, the immense size and much-indented shoreline characteristic of Lake Victoria, coupled to habitat displacement of many endemic species (Witte *et al.* 1992, 1995) may add to the observed prolific egg production by fish due to a competitive release effect (Goldschmidt *et al.* 1993) and subsequent availability of habitat previously occupied by other species.

Hybrid vigour resulting from crossings between *O. niloticus* and other tilapias as reported (e.g. Welcomme, 1964, 1967; Fryer and Iles, 1972; Lowe-McConnell, 1975 and Moreau *et al.* 1988) and observed in specific morphs, could contribute to the observed high fecundities in Lakes Victoria and Kyoga. From the relatively small founder population and the numerous sources of seed material used in the stockings (Lowe-McConnell, 1958; Welcomme, 1966; Trewavas, 1983), the dominant phenotype of the Nile tilapia in the two lakes may represent a genotype with a higher reproductive potential.

### Seasonal cycle of breeding

In Lake Victoria and probably also in Lakes Albert and Kyoga, *O. niloticus* breeds throughout the year as shown by monthly changes in the GSI (Fig. 6) and monthly trends in percentages of ripe and spent fish from Lake Victoria (Fig. 7). Sexual ripeness was also correlated with decreased condition, indicating erratic feeding during brooding (Lowe-McConnell, 1975) and depletion of food reserves (Fryer and Iles, 1972). Results of this study also show that there are two peaks in breeding, the first and more prolonged phase appearing to commence sometime after the onset of the main rainy period (towards the end of May) and stretching into the short dry cool season (July - September). The second peak in breeding followed a similar pattern, commencing after the onset of the short rainy season towards the end of October and beginning of November. The observed breeding patterns agree with the observations that Nile tilapia tend to spawn throughout the year but show increased breeding activity in periods correlated with rainy seasons (Lowe-McConnell, 1958, 1975; Twongo, 1992). Therefore, individual fish may not necessarily breed continuously. In addition, the present results also show that the bi-annual peaks commence sometime after the onset of the rains and extend into the dry seasons. Water level changes which show a lag phase between the onset of the rains and the maximum lake level (Piper *et al.* 1986) could determine the spawning peaks. Peak spawning in the Nile tilapia of Lake Victoria may therefore

be primarily associated with water level changes (Fig. 8) even though rainfall and temperature may be the principal climatic variables.
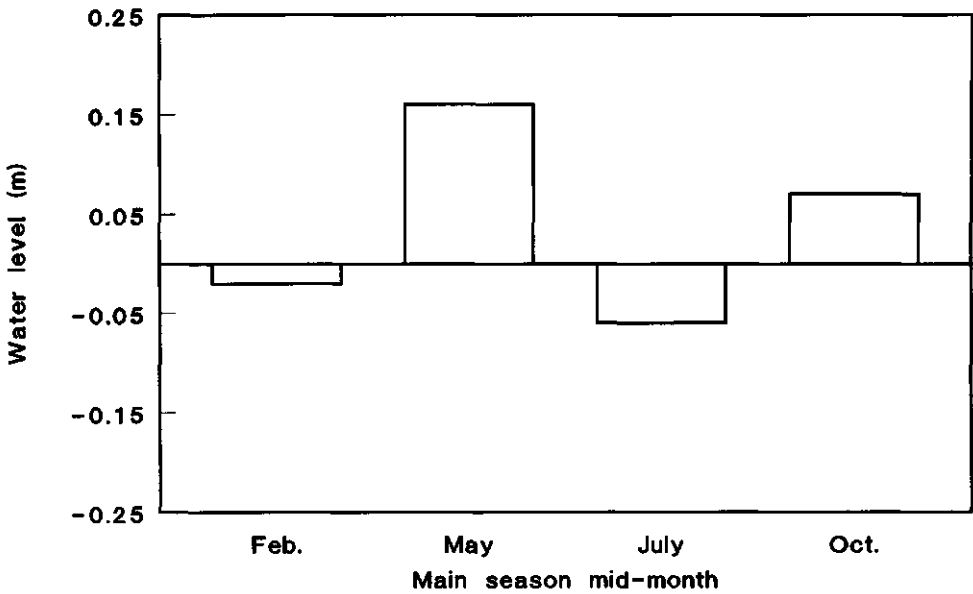


Fig. 8.      The pattern of water level changes in Lake Victoria according to season (indicated by mid month: Feb = long dry season; May = long rainy season; July = short dry cool season; Oct. = short rainy season).

The observed pattern of breeding is similar to Lake Turkana's in which Kolding (1993) noted that when the lake level rises, shoals of tilapia disperse, and also corresponds to other observations by Hickley and Bailey (1987) in a Sudan floodplain. The results therefore might explain the decrease in catches during the dry months reported by Lowe-McConnell (1958), as brooding females (carrying as many as 700 young in a 30 cm female fish, Lowe-McConnell, 1958) could still be in the shelter of flooded plant beds (Lowe-McConnell, 1955) for between 20 and 30 days (Fryer and Iles, 1972; Trewavas, 1983) when young fish will have reached a length of 14 mm (Lowe-McConnell, 1958). Furthermore, the patterns could account for differences in the timing of peak reproduction in different parts of the lake or in lakes at different latitudes within the tropics. For example, according to Kolding (1993), the pattern observed in Lake Turkana appeared to be out phase with the general pattern described by Lowe-McConnell (1958, 1975).

The dependency of the spawning phase on an increase in water level provides some advantages depending on habitat features particularly slope and vegetation, and, low lake levels have been associated with drastic reduction in spawning/ nursery areas (Stewart, 1988). Of the investigated habitats, *Typha* and *Vossia*

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were shown to undergo deeper flooding owing to their more gentle slope (Chapter 3). Coupled to the type of vegetation at these shores, these more deeply flooded areas may provide cover for brooding females and for juvenile fish, as well as food (epiphytic algae, small invertebrates, allochthonous materials) for the juvenile fish. The lag period between onset of the rains and an increase in water level is most likely associated with gradual nutrient inputs from the catchment (Chapter 3) and a build-up of primary production. Together with *Phragmites*-dominated habitats, the three habitats also provide the higher temperature regimes which juvenile *O. niloticus* tolerate better than other fishes (Welcomme, 1964b), a pattern which is partly supported by the April-June high densities (120,000-300,000 ind. ha$^{-1}$) occurring there between 09.00-13.00 h (Chapter 5). Similar temperature and oxygen gradients occur in other interface vegetation-dominated habitats (Chapter 3) but the deeper *C. papyrus* and *Eichhornia*- dominated types may be more suitable habitats for post-spawning adults. In addition, there is in general a related differential use of vegetation-dominated habitats according to sex (Fig. 4; App. 1). The empirical relationships between depth of flooded vegetation and length characteristics of the fish populations observed by Welcomme (1965), the significant interaction effects of vegetation dominated habitats and season in the abundance of immature fish reported in Chapter 5, and results of this study demonstrate the importance of the littoral zone in the life history of the Nile tilapia. Other areas such as rocky shores (Seehausen, 1996a, b), lagoons or open water deeper habitats where Nile tilapia have been found indicate the species' wide ecological niche.

In conclusion, this study demonstrates that maturation size in the Nile tilapia varies with habitat, depends on space, and vegetated shoreline areas depress the size at first maturity mainly as a result of physical (water level and temperature) rather than chemical factors (ionic concentration, pH and alkalinity). Competition for food and its utilization are other factors which seem to influence size at first maturity. The effective size at first spawning is higher than the size at first maturity. The higher fecundity in fish from new environments (Lakes Victoria and Kyoga) in comparison to Lake Albert fish may be due to differences (some of them possibly genetic) between populations in these environments and those in their natural systems. Furthermore, higher fecundity and the better condition of fishes in the new habitats could be a result of differences in dietary quality between habitats. The utilisation by the Nile tilapia of the littoral zone depends on seasonal changes in water level (hydrology) and temperature, and these changes are correlated with two breeding peaks in a continuous cycle. The most extensive vegetation-dominated habitats in both Lakes Victoria and Kyoga (*C. papyrus* and *E. crassippes*) though not suitable for juvenile fishes are occupied by adult fishes both before and after spawning, but there appear to be considerable shifts in habitat as the fish grow but other movements may be for feeding.

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Appendix 1.    Sex ratio distribution patterns in the Nile tilapia (>25 cm TL) of Lake Victoria according to vegetation dominated habitat type (a = *Cyperus*, b = *Eichhornia*, c = *Vossia*, d = *Typha*, e = *Phragmites*), season (Dec. - March 15 = long dry season; March 16 - June = long rainy season; July - Sept. 15 = short dry cool season; Sept. 16 - November = short rainy season) and for all habitats as a whole.

| Season | # males | # females | Sex ratio | % male |
|---|---|---|---|---|
| a. *Cyperus papyrus* - dominated habitats | | | | |
| Dec - March 15 | 18 | 13 | 1.4:1.0 | 58 |
| Mar 16 - June | 37 | 40 | 1.0:1.1 | 48 |
| July - Sept 15 | 22 | 15 | 1.5:1.0 | 60 |
| Sept 16 - Nov | 11 | 4 | 2.7:1.0 | 73 |
| Total | 88 | 72 | 1.2:1.0 | 55 |
| b. *Eichhornia crassipes* - dominated habitats | | | | |
| Dec - March 15 | 7 | 8 | 1.0:1.4 | 47 |
| Mar 16 - June | 28 | 22 | 1.3:1.0 | 56 |
| July - Sept 15 | 13 | 12 | 1.1:1.0 | 52 |
| Sept 16 - Nov | 18 | 15 | 1.2:1.0 | 55 |
| Total | 66 | 57 | 1.2:1.0 | 54 |
| c. *Vossia cuspidata* - dominated habitats | | | | |
| Dec - March 15 | 14 | 5 | 2.8:1.0 | 74 |
| Mar 16 - June | 4 | 7 | 1.0:1.8 | 36 |
| July - Sept 15 | 3 | 2 | 1.5:1.0 | 60 |
| Sept 16 - Nov | 2 | 13 | 1.0:6.5 | 13 |
| Total | 23 | 27 | 1.0:1.2 | 46 |
| d. *Typha domingensis* - dominated habitats | | | | |
| Dec - March 15 | 7 | 12 | 1.0:1.7 | 37 |
| Mar 16 - June | 35 | 35 | 1.0:1.0 | 50 |
| July - Sept 15 | 5 | 3 | 1.7:1.0 | 67 |
| Sept 16 - Nov | 7 | 12 | 1.0:1.7 | 37 |
| Total | 54 | 62 | 1.0:1.2 | 47 |
| e. *Phragmites mauritianus* - dominated habitats | | | | |
| Dec - March 15 | 5 | 8 | 1.0:1.6 | 38 |
| Mar 16 - June | 7 | 11 | 1.0:1.6 | 39 |
| July - Sept 15 | 6 | 5 | 1.2:1.0 | 55 |
| Sept 16 - Nov | 1 | 7 | 1.0:7.0 | 14 |
| Total | 18 | 31 | 1.0:1.7 | 37 |
| **Total of all habitats** | **499** | **498** | **1.0:1.0** | **50** |

Appendix 2. Relationships between Weight (Wt, g), total length (TL, cm) and absolute fecundity (Fec., Fec.g$^{-1}$ and Fec.g$^{-1}$ number), GSI and condition index (K) data (means ± SE) in the Nile tilapia from Lakes: (a) Victoria, (b) Albert and (c) Kyoga according to length class (age) and season (as in Table 2).

|  | Dec - Mar15 | | Mar16 - June | | Jul - Sep15 | | Sep16 - Nov. | |
|---|---|---|---|---|---|---|---|---|
| **a.  Lake Victoria** | | | | | | | | |
| **Length class: 25 - 35 cm** | | | | | | | | |
| n | 9 | | 5 | | 1 | | 6 | |
| Wt | 693 ± | 51 | 683 ± | 61 | 565 | | 782 ± | 90 |
| TL | 32.0 ± | 0.8 | 31.9 ± | 0.8 | 30.8 | | 33.0 ± | 1.0 |
| Fec. | 2694 ± | 482 | 2229 ± | 373 | 1816 | | 2285 ± | 257 |
| Fec.g$^{-1}$ | 4.3 ± | 1.0 | 3.2 ± | 0.4 | 3.2 | | 3.0 ± | 0.3 |
| Fec.cm$^{-1}$ | 80 ± | 18 | 69 ± | 10 | 59 | | 69 ± | 7 |
| GSI | 0.02 ± 0.00 | | 0.03 ± 0.01 | | 0.01 | | 0.02 ± 0.00 | |
| K | 2.09 ± 0.04 | | 2.09 ± 0.04 | | 1.93 | | 2.13 ± 0.08 | |
| **Length class: >35 cm** | | | | | | | | |
| n | 26 | | 21 | | 9 | | 37 | |
| Wt | 1720 ± | 139 | 1481 ± | 100 | 1655 ± | 232 | 1470 ± | 138 |
| TL | 41.7 ± | 1.0 | 40.6 ± | 0.8 | 42.7 ± | 2.0 | 41.3 ± | 1.2 |
| Fec. | 4818 ± | 1262 | 3959 ± | 283 | 4742 ± | 788 | 4082 ± | 414 |
| Fec.g$^{-1}$ | 2.7 ± | 0.4 | 2.7 ± | 0.1 | 2.9 ± | 0.2 | 2.9 ± | 0.2 |
| Fec.cm$^{-1}$ | 109 ± | 23 | 98 ± | 6 | 107 ± | 14 | 98 ± | 8 |
| GSI | 0.02 ± 0.00 | | 0.03 ± 0.00 | | 0.03 ± 0.00 | | 0.02 ± 0.00 | |
| K | 2.25 ± 0.07 | | 2.21 ± 0.13 | | 2.02 ± 0.05 | | 2.05 ± 0.12 | |
| **b.  Lake Albert** | | | | | | | | |
| **Length class: 25 - 35 cm** | | | | | | | | |
| n | 6 | | 4 | | 4 | | 2 | |
| Wt | 518 ± | 49 | 541 ± | 90 | 831 ± | 45 | 655 | |
| TL | 29.6 ± | 1.0 | 29.3 ± | 1.8 | 33.8 ± | 0.3 | 32.5 | |
| Fec. | 1954 ± | 399 | 1327 ± | 101 | 2099 ± | 279 | 1881 | |
| Fec.g$^{-1}$ | 3.7 ± | 0.6 | 2.6 ± | 0.4 | 2.5 ± | 0.4 | 4.0 | |
| Fec.cm$^{-1}$ | 65 ± | 12 | 46 ± | 4 | 62 ± | 9 | 59 | |
| GSI | 0.02 ± 0.00 | | 0.02 ± 0.00 | | 0.02 ± 0.00 | | 0.02 | |
| K | 1.97 ± 0.07 | | 2.11 ± 0.04 | | 2.16 ± 0.11 | | 1.90 | |
| **Length class: >35 cm** | | | | | | | | |
| n | 4 | | - | | 2 | | - | |
| Wt | 1210 ± | 175 | - | | 475 | | - | |
| TL | 38.5 ± | 1.7 | - | | 36.5 | | - | |
| Fec. | 3359 ± | 700 | - | | 602 | | - | |
| Fec.g$^{-1}$ | 2.5 ± | 0.2 | - | | 1.3 | | - | |
| Fec.cm$^{-1}$ | 86 ± | 14 | - | | 17 | | - | |
| GSI | 0.02 ± 0.00 | | - | | 0.02 | | - | |
| K | 2.08 ± 0.03 | | - | | 1.00 | | - | |

Appendix 2 (continued)

|  | Dec - Mar15 | | Mar16 - June | | Jul - Sep15 | | Sep16 - Nov. | |
|---|---|---|---|---|---|---|---|---|
| **c.** *Lake Kyoga* | | | | | | | | |
| Length class: 25 - 35 cm | | | | | | | | |
| n | 3 | | 1 | | 4 | | 1 | |
| Wt | 628 | ± 17 | 750 | | 584 | ± 89 | 600 | |
| TL | 30.4 | ± 0.3 | 34.6 | | 29.3 | ± 0.3 | 29.9 | |
| Fec. | 2401 | ± 264 | 1829 | | 2764 | ± 587 | 2482 | |
| Fec.g$^{-1}$ | 3.8 | ± 0.3 | 2.4 | | 4.7 | ± 0.5 | 4.1 | |
| Fec.cm$^{-1}$ | 79 | ± 15 | 53 | | 92 | ± 15 | 83 | |
| GSI | 0.03 | ± 0.00 | 0.02 | | 0.03 | ± 0.01 | 0.03 | |
| K | 2.23 | ± 0.08 | 1.81 | | 2.29 | ± 0.17 | 2.24 | |
| Length class: >35 cm | | | | | | | | |
| n | 1 | | 7 | | 3 | | 5 | |
| Wt | 1200 | | 1283 | ± 76 | 1623 | ± 332 | 1310 | ± 148 |
| TL | 38.2 | | 39.1 | ± 0.9 | 42.1 | ± 1.9 | 39.7 | ± 1.4 |
| Fec. | 3499 | | 3319 | ± 439 | 4250 | ± 1289 | 3975 | ± 280 |
| Fec.g$^{-1}$ | 1.9 | | 2.5 | ± 0.2 | 2.5 | ± 0.3 | 3.3 | ± 0.6 |
| Fec.cm$^{-1}$ | 92 | | 84 | ± 10 | 99 | ± 25 | 101 | ± 10 |
| GSI | 0.02 | | 0.04 | ± 0.02 | 0.02 | ± 0.00 | 0.02 | ± 0.01 |
| K | 2.15 | | 2.15 | ± 0.10 | 2.11 | ± 0.14 | 2.05 | ± 0.05 |

# Chapter 7

# Trophic characterisation in the Nile tilapia, *Oreochromis niloticus* L. in the shallow habitats of northern Lake Victoria, Uganda[*]

## ABSTRACT

The food and feeding habits of the Nile tilapia, *Oreochromis niloticus* in the shallow habitats of northern Lake Victoria were investigated between December 1995 and December 1996. Quantitative analysis of stomach contents from samples of trawl caught fish was carried out to determine peak feeding periods, relative importance of ingested food items, seasonal feeding patterns, and to resolve suspected omnivory in the species. Feeding in most fish increased between 09.00 h and 13.00 h, and fish appeared not to feed during the night. Detrital material and insects especially chironomid larvae were the most important regularly ingested items; the two items accounted for 65 % of mean stomach contents but the source of detritus appeared to depend on the distance from the shore. Generally, small fish less than 15 cm in length ingested mostly invertebrates, but seasonal patterns explained most of the variation in ingested items in all fish. Fish ingested mostly chironomids during the long dry season (December to March) when 192 chironomids per fish recorded; detrital material was more important during the short wet season (September to November). In the short dry season (July to September), detrital material was replaced by *Caridina* shrimps and molluscs which together made up at least 50 % of mean stomach contents during this period. Phytoplankton and higher plant material were among the main stomach contents considered but they never together made up more than 15 % on average of the quantity of ingested items. From the wide range of food items ingested by fish of all sizes, omnivory and opportunistic feeding habits were confirmed. The shallow vegetated habitats were found to be important feeding grounds for young fish but a high sediment carbon: nitrogen ratio (40:1) associated with *Eichhornia* dominated habitats in comparison to a ratio of 20:1 further away from the shore towards open water indicated that detrital material could be nutritionally more beneficial in areas where large fish apparently feed. Feeding patterns observed in the Nile tilapia of Lake Victoria may be a result of the species phenotypic plasticity and response to changed ecological conditions prevailing in the lake. The apparently wide-spectrum food base which includes invertebrates could partly account for the better condition and higher fecundity in Lake Victoria Nile tilapia in comparison to the species in other lakes.

## INTRODUCTION

In Lake Victoria, East Africa, the Nile tilapia (*Oreochromis niloticus* L.) is one of the most dominant fish species in the shallow vegetated littoral zone where it contributes at least 45 % to the total fish biomass (Chapter 5). The same distribution pattern has been observed in many other freshwater ecosystems in Africa where the species occurs naturally (Lowe-McConnell, 1958; 1975; Welcomme, 1967; Burgis *et al.*, 1973; Kolding, 1993). In these water bodies, the Nile tilapia has been described as primarily herbivorous i.e. feeding on phytoplankton (Appendix 1). However, since the Nile tilapia apparently follows a day-time feeding regime (Moriarty and Moriarty, 1973; Harbott, 1975), the use of few over-night gill net samples in many of the previous studies (Appendix 1) could have masked the relative importance of some food items. Foods of animal origin, due in part to lack of cellulose, probably disappear from the guts within a short

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period of consumptionin comparison to phytoplankton or higher plant material. Other methodological limitations such as sampling across habitats could also result in less clear resolution of trophic effects (e.g. preferences, fish size and habitat effects, species changes, seasonality) in some of the habitats. The apparent success of the Nile tilapia in new habitats (Balirwa, 1992), and the significant differences shown in fecundity and condition of the fish among lakes (Chapter 6) may therefore indicate differences in the quality and quantity of food available to the species in different habitats.

Food habits of fish are studied often to understand the qualitative and quantitative relationships between fishes and food organisms in their environment (trophic organisations) (e.g., Gascon and Legget, 1977; Crowder and Cooper, 1982; Pierce et. al., 1994). Among factors which influence food habits are habitat, preferences, season, temperature, fish size, daily feeding periodicities and competitor species (Ricker, 1971). The influence of these factors on trophic organisation is complex but probably more pronounced in shallow fish-rich habitats, where conditions are less predictable and more subject to environmental changes in comparison to deeper habitats. In Lake Victoria, changes in nutrient concentrations and primary productivity (Ochumba, 1988; Ochumba and Kibaara, 1989; Mugidde, 1992; Hecky and Bugenyi, 1992; Hecky, 1993), predation and fishing impacts on species composition and abundance (Ssentongo and Welcomme, 1985; Ogari and Dadzie, 1988; Ogutu-Ohwayo, 1990; Kudhongania et al., 1992; Witte et al., 1992a) are thought to have resulted in changes in the feeding habits of most sub-littoral zone fish (Ligtvoet and Witte, 1991; Witte et al., 1992b; Goldschmidt et al., 1993) as described by Witte and van Oijen (1990). For the shallower vegetated Lake Victoria littoral, habitat alterations (Lowe-McConnell, 1994a, b; Balirwa, 1995), hydrological regimes, catchment influences or water hyacinth (Eichhornia crassipes Mart. Solms-Laub) infestations (Chapter 3) could add to uncertainty about trophic characteristics of fish species. However, Witte and van Oijen (1990) did not provide quantitative data on the feeding habits of the Nile tilapia which is associated more with the shallower littoral habitats (Chapter 5). Instead, in the resulting simplified food web (Fig. 4 of Ligtvoet and Witte, 1991), O. niloticus, despite its wide ecological tolerance (Lowe-McConnell, 1958; Balirwa, 1992), is depicted as retaining food habits similar to those of the indigenous tilapiine species (O. esculentus and O. variabilis) which it replaced. This conclusion seems to be based more on dated and limited data (e.g Fish, 1952; Welcomme, 1967), and observations in other lakes (App. 1). A recent study suggests that in Lake Victoria, the Nile tilapia seems to show more omnivory than previously reported (Balirwa, 1990) but this study was spread out over a wide range of depths and sizes of fish, and did not include all seasons.

In short, the purpose of the present study was to resolve whether O. niloticus, in spite of its commonly reported herbivorous diet, would show omnivory in Lake Victoria's littoral zone. In addition, the study aimed at comparing the present trophic characteristics of the Nile tilapia with what has been reported in the sub-littoral zone concerning the effects of species changes on the food web. Based on

literature data, it would be expected that the major food items utilised by *O. niloticus* do not differ from what has been reported. Furthermore, there was a relatively higher fish species diversity and abundance in the inner littoral zone in contrast to further offshore (Chapter 4). According to some literature (e.g Crul, 1995) a high species diversity would be expected to maintain stable food chains in the shallow areas, probably implying stability of the Nile tilapia's reported herbivorous habits. However, as there were apparent size differences in relation to distribution of the Nile tilapia in the littoral zone (Chapter 5), the study also aimed at investigating variation in ingested food items among size classes which could have been missed in previous studies. Of particular consideration were dietary items ingested in relation to feeding habitats (near shore vs further away from shore), and food availability (macrofauna) demonstrated in previous studies (Chapter 3).

As omnivory and flexibility in feeding habits have been suspected (Balirwa, 1990), the study attempted to link major food items in stomach contents with differences in availability demonstrated in macrofauna distribution patterns found in a previous study (Chapter 4). It was considered that differences from herbivory in the trophic status of the Nile tilapia, if observed, could be due to different environmental factors. In addition, quantitative differences from herbivory would provide more evidence for the observed simplification of the food web in the sub-littoral zone (Witte and van Oijen, 1990; Ligtvoet and Witte, 1991; Goldschmidt *et al.*, 1993) where the species also feeds. The study therefore also aimed at reducing on apparent artifacts inherent in methodologies of some previous studies (e.g the use of gill nets in feeding studies, pooling of samples across sizes, habitats and seasons).

## MATERIALS AND METHODS
### Habitats
In contrast to many previous studies, fish specimens for this study were actively collected by trawls in the shallow littoral zone in northern Lake Victoria (Fig. 1) between December 1995 and December 1996. Sampling included a 24-hour regimen and covered four seasons according to the previously recognised climatic patterns. The seasons were: the main dry season (15 December to 15 March), the main rainy season (16 March to June), the short dry cool season (July to 15 September) and the short rainy season (16 September to November).

The shoreline in the sampled area is fringed by different wetland plant species dominated by *Cyperus papyrus* L. but has come under heavy infestations with *Eichhornia crassipes* (water hyacinth). Close to the vegetation fringe, the water is about 0.5 m deep increasing to between 2 m and 4 m in depth at the outer fringe of the littoral zone. Bottom substrata are dominated by plant litter, coarse organic mud and clay near *C. papyrus* and *E. crassipes*, and sand and gravel off *Vossia* and *Typha* fringes. From about 400 m further offshore in deeper (4 - 6 m) water, bottom deposits contain fine soft mud with a high silt content. This bottom type may extend to deeper (10 m) areas where it is much more firm and compact with

some sandy and gravelly substrates (Macdonald, 1956). The habitats were previously investigated for seasonal physico-chemical aspects and fish populations (Chapter 3 to 6). Phytoplankton and invertebrate densities in this area are also described in these studies. Fish community structure in the study area was dominated by three stocked species (the Nile perch, *Lates niloticus*, the Nile tilapia, *Oreochromis niloticus* and another, *Tilapia zillii*). Three endemic species (*Brycinus jacksonii*, *Astatoreochromis alluaudi* and *Protopterus aethiopicus*), and haplochromine cichlids are also common (Chapter 4).
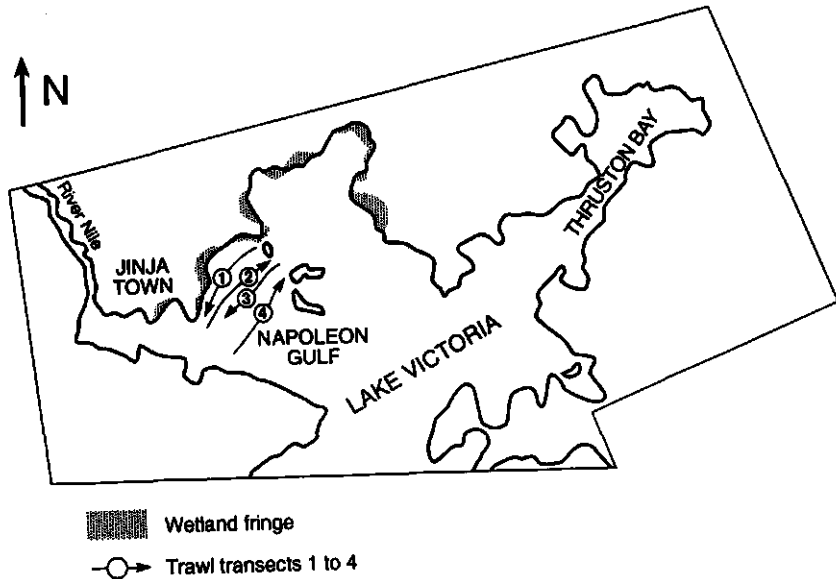


Fig. 1.    Map of the northern part of Lake Victoria showing the Jinja study area with trawl transects 1 to 4 as the specimen collection areas.

### Field procedures

Initially trawling was conducted over 24-hour periods to determine activity patterns and periods of intense feeding according to sex and size (age). In order to improve on past sampling methodologies (dusk to dawn gill netting) and the day time fishing patterns (Moriarty, 1973; Harbott, 1975), the following five periods were used: 06.00 to 09.00 h, 09.00 to 12.00 h, 12.00 to 15.00 h, 15.00 to 18.00 h and after 18.00 h until 06.00 h. In general, trawling was carried out in 2 to 4 m deep areas along transects parallel to the vegetation fringe at the shore (Fig. 1). A total of 46 trawls were made during this period, each with an average duration of about 35 minutes. It was estimated that most areas trawled were within 300 - 500 m from the shore which corresponded to the outer limit of the littoral zone (Chapter 3) though on occasions some trawl cruises passed through deeper (6 - 10 m) water further offshore. As the trawls could not be restricted to shorter time cruises nearer to the shore, they traversed various depths and bottom types. However, an attempt was made to restrict trawl locations within definable areas as described below:

Transect 1: closest to the vegetation fringe which was dominated by *C. papyrus* and *E. crassipes* in about 2 m deep water; usually within 100 m from the shore;

Transect 2: about 300 - 500 m further away from, but parallel to transect 1 in about 2 to 3 m deep water; trawling in this transect usually started from the shallower (1 m deep) end, off a papyrus to *Typha* zone at the shore;

Transect 3: in about 3 - 4 m deep water with some parts up to 6 m;

Transect 4: furthest away from the shore in deeper (6 - 10 m) water.

Following specimen collection, biometric data (fresh weight, g; total length, cm) were taken. Specimens were sexed as described in Chapter 5 and 6, and sorted according to the four size classes used there: 0 - 15.0 cm, 15.1 - 25.0 cm, 25.1 - 35.0 cm and above 35.0 cm. Stomach fullness and fat content were assessed at four levels by visually determining the level of stomach fullness and fat content of the abdominal cavity respectively. A subjective scale of scores ranging from empty (0) to full (1) stomachs or no fat to very fatty abdominal cavities was used. Stomachs containing food and their associated guts were dissected out and preserved in 5 % formalin.

**Laboratory procedures**
At the laboratory, total weights of the stomachs and stomach contents were taken to 0.1 g on a Mettler balance after soaking in water, and blotting off the excess water. Further analyses on stomach contents were based on the four size classes. The volume of the stomach contents (ml) was measured by water displacement of the stomach wall and of the contents, and a second time of the stomach wall separately. The contents were emptied in a petri dish and larger identifiable organisms were sorted from what appeared to be phytoplankton or detrital material. Based on relative sizes of ingested items, the larger organisms such as chironomids, *Caridina*, *Chaoborus* and molluscs were regarded as the main contents constituting the bulk of food. Chironomids were counted. Stomach contents were initially examined under a binocular microscope (magnification X 50) to ascertain the classification of main contents and evaluate the volumetric importance of all the ingested items. At this level of analysis, items such as higher plant material and some semi-digested invertebrates were identified. The detrital-plant and plankton material was thoroughly mixed with water and three sub-samples were taken with a pipette. The three sub-samples were separately examined under a compound microscope (up to magnification X 600) to identify different species or groups of phyto- and zooplankton, and to assess the percentage contributed by different planktonic taxa to the total microscopic food items. Phytoplankton food which was uncontaminated by detritus could be distinguished by its algal cells from heterogeneous detritus, and was also classified as main contents. Evidence of the digestibility of algae was obtained from

differences in appearance under high power magnification of algal cells between the stomach and hind intestinal-rectal contents.

An evaluation of several methods used in fish stomach content analysis (Hynes, 1950; Hyslop, 1980; Balirwa, 1984) revealed that volumetric and percentage occurrence methods were the most practical choices for the Nile tilapia and were therefore used. As the volume or weight of stomach contents was made up of various percentages of individual relatively large items, it was possible to evaluate the proportional importance of most of the main food items found in the stomachs from visual and microscopic analyses.

Catch rates (mean no. of Nile tilapia.hr$^{-1}$) and stomach fullness (percentage of filled stomachs) were evaluated for activity and feeding patterns respectively. In analyzing feeding habits, samples from the five main catch periods were sorted into approximately two-hourly intervals to examine diurnal feeding patterns. Male and female fish were initially treated separately. The significance of season and catch period on fish activity (fish movements between the vegetation fringe and the limit of the littoral zone i.e. within 300 - 500 m off the shoreline, and on peak feeding) were tested by ANOVA ($p < 0.05$). The degree of stomach fullness (percentages) was based on stomach states across different times of the day. In order to analyze peak feeding times by size and by sex in the Nile tilapia, two length groups (10 - 25 cm and $> 25$ cm TL) were used as it was easier to identify maturity stages in these size classes.

## RESULTS
### Catch rates as indices of activity periods
A total of 665 specimens were caught in 46 trawls over a 24 hour period pooled from several catches. In general more female fish were represented in the catches. The regression predicting catchability of the number of male and female fish according to the expression $y = a + bx$ gave the following parameter values: $a = -1.4 \pm 2.4$ and $b = 0.7 \pm 0.6$ (means $\pm$ se), where $y =$ male fish, $x =$ female fish, with a and b as intercept and slope respectively ($r^2 = 0.79$, $p < 0.0001$, $n = 665$).

Both season and catch period were significant factors in peak catch rates (number) but variations in weight were explained mostly by season and interaction between the two (catch period * season) (Table 1).

Catch period accounted for much (44 %) of the variation in numbers but interaction between season and catch period explained most (45 %) of the variation when weight (kg.hr$^{-1}$) was considered, indicating that large fishes dominated the catches only in certain seasons.

Most fish were caught during day time. Significantly ($p < 0.0001$) more fish were caught between 10.00 h and 14.00 h than in any other period of the day (Fig. 2).

Table 1.    Two-way ANOVA for assessing the effect of season (see Materials and Methods), catch period 1 to 5 (06.00 - 09.00 h, 09.00 - 12.00 h, 12.00 - 15.00 h, 15.00 - 18.00 h and after 18.00 h to 06.00 h respectively) and their interaction on fish density (mean numbers, and weight (kg) per hour (levels of significance = p, SS = sum of squares, % SS = factor SS/explained SS * 100, a measure of variation explained by that factor .

| Factor | Season | | Catch period | | Interaction | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| no.hr$^{-1}$ | 0.045$^*$ | 18 | 0.007$^*$ | 44 | 0.081$^{ns}$ | - |
| kg.hr$^{-1}$ | 0.023$^*$ | 26 | 0.097$^{ns}$ | - | 0.040$^*$ | 45 |

$^*$ = significant $p < 0.05$, $^{ns}$ = not significant
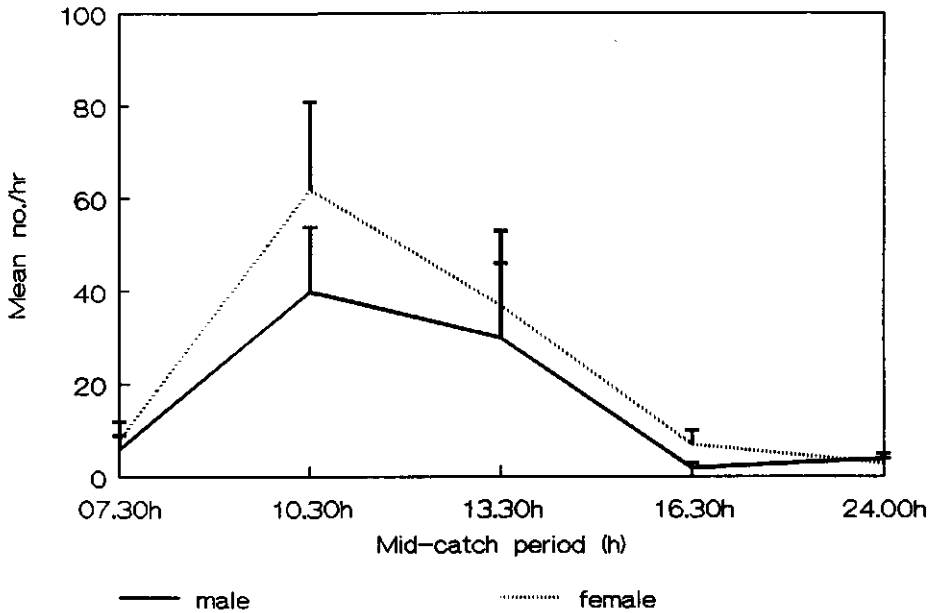


Fig. 2.    Diurnal variation in fish catches as an index of activity (mean no.hr$^{-1}$ of trawl time ± se) for male and female Nile tilapia from the littoral zone of northern Lake Victoria.

**Feeding patterns**
The relative feeding intensity (expressed as percentage of stomach fullness) varied with size and sex but feeding in most fish increased between 09.00 and 13.00 h (Fig. 3a-d). Generally, peak feeding fell within the period of maximum activity identified in Figure 2.

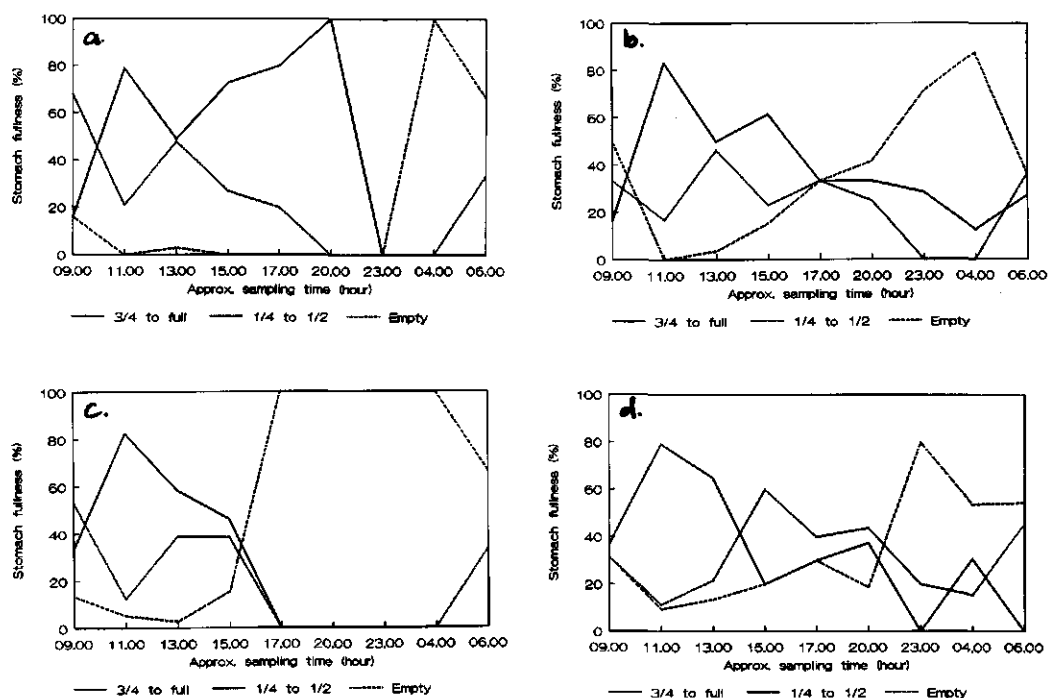Fig. 3a-d.   Percent stomach fullness (as an index of the diurnal pattern of feeding according to sex and size in the Nile tilapia from the littoral zone of northern Lake Victoria.
a. males, 10-25 cm TL, n = 214; b. males, > 25 cm TL, n = 124; c. females, 10-25 cm TL, n = 263; d. females, ≽ 25 cm TL, n = 179.

Comparable sample sizes made up the length distribution of 451 specimens examined for stomach contents according to season (Table 2). These were specimens mostly caught between 09.00 h and 18.00 h.

**Mean stomach fullness and quantity of food ingested**
Mean stomach fullness was 0.70 while the mean weight of food per stomach ranged between 0.63 ± 0.08 g in small (< 15.0 cm) fish to 7.76 ± 0.75 g in larger (> 15.0 cm) fish. There were no significant differences (p > 0.05) between the mean weight and mean volume of stomach contents (food consumed) indicating that food items could be picked either from the water column or from the sediment-water interface.

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Table 2.    The catch composition by size class (mean total length, TL in cm) and season in samples examined for stomach contents of the Nile tilapia caught in day time pooled trawls from the littoral zone in northern Lake Victoria between 1995 and 1996. n = number of samples.

| Season: | 0-15.0 | | 15.1-25.0 | | 25.1-35.0 | | > 35.0 | |
|---|---|---|---|---|---|---|---|---|
| | n | TL | n | TL | n | TL | n | TL |
| Long dry | 14 | 13.4 | 30 | 20.4 | 37 | 28.9 | 33 | 39.7 |
| Long wet | 63 | 11.1 | 44 | 19.8 | 28 | 29.2 | 15 | 38.7 |
| Short dry | 34 | 9.8 | 16 | 21.6 | 17 | 29.2 | 20 | 40.0 |
| Short wet | 19 | 11.8 | 38 | 20.9 | 19 | 29.5 | 24 | 40.1 |

The composition of food items in stomach contents of the Nile tilapia varied widely and included at least 10 items which could be classified as main contents (Table 3).

Table 3.    The composition of food items which could be classified as main stomach contents in Nile tilapia from the littoral zone in northern Lake Victoria between 1995 and 1996.

| Type of main contents | recognised items |
|---|---|
| Detritus | bottom material of mostly unidentifiable deposits mixed with algae, bacteria, rotifers, copepods and occasionally sand grains; |
| Phytoplankton | uncontaminated algal cells, dark blue to green or grey in colour; |
| Higher plant material | plant tissues, roots suspected to be from *Eichhornia* plants; |
| Crustacea | *Caridina*, Cladocera, Ostracoda |
| Mollusca | Gastropoda, Bivalvia |
| Chironomidae | larvae |
| *Chaoborus* | mostly as larvae but also some pupae |
| Trichoptera | mostly as larvae |
| Ephemeroptera | mostly as nymphs |
| Oligochaeta | body segments |
| Fish remains | vertebrae, myotomes, scales |

Among the phytoplankton, the dominant taxa identified were the Cyanobacteria (blue-green algae): filamentous forms (the most dominant), *Microcystis, Anabaena,*

*Merismopedia*, *Lyngbya/Planktolyngbya*; Bacillariophyceae (diatoms): *Nitzschia*, *Melosira* (*Aulosira*) and *Navicula*. Though present, green algae were rarely important among algal contents. A similar pattern was observed in the algal species composition of the detritus, indicating that these taxa had been in the plankton. Analysis of the overall importance of stomach contents pooled across seasons, sizes and locations (Table 4) showed that detritus and chironomids together accounted for more than 65 % of mean stomach contents.

Table 4.     Percentage composition of main contents in stomachs of the Nile tilapia caught in northern Lake Victoria between 1995 and 1996.

| Type of main contents | % of total weight or volume |
|---|---|
| Detritus | 43  ± 2 |
| Phytoplankton | 6  ± 1 |
| Higher plant material | 6  ± 1 |
| *Caridina* | 4  ± 1 |
| Mollusca | 5  ± 1 |
| Chironomidae | 22  ± 1 |
| Trichoptera | 2  ± 1 |
| Ephemeroptera | < 1 |
| Oligochaeta | 2  ± 1 |
| Fish remains | 3  ± 1 |
| Total | 93 |

Phytoplankton (recognised as uncontaminated algae) together with higher plant material contributed about 12 % of the biomass of ingested items. In terms of numbers, each fish stomach contained $86 \pm 9$ chironomids. Other types of main food items assessed on the same scale made up the reminder of stomach contents in minor proportions of: Cladocera, Ostracoda, *Chaoborus* mostly as larvae but also some pupae. Detrital algae, copepods and insect remains, which occasionally included ephemeropteran parts, were also part of this category even though they included several unidentifiable items.

**Season, size and habitat influences in the diet of the Nile tilapia**
Season was the most important factor explaining most of the variation shown in main stomach contents (Table 5) and therefore food ingested. However, for some food items (e.g., phytoplankton, fish, Trichoptera, Ephemeroptera and molluscs), the size of fish explained most of the variation in the food items apparently selected for.

Table 5. Three-way ANOVA for assessing the effect of size class (0-15.0 cm, 15.1 - 25.0 cm, 25.1 - 35.0 cm, > 35.0 cm), trawl location (close to shore, further offshore), and season (long dry, long wet, short dry and cool, short wet) on the 14 types of main food items recognised as mean % main contents (for chironomids, also as mean numbers), and K = condition factor in Nile tilapia stomachs (Levels of significance = p, % SS = factor SS/explained SS * 100, a measure of variation explained by that factor; a significant factor = p < 0.05).

| factor | size class | | trawl transect | | Season | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| Detritus | 0.000* | 20 | 0.000* | 16 | 0.000* | 44 |
| Phytoplankton | 0.019* | 51 | 0.729 | ns | 0.077 | ns |
| Higher plant material | 0.829 | ns | 0.124 | ns | 0.014* | 51 |
| Caridina | 0.063 | ns | 0.101 | ns | 0.000* | 81 |
| Cladocera | 0.050 | 21 | 0.034* | 20 | 0.000* | 47 |
| Ostracods | 0.489 | ns | 0.074 | ns | 0.047* | 56 |
| Mollusca | 0.001* | 25 | 0.444 | ns | 0.000* | 73 |
| Chironomidae | 0.000* | 7 | 0.000* | 27 | 0.000* | 71 |
| Chironomid nos. | 0.000* | 34 | 0.073 | ns | 0.000* | 52 |
| Chaoborus | 0.220 | ns | 0.480 | ns | 0.032* | 46 |
| Trichoptera | 0.000* | 81 | 0.385 | ns | 0.005* | 22 |
| Ephemeroptera | 0.000* | 67 | 0.928 | ns | 0.224 | ns |
| Oligochaeta | 0.000* | 41 | 0.007* | 18 | 0.007* | 18 |
| Fish remains | 0.014* | 76 | 0.085 | ns | 0.601 | ns |
| K | 0.000* | 66 | 0.973 | ns | 0.367 | ns |

* = significant, ns = not significant, Trawl trans. = trawl transect as the fished location approximating to habitat type according to distance from the shore and composition of bottom deposits (see, Materials and Methods).

According to individual percentage contribution to the total weight or volume of stomach contents (see Materials and Methods), seasonal effects on the type of food ingested by Nile tilapia was clearly shown by selection for detritus, chironomids, molluscs, higher plant material and Caridina shrimps (Fig. 4) from among the main ingested items. Detrital material was most important (64 % contribution to main stomach contents) during the short wet season (end of September to November) and to a lesser extent (47 %) during the dry season (i.e from December to the end of June). In the short dry cool season, detrital material was replaced mostly by Caridina shrimps (20 %) and molluscs (20 %). The long dry season was dominated by chironomids (31 %) equivalent to 192 chironomid individuals ingested per fish. Higher plant material (11 %) was an additional long dry season component in stomach contents.
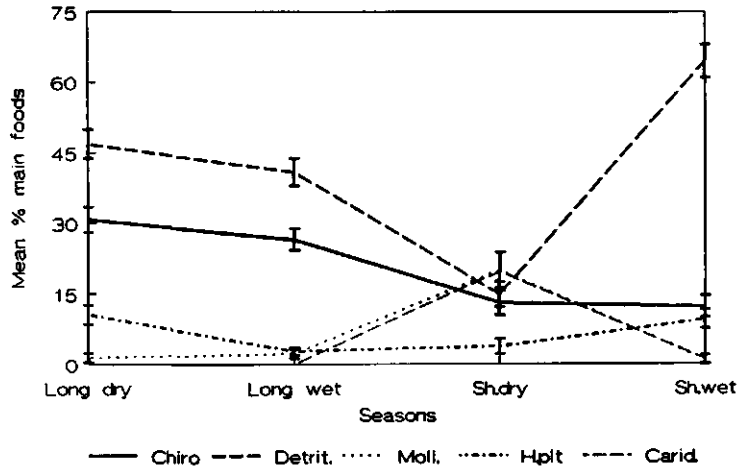
Fig. 4.    Seasonal variation (mean percentages ± SE) in relative importance of main food items according to the quantity of food items found in stomachs of *O. niloticus* (pooled across size classes) from the littoral zone of northern Lake Victoria between 1995 and 1996. Values are given for the main food items recognised as mean % main contents (according to levels of volumetric importance, see Materials and Methods).

The importance of seasonal variation in the diet of Nile tilapia was most clearly illustrated by the pattern of molluscs, *Caridina* and chironomid abundance among stomach contents. Molluscs and *Caridina* had a remarkable impact on stomach contents during the short dry but cool season. In addition, fish clearly ingested more chironomids (numbers per fish) during the long dry season than at any other time (Fig. 5) even though the biomass ingested may have been less than that of detrital material.

The size of fish was a significant factor in the composition and quantity of main contents in fish stomachs (Table 5). Size accounted for significant differences in presence among stomach contents of detritus, molluscs, chironomids, Oligochaeta (Fig. 6), Trichoptera, Ephemeroptera and fish prey from the list of the recognised major foods (Table 3). Small fish (0 - 15 cm TL) contained the least amount of detritus but ingested significantly more molluscs and oligochaetes than larger sized fish (above 15.0 cm TL). Intermediate sizes of fish (15.1 - 35.0 cm TL) contained more higher plant material and Trichoptera than the very small or the largest fish. There was also an apparent increase in the amount of fish prey ingested with increasing fish size (Fig. 6) but no systematic pattern was found with respect to phytoplankton even though in fish above 25.0 cm, stomachs contained relatively more of this item than in the smaller fish sizes.
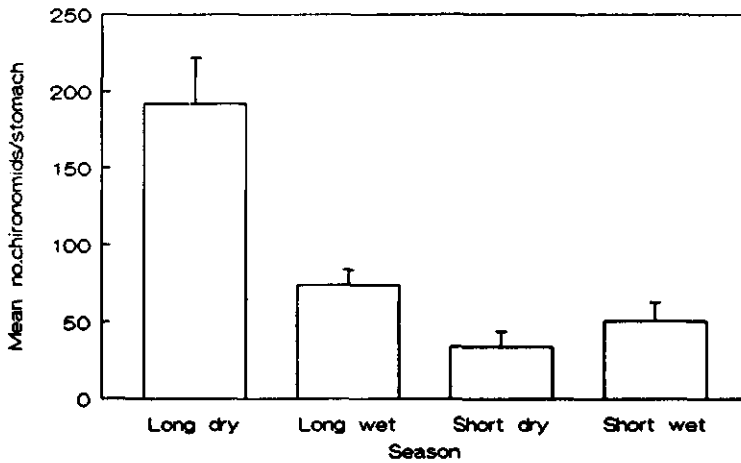
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Fig. 5.  Seasonal variations in the quantity (mean number per stomach ± SE) of chironomids found in *O. niloticus* stomachs (n = 451) between 1995 and 1996 in the littoral zone of northern Lake Victoria (seasons are explained in Materials and Methods).

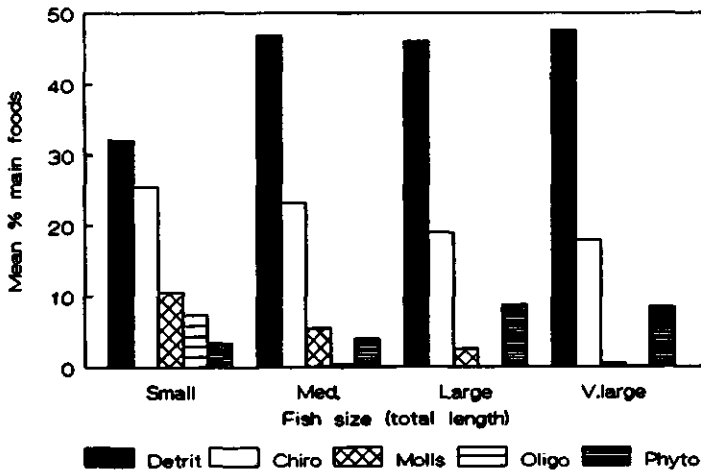

Fig. 6.  Size (small = 0 - 15 cm, medium = 15.1 - 25.0 cm, large = 25.1 - 35.0 cm and very large fish = > 35.0 cm) related utilisation of main foods (% of major food items, see Table 2) (Detrit. = Detritus, Chiro = chironomids = molls = molluscs, Oligo. = oligochaetes, Phyto. = phytoplankton) by the Nile tilapia caught in the littoral zone of northern Lake Victoria between 1995 and 1996.

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Although as would be expected large fish ate more chironomids (in terms of mean number per fish), the pattern was different when number of chironomids per cm total length or when volume in stomachs were considered. In this respect, small fish ate more chironomids per length or weight than was eaten in the large fish. Seasonal use of different items in the main stomach contents category was generally similar to the one in pooled samples shown earlier (Fig. 4).

Habitat, represented here as trawl location was less important (Table 4) than either fish size or season in food selection by fish hence confirming mixtures of habitat types traversed by the trawls. However, the significant effects of habitat could still be discerned from the use of detritus, chironomids and oligochaetes (Fig. 7).

The condition of the fish (as described in Chapter 5) (mean $2.03 \pm 0.08$ to $2.35 \pm 0.08$ between large and small size classes) variedly independently of season or habitat, and was explained most (66 % of total variation) by size differences in samples.
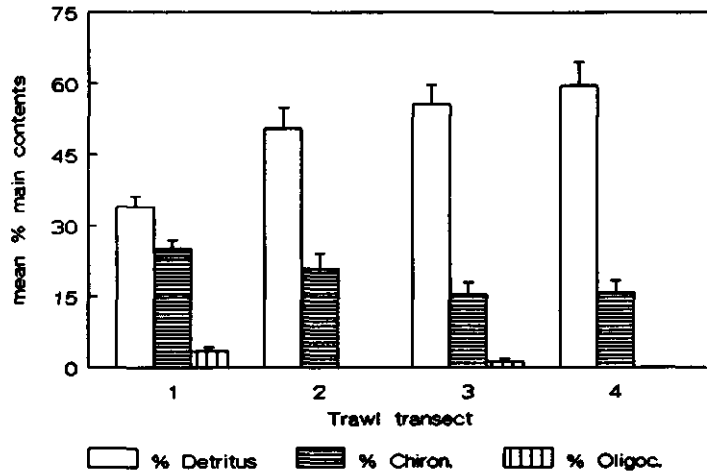


Fig. 7.     The influence of habitat (location of trawled areas) on the quantity (mean % of stomach contents) of detritus, chironomids and oligochaetes ingested by Nile tilapia between 1995 and 1996.

Although detritus and chironomids together accounted for more than 60 % of main contents in all areas sampled, fish tended to ingest more detritus further away from the shore (Fig. 8). In contrast, chironomids and oligochaetes were more important in samples from nearer to the shore. Apart from the dependence of this pattern on the earlier defined two factors (season and size), time of the day was also important in the quantities of detritus and chironomids ingested (Fig. 8).

Fig. 8. Ingestion of detritus and chironomids by the Nile tilapia in the littoral zone of Lake Victoria according to time of day represented by catch period (1 = 06.00 - 09.00 h, 2 = 09.00 - 12.00 h, 3 = 12.00 - 15.00 h, 4 = 15.00 - 18.00 h; night samples had mostly empty stomachs and are not included).
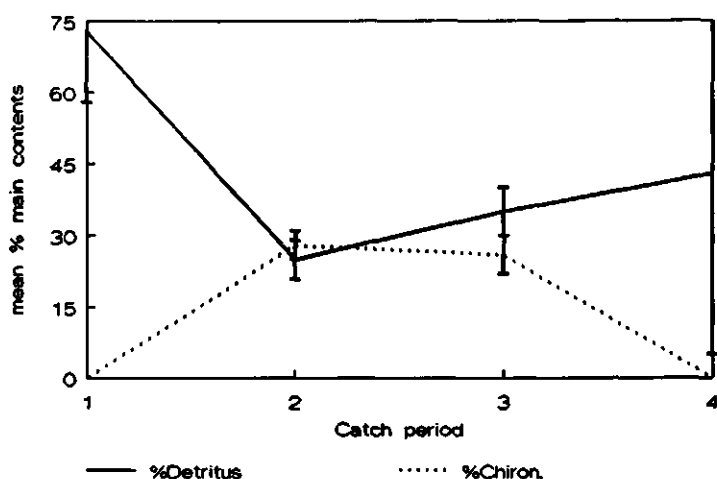
Detrital material was ingested early in the day and towards the end of feeding periods. The amount of detritus in stomach contents fell sharply by 09.00 h as chironomids started to increase. Chironomids by number and weight increased among stomach contents between 09.00 and 15.00 h and disappeared from stomach contents towards the end of the day. Chironomid numbers per stomach followed the same pattern increasing to about 50 per stomach between 09.00 and 15.00 h, and falling to zero thereafter. No systematic pattern for algae was found, but there appeared to be more phytoplankton in stomach contents between 15.00 and 18.00 h.

## DISCUSSION

Results presented here clearly support the hypothesis that Nile tilapia in the study area did not exhibit the same feeding habits (i.e. a herbivorous diet) as has been reported in many previous studies on the food of the species (e.g. Harbott, 1975; Getachew and Fernando, 1989; Getabu, 1994). A majority (at least 60 %) of such studies (Appendix 1) have used gill nets as the principal capture method. Therefore, the present results also indicate that although gill nets may be simple and relatively inexpensive to operate, they may not provide a full indication of the feeding habits of the Nile tilapia in Lake Victoria. As the nets are usually set in the late afternoons and left over night, only part of the available food spectrum will have been ingested, and therefore likely to appear in stomach contents. In addition, fish captured at various times and in various stomach fullness states may continue with the digestive and egestion processes at various rates. Often, this results in

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analyses based on a poor state of stomach contents. These factors may explain the generally high frequency of stomachs reported with little or no food items. Hence, the use of over-night gill net samples (Appendix 1) could partly explain under-representation of particular food items e.g., chironomids (Fig. 8) which could have disappeared from stomach contents by the following day. Also, such samples would over-represent food items ingested towards the end of the day e.g., algae as shown by Moriarty (1973), and detritus (Fig. 8), and could be a major factor in the description of *O. niloticus* as herbivorous.

For purposes of characterising food habits of the Nile tilapia in northern Lake Victoria, it was essential to analyze diurnal variation in activity and stomach fullness (Fig. 2 and 3) in order to be able to examine specimens which had stomachs containing food from within a relatively short time of capture. The day time feeding regime (Moriarty, 1973; Moriarty and Moriarty, 1973; Harbott, 1975) in the species was confirmed by these analyses. In general, stomachs appeared to start filling from about 11.00 h to 14.00 h and specimens tended to have empty stomachs between 20.00 h and 08.00 h (Fig. 2), justifying the use of catch periods (Table 1). But these patterns could also be influenced by the type of food. For example, while detritus appeared among stomach contents early and towards the end of the day (Fig. 8), chironomids increased in abundance between 09.00 h and 15.00 h after which they disappeared from stomach contents. No systematic pattern for algae was found, probably due to its minor importance in comparison to animal food items. However, there appeared to be more phytoplankton in stomach contents between 15.00 h and 18.00 h just as has been shown in some studies (e.g., Moriarty, 1973; Moriarty and Moriarty, 1973).

The wide variety of main food items in the analyzed stomachs of *O. niloticus* (Table 2) was due to sampling at appropriate feeding times in the species. It is clear that many food categories previously considered as unimportant could be classified as major dietary items (i.e. more than 50 % of guts on average, but repeatedly filling 100 % of stomachs). The relatively low percentage of phytoplankton (uncontaminated algae) (Table 2) in all size groups in comparison to the emphasis given to the importance of the food category in literature data (Appendix 1), particularly values of at least 70 % (Moriarty, 1973), shows that the examined Nile tilapia in Lake Victoria cannot be classified as a pure herbivore or phytoplanktivore. The under-representation of other food items such as molluscs and chironomids may have been due to inadequate sampling. The ingestion of such a wide variety of food items suggests that the Nile tilapia in this lake is best described as omnivorous, with phytoplankton also featuring as part of the food spectrum. Phytoplankton could be more important in the diet of *O. niloticus* in other lakes than was found for the species in Lake Victoria, but it is likely that due to methodological limitations (e.g., the use of over night gill net samples, reliance on frequency occurrence methods, identification of food organisms) the importance of other major items would still be underestimated.

From the specimens containing pure phytoplankton (especially blue-green algae and diatoms), it may be concluded that the species is able to filter feed, confirming earlier reports of the mechanism (Greenwood 1953; Moriarty, 1973). The relative amounts and composition of phytoplankton species in stomach analyses was likely a reflection of the variations earlier observed in the plankton (Chapter 3), and apparent in the dominance among stomach contents of filamentous forms, *Microcystis, Nitzschia, Anabaena, Lyngbya*. The same groups and diatoms (*Melosira, Navicula*) were found in abundance among stomach contents (Welcomme, 1967; Balirwa, 1990; Getabu, 1994) but the use of the frequency of occurrence method (cf. Hynes, 1950) could lead to overemphasis of their importance.

Nile tilapia also feeds near the bottom and includes detrital material in its diet. The high proportion of specimens in which phytoplankton was associated with detrital material suggests that some components of organic detritus (dead phytoplankton, bacteria, rotifers, etc) are a source of nutrition but as a whole, the quality and digestibility of detritus may depend on its C:N ratio, and therefore the type of habitat sediments. However, Moriarty and Moriarty (1973) and Moriarty *et al.* (1973) alluded to the possibility that as faeces from the algae accumulated in the stomach, would have been subjected to strong acid, the brown colour associated with bottom sediments (Fish, 1955) was in fact digested algae. In this study, it was possible to distinguish pure phytoplankton from detrital material (Table 3) in the stomach through the intestines up to rectal contents. As there appeared to be a transformation (due to digestion) of algal cells which could still be distinguished from the detrital material, it is considered that detrital material was a separate ingested category found among stomach contents. This is supported by quantitative differences in its ingestion in relation to the size of fish (Fig. 6) and approximate habitat types (Fig. 7).

The paucity of zooplankton among stomach contents of tilapia in earlier studies (Greenwood, 1953) and, in particular *O. niloticus* stomachs (Moriarty and Moriarty, 1973) was ascribed to feeding currents generated by the fish. In this study, planktonic *Chaoborus* (Macdonald, 1953) and Cladocera formed important food items and, in some specimens were main contents. The presence among stomach contents of Cladocera, *Caridina* shrimps and molluscs, and the observed 1:1 ratio of the mean weight and volume of stomach contents further suggest that various feeding modes (including active pursuit and gulping) are used in addition to filter feeding and benthic habits. Hence, apart from its omnivorous feeding habits, Nile tilapia may also be described as opportunistic. This makes the present trophic organisation of Nile tilapia in Lake Victoria (Fig. 9) more complex than previously predicted (Ligtvoet and Witte, 1991; Witte *et al.*, 1992b).

```
                    Oreochromis niloticus

        35 %          10 %          40 %          15 %

    Molluscs      small fishes
    Caridina      Trichoptera     Detrital       Higher plants
    Chironomid    Ephemeroptera   material       Algae
    larvae        Chaoborus
    Oligochaeta
```
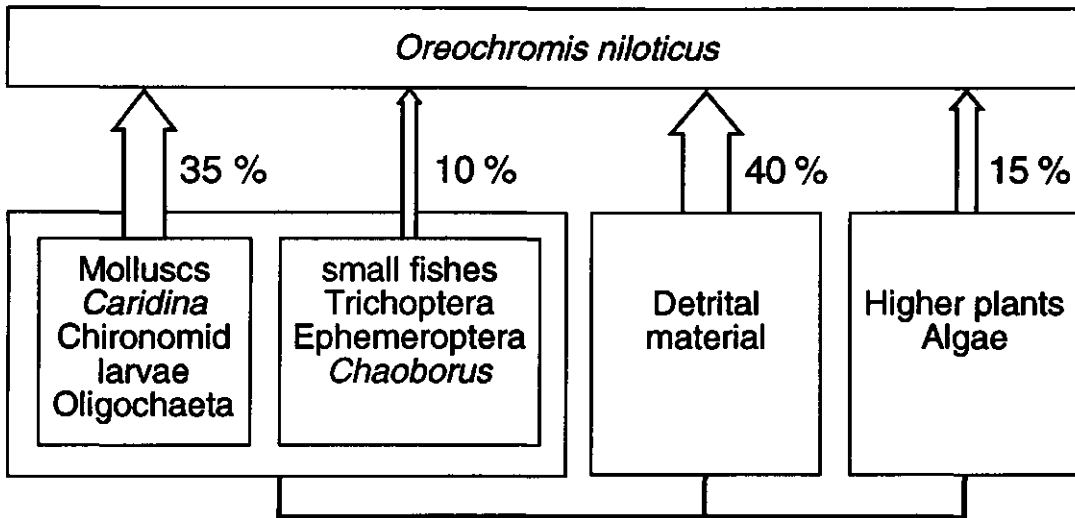
Fig. 9.     Links in the trophic structure involving *O. niloticus* from the littoral zone of northern Lake Victoria; only food items regarded as main contents in stomachs of the fish between 1995 and 1996 are considered; size classes are not considered; the percentages given are estimates of the likely nutritional value in energy terms according to the relative importance of grouped categories in relation to assumed C:N ratios.

It is doubtful that apart from the over-emphasis of a herbivorous diet resulting from sampling methodologies, previous investigations would totally fail to detect the increasing importance of animal foods in the diet of the Nile tilapia in Lake Victoria. There have been relatively few studies on the ecology of the species particularly on its feeding habits in the lake since it was introduced in the 1950s. In the earliest study of the species' feeding habits in the lake, Welcomme (1967) recorded 57 % (frequency method) of the specimens as containing planktonic (phytoplankton) material in contrast to 20 - 30 % frequency in this study. Bottom material with phytoplankton constituted 37 % and bottom plants 40 %, while diatoms (*Melosira* = 91.5 %, *Surirella* = 57 %) occurred in all specimens. These studies were carried out when the lake level was still high, and its effects (Chapter 3) had not stabilised. Also, this was before the reported decline in diversity and abundance of fish species as depicted recently (Ligtvoet and Witte, 1991; Witte *et al.*, 1992b; Goldschmidt *et al.*, 1993; Witte *et al.* 1995). It is therefore reasonable to consider the impact of species changes and trophic cascades in the lake on the present feeding habits of the Nile tilapia in light of other known aspects of the species ecology (Chapter 4, 5, 6). Being phenotypically plastic (Lowe-McConnell, 1958; 1975), Nile tilapia could have filled the trophic niches previously occupied by various haplochromine cichlids (Witte and van Oijen, 1990) and several non-cichlids (Corbet, 1961; Balirwa, 1984). However, as described in Chapter 4, with the exception of some cyprinids, many endemic haplochromines still occur in the

vegetated littorals in spite of Nile tilapias dominance there. The species also exhibits ontogenetic distribution patterns for breeding, shelter, and apparent habitat differences between size (age) classes have been demonstrated (Chapter 5 and 6). Similar patterns have been observed in Lake George (Burgis *et al.*, 1973) where apart from Nile tilapia, other species were also found apparently in the same niche.

Omnivory and opportunistic feeding patterns shown by the Nile tilapia in Lake Victoria could result from its phenotypic plasticity under changed ecological conditions prevailing in the lake, in contrast to the time of the first studies on the species (Welcomme, 1967). Changes such as increases in phytoplankton abundance (Ochumba, 1988; Ochumba and Kibaara, 1989; Mugidde, 1992; Hecky and Bugenyi, 1992; Hecky, 1993), and a major reduction in the intensity of the grazing food chain are suspected to have led to an increase in the abundance of various invertebrates (Witte *et al.*, 1992b; Mbahinzireki, 1994; Mwebaza-Ndawula, 1994; Witte *et al.*, 1995). It would then appear that a pool of invertebrates have become more available to Nile tilapia, and being more nutritionally beneficial, may at present contribute more to the diet than phytoplankton and higher plant material. The impact of phytoplankton abundance seems more reflected in the composition of detrital material which was largely made up of the abundant blue green algae (filamentous forms, *Microcystis*) and diatoms (*Nitzschia*) as reported in Chapter 4, in contrast to *Melosira* reported by Welcomme (1967). However, the nutritional quality of detritus could also depend on location, with areas near to the shore being less suitable than further away due to the high fraction of coarse organic matter with a high plant content. In addition, besides phenotypic plasticity, a genetically influenced response (hybridisation) which has been implicated in the species' dominant role in new habitats (Welcomme, 1967; Lowe-McConnell, 1975; Balirwa, 1990) could be another factor explaining the apparent plasticity in feeding habits and efficient utilisation of the many food items found in stomach contents.

The nutritional importance of various items ingested can be evaluated with respect to their carbon to nitrogen (C:N) ratios. These ratios have been correlated with growth and fecundity of second trophic levels (McMahon *et al.*, 1974). It has been indicated in these studies that freshwater macrophytes have C:N ratios above 17:1 (in comparison to ratios of 45:1 to 50:1 given for organic matter of allochthonous origin by Wetzel, 1983) while ratios for phytoplankton range between 4:1 and 8:1. These ratios are thought to vary with season and with habitat (Wetzel, 1983; Duarte, 1992), and variations in both TOC and total-N of sediments and plants in the study area were observed (Chapter 4). However, in spite of the variations in total organic carbon and nitrogen content of sediments with habitat, plant species and with season (Chapter 4), typical values could be derived from average conditions. For the trawled transects, the following detrital (sediment) C:N values have been estimated: Transect 1 = 40:1, Transect 2 = 30:1, Transect 3 = 20:1. For habitats associated with sandy silt sediments e.g., off *Vossia*, *Typha* and *Phragmites* as well as areas at the outer littoral fringe (Chapter 4), the C:N ratio could be less than 15:1 due to a TOC content of less than 40 % and likely contribution of aufwuchs. Using a ratio of (8:1) for phytoplankton (McMahon *et al.*,

1974), and assuming a value of 5:1 for animal foods in general, a pattern in the nutritive value of detritus with distance from the shore may explain both the increasing importance of detritus with distance from the shore, and the use by juvenile fish of shallow sandy habitats in the vicinity of vegetated shore. It is also noteworthy that transect 2 was operated from a shallow end associated with *Typha* beds where, together with *Vossia* and *Phragmites* dominated areas, the highest species diversity and densities of small fishes were found (Chapter 5 and 6).

The feeding habits of the Nile tilapia in Lake Victoria illustrate the ecological importance of the littoral zone particularly the relative importance of the associated wetland habitats in the life cycle of the species. The great abundance of invertebrates such as molluscs are known to be associated with vegetated habitats because such habitats provide a greater colonisable surface (Brown and Lodge, 1993) in comparison to other habitats in open water. Despite small samples, a similar pattern was observed in the vegetated habitats in the study area (Chapter 3) where small fishes were more abundant than in open water habitats (Chapter 5). Together with chironomids and oligochaetes, gastropods were especially important for small fish (Fig. 6) and with *Caridina*, their importance increased during the short dry cool season (Fig. 4). This season was correlated with an influx of juvenile fishes in some of the vegetated habitats, and a general increase in the biomass of all fish (Chapter 4 and 5) in all habitats. For small fishes, vegetated habitats afford protection from predation while also providing food resources for their relatively high energy demands. Their diet at this stage therefore partly accounts for the use of shallow vegetated areas. Detrital material in some of the habitats (near papyrus and water hyacinth shores) may be less nutritionally beneficial due to a high coarse litter content and a high (40:1) carbon: nitrogen ratio. For the big fishes, an invertebrate diet could be supplemented with a nutritionally better source of detrital material (C:N of 15:1) further away from the shore where their main feeding grounds occur. In this region, another pattern of invertebrate density and diversity similar to one nearer to the vegetation fringe has been demonstrated (Chapter 4). However, the relative importance in use of invertebrates especially chironomids alternates with the use of detritus according to size and season (Fig. 4 and 5) which could also be correlated with breeding seasons and habitats (Chapter 6).

The source and use of chironomids and detritus deserve further consideration. The distribution of chironomids in the lake has been described variously. According to Macdonald (1956) both chaoborids and chironomids are most abundant (density about 2000 - 2500 larvae.$m^{-2}$) in 5 - 10 m of water, and have an 8 weeks life cycle which includes 2 weeks when the first and second larval instars are planktonic. Other accounts associated chironomids either with shallow muddy areas (e.g. Okedi, 1990; Mbahinzireki, 1994), or with a wide range of habitats (Mothersill *et al.*, 1980). In a related study (Chapter 4), chironomid abundance was high off *Vossia* and *Phragmites* dominated habitats (density of 120 - 1760 and 1370 ind.$m^{-2}$ respectively) and larvae were commonly distributed in most habitats near papyrus. However, a similar pattern was identified at 400 m away from the shore (Chapter

3) suggesting that the feeding niches of small and adult Nile tilapia are most likely to be spatially separated. A considerable proportion of specimens examined during this study contained only chironomid or chaoborid larvae and others only detritus. As the Nile tilapia feeds during the day (Fig. 3), the source of larvae may be the planktonic stages in spite their possible avoidance of predators through diel vertical migrations (Irvine, 1997).

When ingested food items other than detritus were evaluated with respect to variation among trawl transects, these transects seemed less important than differences among size classes or seasons (Table 5). However, trawling in this study was restricted to transects off papyrus-water hyacinth fringes or starting from shallow areas assumed to represent *Typha* dominated habitats. A comparative sampling strategy of all vegetation types and distances (Chapter 3 and 4) could not be done. Therefore, initially, it could be assumed that although detritus was the main stomach content in terms of percent of the volume it occupied, its value as a food resource could be of secondary importance. However, a consideration of C:N ratios indicates the relative importance of detritus as a major food resource especially further away from the shore. Therefore, from the present analyses of feeding habits in the Nile tilapia, it appears that a part of the impact of species changes which has been associated with predation by the Nile perch (Ogari and Dadzie, 1988; Ogutu-Ohwayo, 1990; Ligtvoet and Witte, 1991; Kudhongania *et al.*, 1992; Witte *et al.*, 1992a; Goldschmidt *et al.*, 1993) could also have been caused by the Nile tilapia. According to some of these studies (e.g., Goldschmidt *et al.*, 1993), detritivorous haplochromines comprised the highest biomass (31 %) and density (number) (37.7 %) by 1982 down from 54.5 % and 61.3 % respectively in 1979 in the sub-littoral zone. It appears that due to its benthic feeding habits, its high biomass (45 - 60 %) in comparison to all fish in shallow areas (Chapter 5), high fecundity (Chapter 6) and, its use of detrital material some distance away from the shore (i.e. the sub-littoral zone), the impact of the Nile tilapia on haplochromine displacement and other detritivorous fish could be considerable.

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Appendix 1. The major food items identified in *O. niloticus* stomachs from some previous studies.

| Lake | Major food items | source | sampling method |
|---|---|---|---|
| Albert | phytoplankton | Lowe-McConnell, 1958 | gn |
| Edward | phytoplankton and diatoms | Lowe-McConnell, 1958 | gn |
| George | phytoplankton | Lowe-McConnell, 1958 | gn |
| George | Phytoplankton especially blue green algae | Moriarty, 1973 | sn |
| Rudolf (Turkana) | diatoms and blue greens | Lowe-McConnell, | gn |
| Turkana | diatoms and blue greens | Harbott, 1975 | sn |
| Baringo | algae and bottom deposits | Okorie, 1975 | gn |
| Awasa | Phytoplankton especially blue-green algae | Getachew and Fernando, 1989 | gn |
| Victoria | Phytoplankton, bottom deposits | Welcomme, 1967 | gn |
| Victoria | detritus, invertebrates and phytoplankton | Balirwa, 1990 | tr |
| Victoria | blue-green algae, diatoms aquatic invertebrates | Getabu, 1994 | tr |

gn = gill nets, sn = seines, tr = trawls
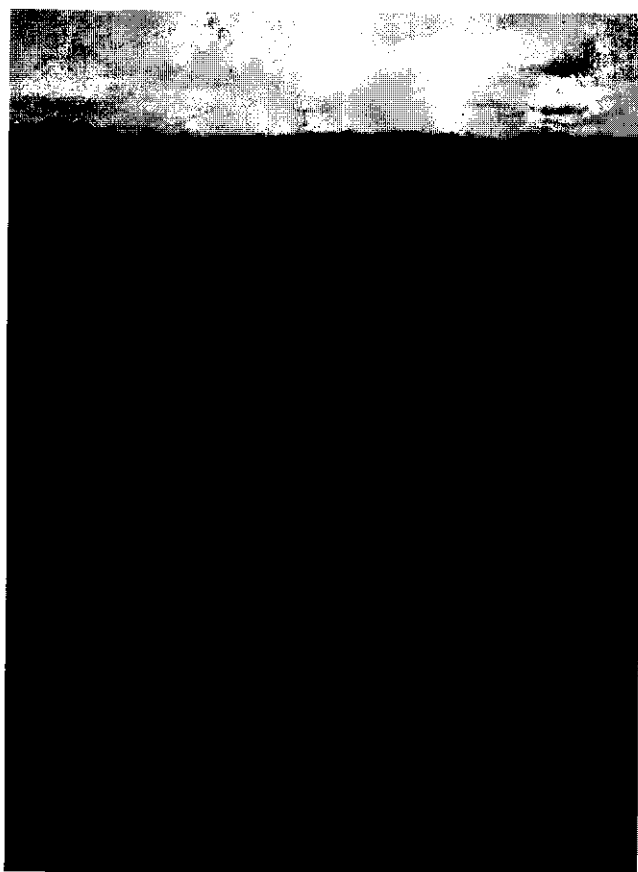
# Chapter 8

# The growing influence of water hyacinth *Eichhornia crassipes* (Martius) Solms-Laubach on the ecology of the shoreline wetlands of Lake Victoria, East Africa[*]

## ABSTRACT

The influence of the alien water hyacinth (*Eichhornia crassipes*) on some ecological aspects of the shallow vegetated habitats in northern Lake Victoria was investigated between 1993 and 1996. Water hyacinth was associated with habitats occupied by *Cyperus papyrus* (papyrus) and *Vossia cuspidata* (hippo grass) on the landward side while the natural water plants (euhydrophytes) such as *Nymphaea*, *Ceratophyllum* and *Pistia* were common at the interface with the dominant emergent macrophytes. Over the study period, the aquatic weed which expanded by 200 %, also led to an increase in the cover of the native emergent macrophyte, *V. cuspidata*. Over the same period, water plants such as *Nymphaea*, *Ceratophyllum* and *Pistia* declined to almost total disappearance in the study area. In terms of water quality, seasonal variations in temperature were small (25 - 27 $^{\circ}$C); others like pH (7.7 - 8.2), DO (6.7 - 6.9 mg.l$^{-1}$) total-P (41 - 48 ug.l$^{-1}$) varied more, but for some parameters like oxygen, pH and temperature, diurnal variations could have also been important. A comparison of *C. papyrus*-dominated shallow habitats with those occupied by *E. crassipes* showed that water hyacinth-dominated habitats had significant (p < 0.05) effects on a range of water quality parameters particularly dissolved oxygen, pH, NO$_3$-N, but no significant effects on conductivity and chlorophyll were apparent. Within *E. crassipes* differences were distinct; dissolved oxygen averaged 5.4 mg.l$^{-1}$ under the mats in comparison to 8.0 mg.l-1 in open water. The % AFDW of the sediments ranges from 60 % under water hyacinth mats to 40 % in areas at about 350 m further away from the fringes of both papyrus and water hyacinth. No significant differences (p > 0.05) in % AFDW between the two habitats were observed but water hyacinth had a significantly higher nutrient (P, N) content particularly in the roots than *C. papyrus* had. A high diversity and abundance of epiphytic invertebrates were associated with the weed's root zone but sediments under water hyacinth were poor in both indices in comparison to sediments in other vegetated habitats.

## INTRODUCTION

A large part of eastern and central Africa is occupied by water bodies many of which are bordered by extensive emergent wetland vegetation often referred to as swamp. In Lake Victoria, although hydrological influences (seasonality) were the main factor explaining variation in structural characteristics of the shallow vegetated habitats, wetland vegetation was also found to be important in determining variations in some aspects including fish populations (Chapter 3). Under the observed hydrological regimes, and with altered land use, native wetland vegetation may attain prolific growth and become a weed problem especially in these shallow habitats. Apart from altered land use, warm moist conditions and ample nutrients could contribute to the prolific growth of the plants; the weeds then form dense floating or submerged mats, and become an environmental and socio-economic nuisance in a variety of ways. The mats choke waterways and navigation routes or smother lake shores, river banks and small water bodies,

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particularly ponds and dams (Thompson, 1991). Such water weeds thus cause mostly undesirable effects on navigation, fishing activities, hydro-power generation, industrial and potable water abstraction and public health. Most of those effects are quickly noticed and easily appreciated by the user communities of the environments impacted by the weeds.

A classic example of such aquatic weeds has been the introduction of alien water plants like the water hyacinth *Eichhornia crassipes* (Martius) Solms-Laubach in many countries of the tropical and sub-tropical world including Africa (Harley, 1993). Apart from the negative socio-economic effects associated with aquatic weeds, the impact of aquatic weeds may also be evaluated in terms of their ecological influence in the new environment. For example, prolific growth of one weed species may lead to competition and displacement of others. Generally, in comparison to socio-economic impacts, ecological transformations may be slow, subtle and difficult to characterise. They could involve a gradual transformation of water quality, sediments, thus fish habitats and fish populations. Although slow to manifest, in the long run the impacts on the environment and resources infested could be far reaching. Such ecological impacts, influenced by infestation with the alien *E. crassipes*, may be starting to show in the shoreline wetlands of Lake Victoria, where the weed was first reported in 1989 (Taylor, 1993).

The water hyacinth is reported to have been introduced into Egypt between 1879 and 1892 (Gopal and Sharma, 1981), South Africa, 1910, Zaire (Congo River) 1952 (Gopal, 1987) and had appeared in Uganda by 1976 (Robson, 1976). The most recent outbreaks of the weed's problems have been in Nigeria, Cote d'Ivoire, on Lake Victoria (East Africa) and on Lake Chivera (Zimbabwe) (Taylor, 1993). In Uganda, *E. crassipes* was recorded in 1988 in Lake Kyoga (Fig. 1), where it was probably introduced around 1985 (Twongo, 1991; 1993). The introduction of the weed in Lake Victoria seems to have been from Rwanda via the Kagera river, a major inflow to Lake Victoria contributing about 12% to its yearly input. In this lake, the weed may have been first observed around 1981 but was reported in 1989 (Taylor, 1993). By 1991 *E. crassipes* had spread up to Kampala and by 1992, the first plants were seen in the Jinja area where the present investigations were carried out (Chapter 1). However, the spread of the weed in Uganda generally appears to have been from east to west in the Lake Kyoga region (Fig. 1); this pattern could not directly be associated with the Victoria Nile infestation (Taylor, 1993).

Given its geographical features (Chapter 1) and its proximity to other impacted water bodies in the region, Lake Victoria was always likely to become infested with the water hyacinth. At present, infestations appear to be concentrated in the Uganda part of the lake. This pattern could be due to several factors. In comparison to the lake's entire shoreline length (3,440 km), the fraction of the shoreline of Lake Victoria in Uganda, excluding islands, is quite large (about 1000 km). In addition, the swampy shoreline in Uganda is comparatively more highly convoluted with many shallow sheltered bays, indentations and numerous inlets. These could

prevailing winds of Lake Victoria generally show a daily shift at about 12.00 h from
north-east to east in the morning, backing to south-west to west in the afternoon
(Welcomme, 1964), extensive mats which are blown towards the different areas
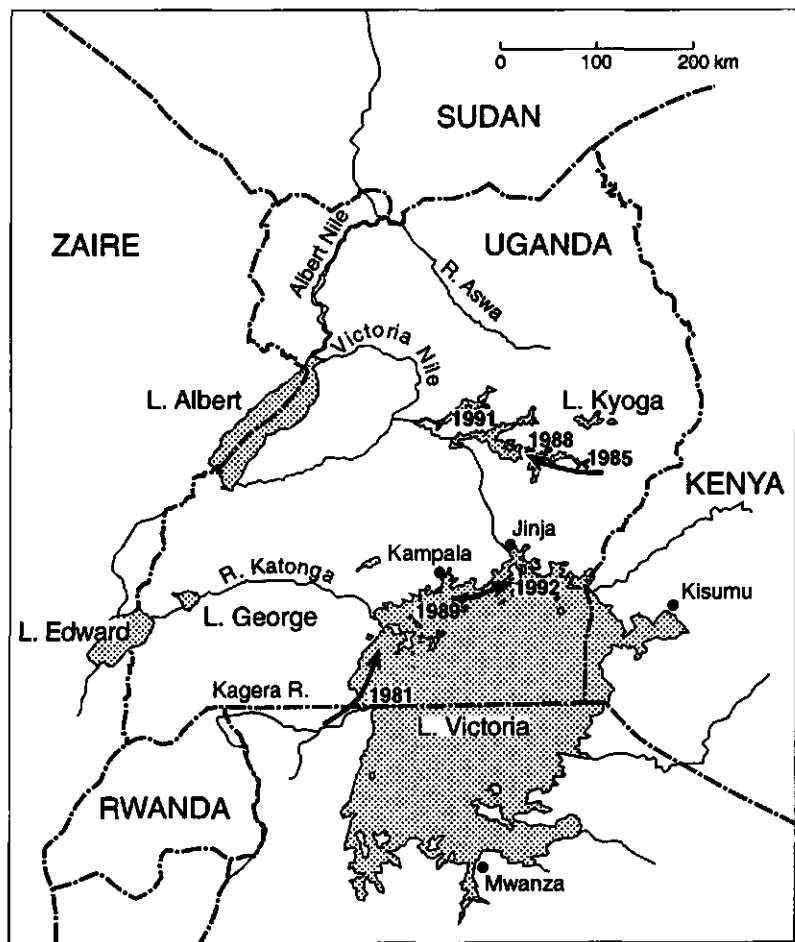


Fig. 1.     The spread of the water hyacinth in Uganda.

of the coastline by onshore winds tend to accumulate in the shallow swampy
sheltered parts of the bays. In some of the very shallow ones, water hyacinth
plants tend to become rooted to the bottom and acquire a semi-permanent status.
In addition, there appears to be a regular influx of extensive *Eichhornia* mats which
are swept into the lake from the River Kagera current and subsequently move along
a north-east axis according to the prevailing wind patterns over the lake. The
distribution pattern of water hyacinth in the lake tends to follow previously
predicted trends (Twongo *et al.*, 1991; Twongo and Balirwa, 1995; Willoughby *et
al.*, 1993). Such situations may provide conditions in which ecological impacts may
be quickly manifested. Many of these localities are associated with other water

plants such as the euhydrophytes (Denny, 1985) and, therefore are ideal for studying the long-term ecological effects of water hyacinth on shallow habitats in the lake. However, despite its rapid spread in the Uganda part of Lake Victoria, only the negative socio-economic impacts have been more fully appreciated.

Most of the shallow interface habitats which are prone to water hyacinth infestations are bordered by native emergent vegetation (e.g. *Cyperus papyrus*, *Vossia cuspidata*, *Typha domingensis* and *Phragmites mauritianus*) and scattered patches of euhydrophytes (true water plants) (e.g., *Pistia stratiotes*, *Nymphaea caerulea* and *Ceratophyllum demersum*). They are areas of high biodiversity particularly of fish (Chapter 4). Even though the euhydrophyte beds may not presently be as common as previously reported (Carter, 1955; Lind and Visser, 1962), the width of the littoral zone in the present studies could still be based on secchi transparency and the influence of emergent vegetation on the adjacent shallow habitats in the lake (Chapter 3). As water hyacinth has become a common feature in the associated bays, often smothering beds of the indigenous euhydrophytes and disrupting traditional inshore fisheries, it is considered that the weed could ecologically alter structural characteristics in the infested habitats. Therefore, in view of the established importance of these littoral environments as habitats with a higher fish diversity in comparison to open water (Ch 4), and as sheltering, breeding, nursery and feeding grounds for the commercially important Nile tilapia, *Oreochromis niloticus* (Chapter 5), there is need to determine the influence of alien *E. crassipes* on the ecology of the zone, and to provide an indication of baseline conditions in the early stages of infestations.

This study therefore investigated the growing influence of *E. crassipes* and its impact on the distribution of indigenous euhydrophytes, on the water quality, the diversity, distribution and relative abundance of the macrobiota (macrofauna) in shallow wetland vegetation-fringed habitats of northern Lake Victoria. *C. papyrus*, *V. cuspidata*-dominated and *E. crassipes*-infested habitats were investigated in detail for several reasons: *C. papyrus* is the most characteristic and most dominant plant species of the shoreline, and *E. crassipes* tended to associate with it only in specific areas; in other areas, *C. papyrus*-dominated habitats appeared to remain relatively clear of the weed. However, from previous multiple comparisons of structural differences among the various shallow aquatic habitat types (Chapter 3), *C. papyrus* and *E. crassipes*-dominated habitats shared some similarities in sediment characteristics and water quality. With *C. papyrus* as the dominant vegetation in the background, it was thus not very clear in what other respects significant differences between the two habitat types could lead to inferences on the ecological impact of water hyacinth. *Vossia cuspidata*, on the other hand, though not as common as these two, had been observed to form what was then considered as a stable successional combination with *E. crassipes*.

## MATERIALS AND METHODS

**Study area and sites**

Studies were carried out near Jinja town in an area (Latitudes 0° 22N; 0° 30N and Longitudes 33° 10E; 33° 26'E) along the northern shores of Lake Victoria in Uganda. The experimental area covered a shoreline length of about 110 km (including islands) and had an open water surface area of about 133 $km^2$. Sampling sites were identified along the shoreline of wetland-fringed bays found in this zone, and have been described in detail in Chapter 3. Selection of the sites for this study was based on the stability of *C. papyrus*, *E. crassipes* and *V. cuspidata* stands which appeared to be undisturbed by human activity. In all, five stands of each of *C. papyrus* and *E. crassipes*, and one of *V. cuspidata* were studied between 1993 and 1996.

**Vegetation characterisation**

Studies along the shoreline were made using a fibreglass canoe powered by an outboard engine. Characterisation of shoreline vegetation was made in 1993 and 1996 according to the methods described in Chapter 3. This characterisation included macrophyte species identification, abundance (cover) estimates, ash-free dry weight (AFDW) determinations as well as analyses of plant nutrients (P, N). Samples for biomass and nutrient analyses of *Cyperus papyrus* were taken in August 1993, February 1994, August 1995 and May 1996. Samples for biomass analyses of *Eichhornia crassipes* were taken in August 1995 and May 1996; nutrients of this macrophyte were analyzed in May 1996.

For the purpose of this paper, emphasis was placed on selected wetland patches of the shoreline, some of which were associated with indigenous euhydrophytes particularly *Pistia stratiotes*, *Nymphaea caerulea*, *Ceratophyllum demersum*, and the alien *Eichhornia crassipes*. The alien weed was also regarded as part of the mosaic of floating and submerged shoreline vegetation (i.e. true water plants).

**Water quality, algal biomass and macrofauna sampling**

Sampling stations bordered selected continuous stands dominated by *C. papyrus* and *E. crassipes*. The design allowed comparison of the influence of the water weed in *E. crassipes* vs *C. papyrus* shallow water habitats. Water quality variables included temperature, electric conductivity, redox potential, pH, dissolved oxygen, alkalinity, Si, ortho-P, total-P and nitrate-N. Water samples were taken (Chapter 3) at the edge of the vegetation (0 m), 10, 20, 40, and at 350 - 400 m offshore, as well as, in the case of *E. crassipes*, at 5 m inside the vegetation mats.

Phytoplankton (chlorophyll-a) was studied according to the methods described in Chapter 3. Bottom samples for sediments and for macrofauna assessment were collected separately using a Ponar Grab; macro-invertebrates associated with water hyacinth roots were sifted from material collected in 0.25 $m^2$ quadrats. The two macrofauna groups (from sediments and from roots) were analyzed separately.

All samples for dissolved oxygen, algal biomass (seston), other water quality parameters and macrofauna assessment were taken in triplicate at each sampling point.

## Survey data collection

A strategy to study the distribution, areal cover, biomass and movement of *E. crassipes* was modified from that descibed by Twongo and Balirwa (1995). In the present study, monitoring initially focused on shoreline areas with a potential for establishment and proliferation of water hyacinth (Twongo *et al.*, 1993). Subsequently, detailed surveys which covered mainland and island shores of Lake Victoria in Uganda, were conducted between August 1994 and December 1996. A similar survey was carried out in parts of Lake Kyoga (Fig. 1) at about the same period.

To estimate areal cover of large fields of mobile water hyacinth, the extent of the weed was demarcated on a map in the evenings when strong landward breezes had piled it along the shoreline. The area covered was then estimated from maps. A similar method was used to estimate continuous mats along the shore; the width across the mat from the open water edge to the shore was often averaged from four independent estimates made by eye. On the other hand, the area of mobile mats offshore was calculated from estimated dimensions obtained from timed steady runs by outboard motor whose speed had been established under prevailing weather conditions. The percentage cover of water hyacinth mats along a given section of shoreline was derived from drawn sketches of weed patches in heavily infested bays in addition to visual impressions of several observers along the sparsely infested shores. Biomass per square metre was determined in triplicate at various locations using a 0.25 m² quadrat, to account for differences in water hyacinth growth habit and vigour.

## Data analyses

Analysis of cover changes was based on percentages following the procedure described in Chapter 3. For other data (water quality, sediments, algal biomass, macrofauna), arithmetic means and standard errors were calculated. Factor levels (as *C. papyrus* or *E. crassipes*-dominated habitats), distance (as horizontal effects of vegetation type from the edge of *C. papyrus* ( 0 m) or from 5 to 10 m (also referred to as -5 m or -10 m) into *E. crassipes* mats outwards into open water), season (as defined in Chapter 3 and 4) and interaction effects between factors, on water quality and macrofauna were tested by ANOVA ($p < 0.05$) using the SPSS software. Unless stated otherwise, this significance level was maintained in all comparisons. Probability levels of 0.05 or less indicated significant effects. Only probability levels (p) of the various factors and the percentage of explained variance due to significant factors are reported.

# RESULTS

## Change in vegetation cover

From isolated sightings of water hyacinth in various parts of Lakes Victoria and Kyoga in 1993, the weed had become a common feature of bays and other shallow indented coastline areas in these two lakes by 1995. Initially, the distribution of the weed was highly dynamic and was strongly correlated with the intensity and direction of the prevailing winds. The mostly mobile water hyacinth mats were periodically blown by violent off-shore storms towards the open lake, resulting into further spread of the weed over the lake and, variations in cover. Table 1 summarizes the 1995/1996 data on water hyacinth cover in selected areas in Lake Victoria and Lake Kyoga. A striking aspect of cover change was the phenomenal increase in cover in Thruston Bay where water hyacinth covered an estimated area of 108 ha (Table 1), thus completely shading out the previously dominant euhydrophytes.

Table 1. Areal cover of mobile mats and mean fresh biomass of *Eichhornia crassipes* in the inshore shallow bays of northern Lake Victoria and selected localities in Lake Kyoga (1995/1996).

| location (bay) | *Eichhornia crassipes* cover (ha) | mean biomass (kg fresh weight.m$^{-2}$) |
|---|---|---|
| **Lake Victoria** | | |
| Pringle | 15 | - |
| Macdonald | 13 | 42.9 |
| Hannington | 96 | 58.8 |
| Thruston | 108 | 59.5 |
| Fielding | 6 | 57.3 |
| Grant | - | 40.8 |
| Buka | - | 68.0 |
| Bay of Kome Island | - | 39.9 |
| Inner Murchison | 620 | 63.9 |
| Entebbe Peninsular | 257 | - |
| Busi | - | 59.6 |
| Katonga | - | 74.2 |
| **Lake Kyoga** | | |
| Kapiokolo | - | 80.2 |
| Kyankole | - | 55.5 |
| Zengebe | - | 62.8 |

In 1993 the dominant indigenous euhydrophytes in the experimental area in northern Lake Victoria (Chapter 3) were the rooted *Nymphaea cearulea*, the floating *Pistia stratiotes* and the submerged *Ceratophyllum demersum* occasionally mixed with *Utricularia* sp. (Fig. 2A). These macrophytes considered together, occurred in
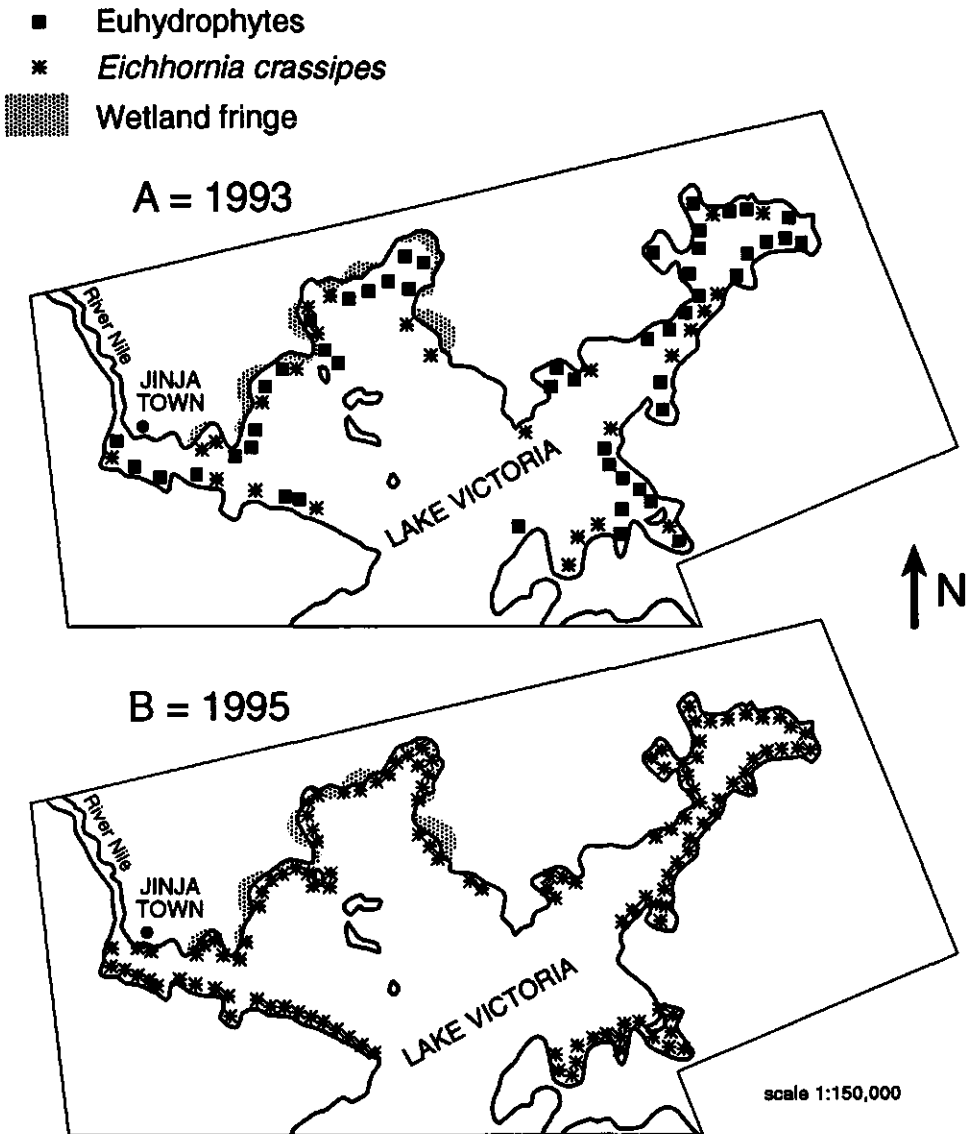
- ■ Euhydrophytes
- * *Eichhornia crassipes*
- ▨ Wetland fringe

A = 1993

B = 1995

N

scale 1:150,000

Fig. 2.    Distribution of euhydrophytes and *Eichhornia crassipes* in Lake Victoria, Jinja area.
a. 1993; b. 1995.

occasionally frequent patches (i.e rated as occupying 5 - 25 % of the shoreline water surface in the study area, see Chapter 3, Materials & Methods) except in Thruston Bay (Chapter 3) where extensive patches of *C. demersum* covering several hectares adjacent to the wetlands were noted. In that bay, euhydrophytes could be rated as abundant (i.e covering 51 - 75 % of the area). In comparison, water hyacinth at that time was rated occasional (rated at less than 5 % of the water surface), occurring in small mats or as individual plants hidden among the emergent vegetation. By the end of 1996 virtually all the beds of indigenous euhydrophytes close to the shore had been smothered by a resident fringe of water hyacinth about 10 to 20 m wide (Fig. 2B).

A comparison of cover abundance of selected euhydrophytes, the introduced *Eichhornia crassipes* and the emergent macrophyte *Vossia cuspidata* in the study area is given in Table 2. Data indicate a dramatic increase of 60 % and 200 % in the cover of *V. cuspidata* and *E. crassipes*, respectively. Conversely, the cover index of the indigenous euhydrophytes declined drastically to near disappearance. The increase in cover abundance of *E. crassipes* over the 110 km shoreline of the study area is also illustrated in Fig. 2B. There was no apparent change in cover of *C. papyrus*.

Table 2.    Percentage change (1993/1996) in cover abundance from the total score in 38 sites of northern Lake Victoria.

| species | 1993 | 1996 | % change |
|---|---|---|---|
| *Vossia cuspidata* | 52.6 | 83.5 | 58.7 |
| *Eichhornia crassipes* | 11.5 | 163.5 | 217.5 |
| *Pistia stratiotes* | 6.1 | 0.1 | - 98.4 |
| *Nymphaea caerulea* | 8.6 | 0.1 | - 98.6 |
| *Ceratophyllum demersum* | 0.6 | 0.0 | - 100 |

**Macrophyte biomass, sediments and nutrient content**
In Fig. 3 the biomass of *C. papyrus* and *E. crassipes* is given as ashfree dry weight of above as well as below water parts of the macrophytes. In 1993 and 1994 *E. crassipes* was present in low quantities in the research area. In 1995 and 1996 the weed had increased to large numbers, although the total biomass, of both above and below water, was still very low, compared to *C. papyrus*. The slight decrease in *E. crassipes* biomass in 1996 could be due to seasonality. The biomass data of *C. papyrus* are very variable from year to year as well as from location to location. It is not clear whether this is the result of the sampling and analyzing procedures used but it could also have been due the uneven terrain and micro-habitat differences in the sampled locations (see also Chapter 3). Variations in nutrient content of the sediment (mgP.g$^{-1}$, mgN.g$^{-1}$ DW of sediment, N:P) in the *C. papyrus*- and *E. crassipes*-dominated habitats were largely influenced by season (Table 3).

**plant biomass**
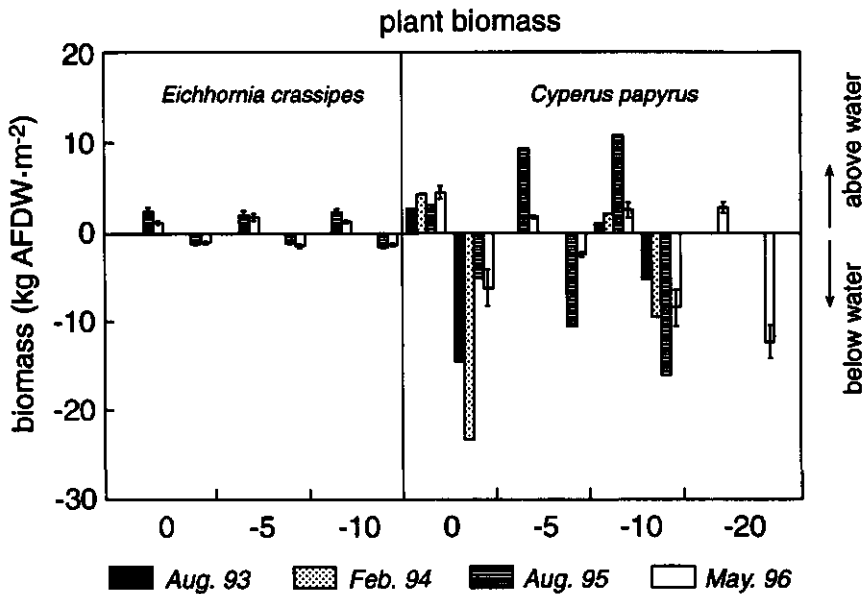
Fig. 3. *Cyperus papyrus* and *Eichhornia crassipes* biomass as ashfree dry weight. Above water as well as below water parts of the macrophytes are indicated.

Table 3. Three-way ANOVA for assessing the effects of vegetation type (as habitat dominated by either *C. papyrus* or *E. crassipes*), season (long wet: 16 March - June, short dry: July - 15 September, long dry: December - 15 March) and distance (from the vegetation edge or 5 m inside water hyacinth mats up to 350 m away towards open water) on sediment nutrient content ($mgP.g^{-1}$, $mgN.g^{-1}$ DW of sediment, N:P, % AFDW). Levels of significance = p, % SS = factor SS/explained SS * 100, a measure of variation explained by that factor; a significant factor = $p < 0.05$.

| Factor: | Vegetation | | Season | | Distance | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| $mgP.g^{-1}$ | 0.471[ns] | - | 0.000[*] | 81 | 0.002[*] | 8 |
| $mgN.g^{-1}$ | 0.001[*] | 21 | 0.000[*] | 74 | 0.212[ns] | - |
| N:P | 0.000[*] | 13 | 0.000[*] | 80 | 0.005[*] | 13 |
| % AFDW | 0.047[*] | 6 | 0.000[*] | 26 | 0.005[*] | 15 |
| C:N | 0.901[ns] | - | 0.074[ns] | - | 0.666[ns] | - |

[*] = significant, [ns] = not significant.

Seasonal influences (rainy-dry periods) explained more than 70 % of the observed variation in three of the tested parameters. Distance from the vegetation edge in papyrus (or -5 to -10 m into *Eichhornia* mats) was the major factor accounting for variation in % AFDW (a measure of the carbon content of the sediments). To a lesser extent (6 - 21 % of the observed variation), vegetation type also had significant effects on N, N:P and % AFDW but no significant effects of any of the factors were seen when the C:N (in the C:N, the carbon content is obtained by conversion of the % AFDW with a factor of 0.4, Hootsmans and Vermaat, 1991) was used, indicating uniformity in carbon content in the two habitat types. The % AFDW ranged between 40 % $\pm$ 1 % in sites further away from the shore to 62 % $\pm$ 8 % under water hyacinth mats (Fig. 4).
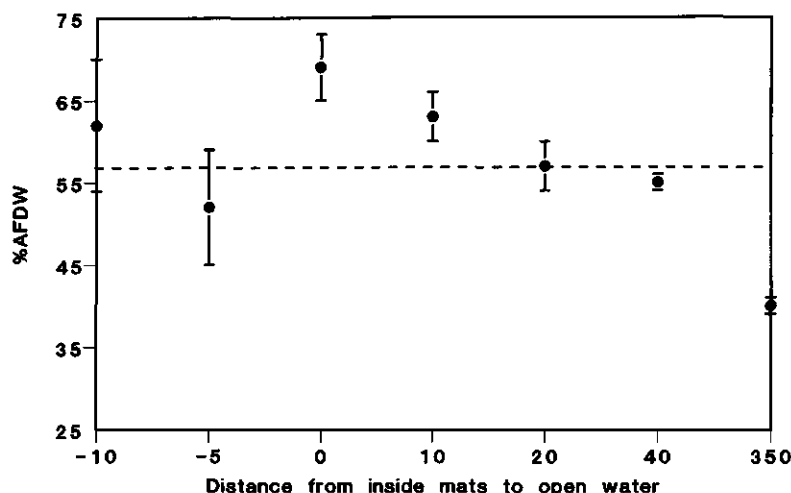


Fig. 4.          Variations in % AFDW with distance (from within the mats of water hyacinth up to further away from the vegetation) in samples pooled across *C. papyrus* and *E. crassipes* habitats.

In Appendix 1 the plant-nutrient composition of different sections of *C. papyrus* and *E. crassipes* is given and is compared with the concentrations in sediment of the habitats examined. In Fig. 5 and 6 the plant-nutrient composition is depicted for the above water plant parts (in *E. crassipes*: petiole and leaves; in *C. papyrus*: culm (base and apex), umbel and inflorescence) and below water plant parts (in *E. crassipes*: roots; in *C. papyrus*: roots and rhizome). Fig. 5 shows the seasonal differences in nutrient content of *C. papyrus* (May vs. August, i.e. long wet vs. short dry season). There is a clear seasonal difference in the total-P content of *C. papyrus* plants at the 2 - 5 m and the 10 m inside the swamp sites, i.e. in August less than 50 % of the May (below water) values is found. The total-P content is fairly constant from the edge of the vegetation to 10 m inside the vegetation; this is true for both the May and the August series.
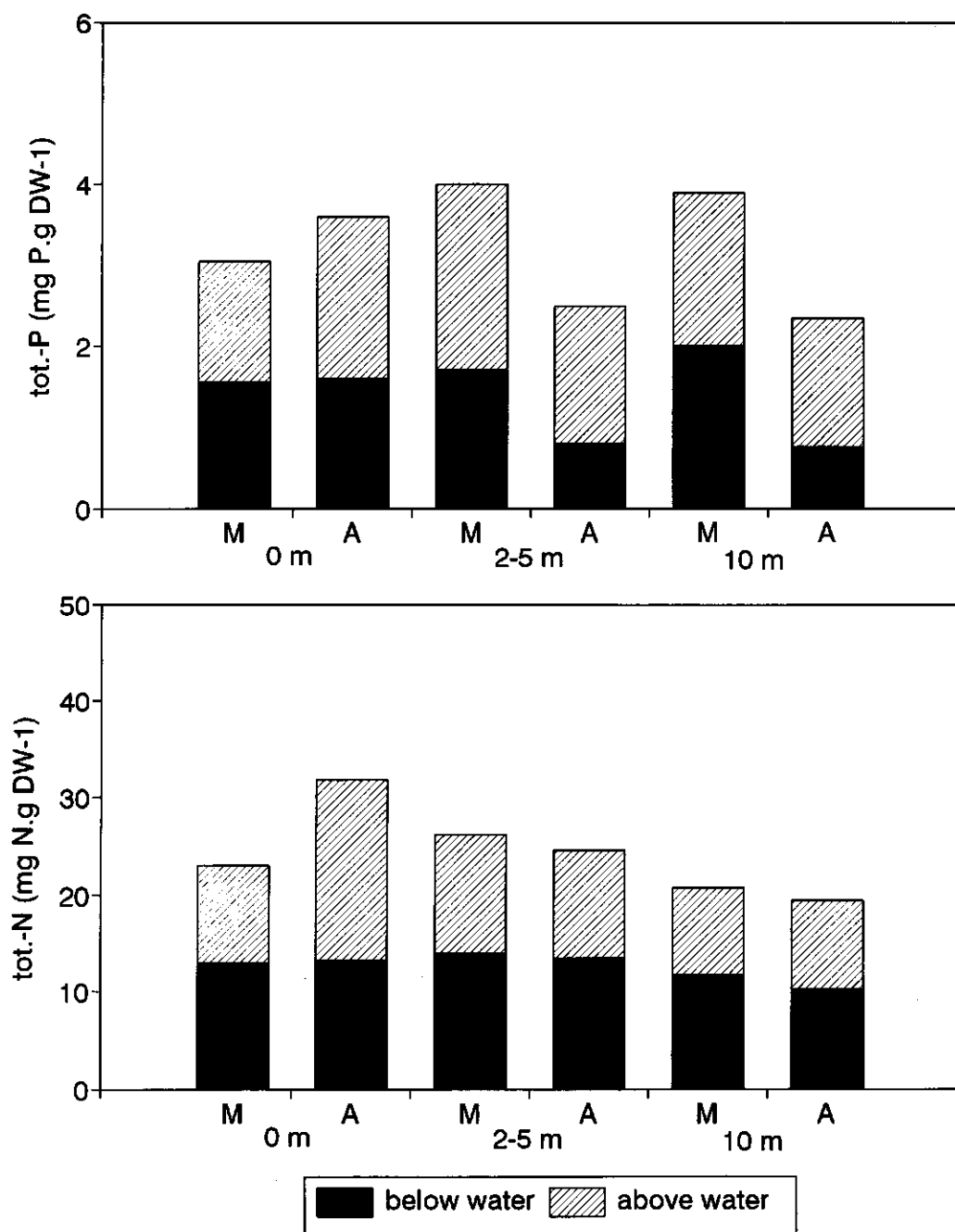
Fig. 5.     Seasonal differences in nutrient content (above: tot.-P; below: tot.-N) of *C. papyrus* (May vs. August, i.e. wet vs. dry season; mg.g DW$^{-1}$).
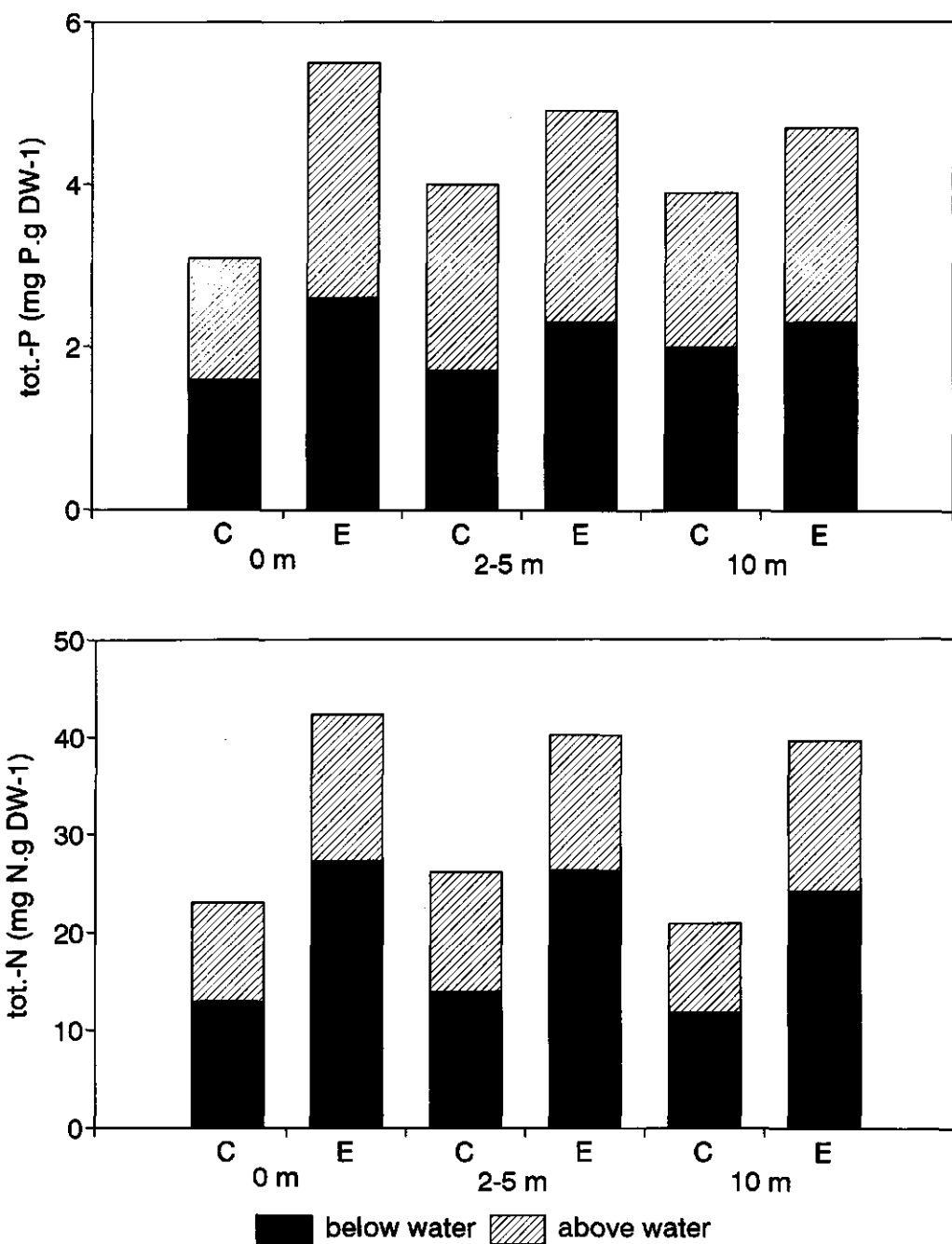
Fig. 6.    Nutrient content (above: tot.-P; below: tot.-N) of *C. papyrus* and *E. crassipes* (May series; mg.g DW⁻¹).

In Fig. 6, the May series of *C. papyrus* and *E. crassipes* plant nutrient content are compared. The most prominent feature of this figure is the much higher nutrient concentration in *E. crassipes* plants. This difference is completely accounted for by the below water plant parts. This indicates that *E. crassipes* retains more nutrients, particularly nitrogen, in its below water parts. In comparing the nutrient storage per unit area (Fig. 7) the differences between the two species appear negligible, except for plants at the edge i.e 0 m (both total-N and total-P) and 10 m inshore (total-P).
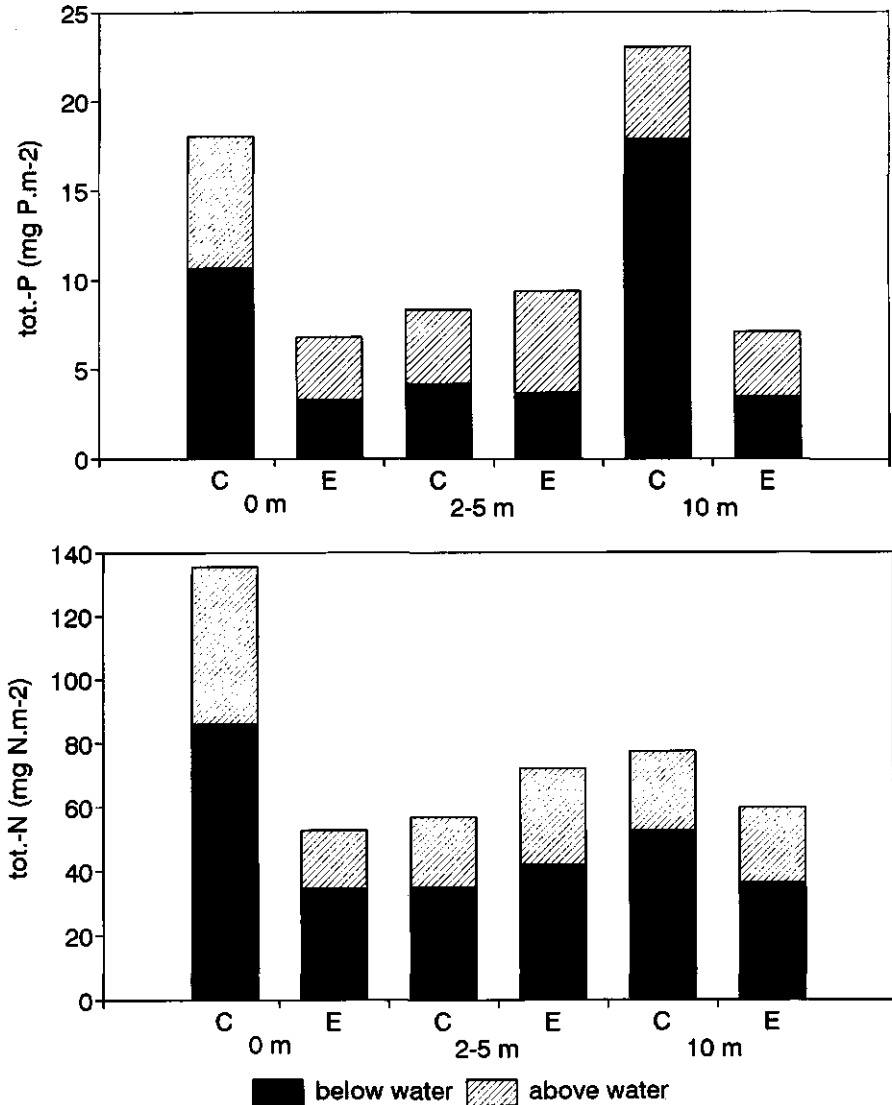


Fig. 7.        Nutrient content of *C. papyrus* and *E. crassipes* (May series; mg.m⁻²).

Appendix 2 illustrates the seasonal change in total-P and total-N content of the sediments in *E. crassipes* and *C. papyrus* habitats at different distances from the edge of the vegetation. From this table it can be seen that the *C. papyrus* sediments have a consistently higher nutrient content than the *E. crassipes* sediments. Different nutrient contents at the various distances are not pronounced.

**Water quality and diurnal measurements**
Appendix 3 summarizes the water quality data for *C. papyrus* and *E. crassipes*-dominated shallow water habitats (mean of 5 sites each). From these tables it appears that differences in water quality between both vegetation types are negligible, except for the higher nitrate-concentrations in *E. crassipes*.

A three-way ANOVA to evaluate the significance of different factors (vegetation as either *C. papyrus* or *E. crassipes* representing habitat type, distance across the width of the shallow littoral from the edge or inside water hyacinth mats up to 350 m away towards open water, season and interaction) in their effects on water quality (Table 4) showed that seasonal influences largely explained most of the observed patterns.

Table 4. Three-way ANOVA for assessing the effects of vegetation type (as habitat dominated by either *C. papyrus* or *E. crassipes*), season (long wet: 16 March - June, short dry: July - 15 September, long dry: December - 15 March) and distance (from the vegetation edge or 5 m inside water hyacinth mats up to 350 m away towards open water) on a range of investigated water quality parameters. Levels of significance = p, % SS = factor SS/explained SS * 100, a measure of variation explained by that factor; a significant factor = $p < 0.05$.

| Factor: | Vegetation | | Season | | Distance | |
|---|---|---|---|---|---|---|
| | p | % SS | p | % SS | p | % SS |
| Si | 0.073 | ns | 0.000* | 97 | 0.340 | ns |
| SRP | 0.962 | ns | 0.000* | 54 | 0.000* | 36 |
| Tot.-P | 0.192 | ns | 0.000* | 21 | 0.000* | 75 |
| $NO_3$-N | 0.000* | 5 | 0.000* | 54 | 0.000* | 37 |
| Chl.a | 0.797 | ns | 0.000* | 84 | 0.050* | 15 |
| Seston | 0.367 | ns | 0.039* | 20 | 0.006* | 79 |
| temp. | 0.033* | 1 | 0.000* | 99 | 0.288 | ns |
| pH | 0.000* | 18 | 0.000* | 68 | 0.000* | 15 |
| DO | 0.616 | ns | 0.040* | 16 | 0.000* | 84 |
| Cond. | 0.826 | ns | 0.000* | 90 | 0.897 | ns |
| Redox | 0.000* | 30 | 0.000* | 76 | 0.999 | ns |

* = significant, ns = not significant.

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Vegetation type explained little of the observed variation; only in NO$_3$-N, temperature, pH and redox were the differences explained by vegetation initially noticeable.

However, data also show that distance had considerable effects on some parameters (NO$_3$-N, pH) in which variation was also explained by vegetation. When season was suppressed in the analyses, significant influences of vegetation on other water quality parameters (Si, SRP, Tot.-P, NO$_3$-N, DO) were discerned in differences between *C. papyrus* and *E.crassipes* dominated habitats (Table 5).

A major difference between the two vegetation-dominated habitats was the nature of variation due to distance. Unlike in habitats dominated by *E. crassipes*, within papyrus distance effects were not significant (p >> 0.3) for all the tested parameters. In *Eichhornia*, significant differences (p < 0.05) due to distance were observed in SRP, Total-P, NO3-N, chl.-a, pH and DO (Table 6).

Table 5.    Mean values ( ± s.e., n = number of analyzed samples) pooled across seasons and distances (from the edge or -5 m up to 350 m towards open water) for water quality parameters (Si, SRP, NO$_3$-N, Chl.-a, seston in $\mu$g.l$^{-1}$; DO in mg.l$^{-1}$, conductivity in $\mu$S.cm$^{-1}$, redox in mV) in which significant (p < 0.05) differences between *C. papyrus* and *E. crassipes* dominated aquatic habitats were found; different characters show significant differences between the two habitats.

| n | C. papyrus 192 | | | E. crassipes 214 | | |
|---|---|---|---|---|---|---|
| Si | 408 | ± | 25b | 302 | ± | 17a |
| SRP | 7.2 | ± | 0.2a | 8.5 | ± | 0.3b |
| Tot.-P | 41.0 | ± | 1.0a | 48.0 | ± | 2.0b |
| NO$_3$-N | 5.4 | ± | 0.4a | 9.7 | ± | 0.9b |
| Chl.a | 24.0 | ± | 1.0 | 23.0 | ± | 1.0 |
| Seston | 12.0 | ± | 0.3 | 11.0 | ± | 0.2 |
| Temp. | 26.6 | ± | 0.0b | 26.5 | ± | 0.0a |
| pH | 8.2 | ± | 0.1b | 7.7 | ± | 0.0a |
| DO | 6.9 | ± | 0.2b | 6.7 | ± | 0.1a |
| Cond. | 110 | ± | 1 | 110 | ± | 1 |
| Redox | 0.14 | ± | 0.00a | 0.24 | ± | 0.02b |

Table 6.    Mean values (± standard error) for water quality parameters (SRP, tot.-P, $NO_3$-N, Chl.-a, in $\mu g.l^{-1}$; DO, $mg.l^{-1}$) in *Eichhornia*-dominated habitats for observed significant (p < 0.05) differences from samples pooled across seasons: 5 m inside water hyacinth mats (within mats) vs 350 m away towards open water.

|  | SRP | TP | $NO_3$-N | Chl.-a | pH | DO |
|---|---|---|---|---|---|---|
| into mats | 12.4 ± 1.1b | 82 ± 9b | 21 ± 3b | 29 ± 2b | 7.3 ± 0.0a | 5.4 ± 0.3a |
| open water | 6.6 ± 0.8a | 38 ± 4a | 5 ± 2a | 25 ± 3a | 8.2 ± 0.3b | 8.0 ± 0.4b |

In Fig. 8 diurnal changes in temperature, oxygen and pH at different places in two vegetation stands of *Cyperus papyrus* (Masese-Wanyange and Kirinya-Masese) have been compared with one of *Eichhornia crassipes* (Masese-*Eichhornia*). The measurements were done in February 1996. The lowest oxygen concentrations were measured within the vegetation mats of both the *C. papyrus* stand at Kirinya-Masese and *E. crassipes*. The oxygen concentrations at all the distances from the vegetation (0, 10, 20, 40 m and open water) was similar in the *E. crassipes* and the Kirinya-Masese *C. papyrus* stand. The Masese-Wanyange *C. papyrus stand* showed with higher oxygen levels at all sampling points. The oxygen saturation level ranged from 40 - 100 % at the *E. crassipes* and the Kirinya-Masese *C. papyrus* stands; at the Masese-Wanyange *C. papyrus* stand it ranged from 60 - 138 %, with a clear maximum at noon. At the Masese-Wanyange *C. papyrus* stand it can be seen that maximum temperature and oxygen levels were reached at noon; also pH shows maximum values from noon till midnight.

**Phytoplankton and macrofauna**
In Table 7 phytoplankton biomass is given, expressed as chlorophyll-a, for both vegetation types at different distances from the edge of the vegetation and at different seasons (data from Chapter 3).
From this table it can be seen that differences between both vegetation types are not significant confirming the ANOVA results in Table 4 and the pooled results in Table 5. A major exception was the seasonal influence of the dry period especially in February 1996, when the *E. crassipes* stands showed significantly lower phytoplankton biomass at all distances apart from a single open water sample.
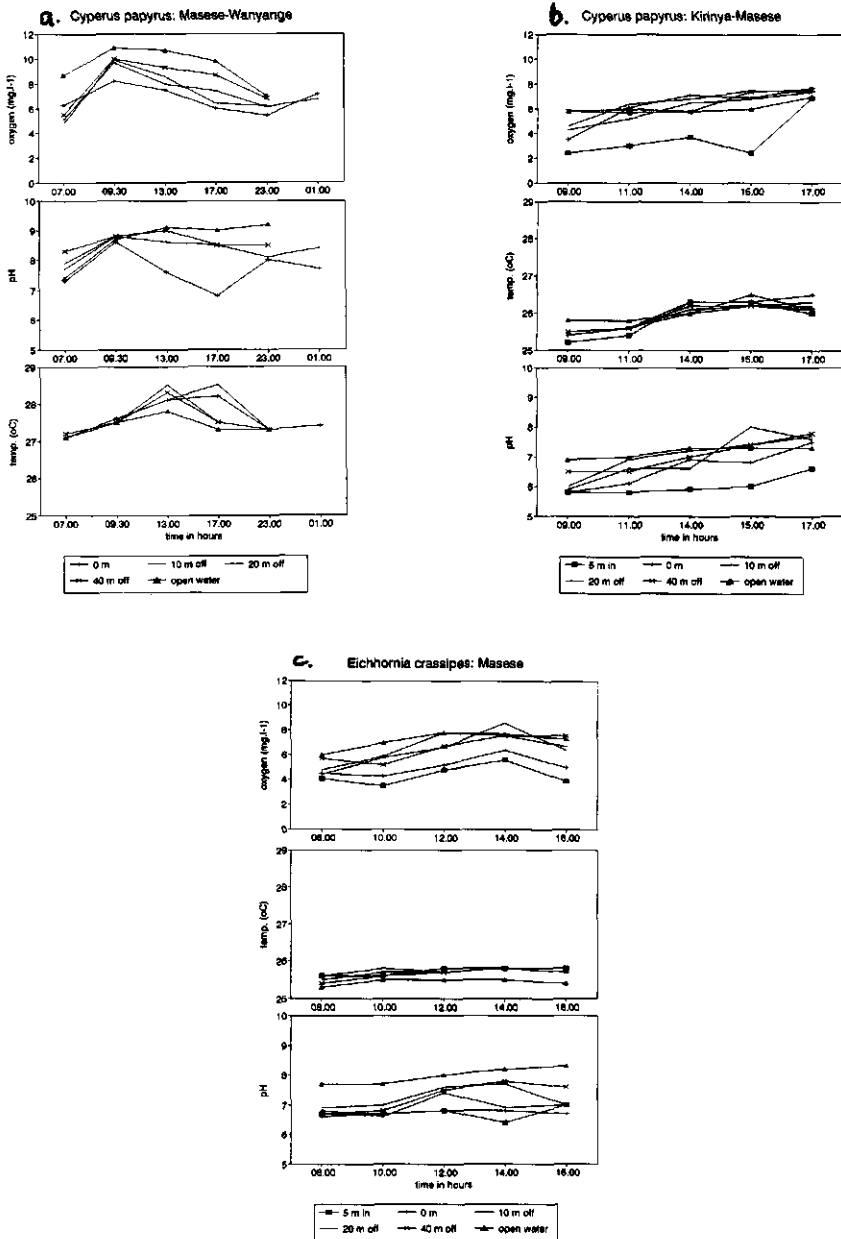
**Fig. 8.** Diurnal changes in temperature, oxygen and pH at different places in vegetation stands of *Cyperus papyrus* (a: Masese-Wanyange and b: Kirinya-Masese) and one stand of *Eichhornia crassipes* (c: Masese). February 1996.

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Table 7.    Chlorophyll-a ($\mu$g.l$^{-1}$) in *Eichhornia crassipes* and *Cyperus papyrus* transects (mean values and standard error). The wet and dry seasons have been indicated.

| | May 1995 (wet) | | | July 1995 (dry) | | | October 1995 (wet) | | | February 1996 (dry) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eichhornia crassipes* | | | | | | | | | | | | |
| shoreline | 23.0 | ± | 1.9 | 16.1 | ± | 1.2 | 23.7 | ± | 2.4 | 16.7 | ± | 0.5 |
| 10 - 40 m off | 21.1 | ± | 0.7 | 18.7 | ± | 0.7 | 26.5 | ± | 1.3 | 20.2 | ± | 0.7 |
| open water | 21.6 | ± | 0.9 | 20.5 | ± | 3.0 | 24.5 | ± | 2.9 | 45.9 | | |
| *Cyperus papyrus* | | | | | | | | | | | | |
| shoreline | 22.4 | ± | 1.1 | 16.6 | ± | 1.9 | 25.1 | ± | 2.6 | 31.1 | ± | 2.9 |
| 10 - 40 m off | 20.6 | ± | 2.0 | 18.5 | ± | 1.2 | 25.2 | ± | 1.3 | 36.4 | ± | 1.4 |
| open water | 22.1 | ± | 1.4 | 21.1 | ± | 2.5 | 29.9 | ± | 0.0 | 40.7 | ± | 2.2 |

Data on the mean abundance and temporal distribution patterns of six macrofaunal groups in *E. crassipes* and *C. papyrus* stands are given in Table 8 (data from Chapter 3). *E. crassipes* habitats had comparatively fewer individuals of most taxa per area at most distances. Areas under the mats were particularly poor in macrofauna. Of the invertebrate taxa recovered in sufficient numbers to allow further analysis, molluscs and chironomids showed more consistent distribution patterns in the two vegetation-dominated habitats. Chironomids were more associated with the papyrus edge (70 - 650 ind.m$^{-2}$) in contrast to many zero scores at the fringes of and inside *Eichhornia* mats. In *Eichhornia* habitats, bivalves were generally more abundant (up to 950 ind. m$^{-2}$) some distance (10 - 20 m) away from the weed's fringe while Gastropods were more represented at 20 - 40 m from the fringe further into the open water.

As there were no clear cut seasonal trends (May data were not available) shown by the taxa, the two-way ANOVA carried out (Table 9) showed that most variation in macrofauna abundance patterns was due to vegetation, distance and interaction between the two (vegetation * distance).

Of the seven taxa, three taxa (Bivalvia, Chironomidae, Gastropoda) were strongly influenced in their distribution by both vegetation and distance with a large proportion (30 - 40 %) of the interaction due to distance. Oligochaeta appear to be strongly affected by vegetation but no effects of distance were significant (p = 0.05) for other groups.

Table 8. Seasonal changes in mean abundance (individuals.m$^{-2}$) of benthic organisms from *Eichhornia crassipes* and *Cyperus papyrus* stands (mean based on 3 samples per distance unit; -m indicates distance from the edge/interface into the *Eichhornia* mats).

*Eichhornia crassipes*: May 1995

|  | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 0 | 0 | 7 | 16 | 21 | 25 | 0 |
| Chironomidae | 0 | 0 | 7 | 16 | 0 | 0 | 8 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | 0 | 0 | 62 | 66 | 103 | 123 | 139 |
| Odonata | 0 | 0 | 7 | 0 | 7 | 0 | 0 |
| Oligochaeta | 0 | 0 | 0 | 25 | 7 | 8 | 16 |

*Eichhornia crassipes*: July 1995

|  | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 57 | 155 | 141 | 570 | 948 | 69 | 402 |
| Chironomidae | 0 | 0 | 0 | 5 | 5 | 5 | 29 |
| Ephemeroptera | 0 | 7 | 5 | 0 | 0 | 0 | 0 |
| Gastropoda | 25 | 41 | 137 | 96 | 137 | 274 | 16 |
| Odonata | 0 | 9 | 9 | 9 | 5 | 0 | 21 |
| Oligochaeta | 16 | 14 | 28 | 46 | 28 | 14 | 28 |

*Eichhornia crassipes*: October 1995

|  | - 10 m | - 5 m | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|---|---|
| Bivalvia | 0 | 129 | 73 | 23 | 250 | 182 | 14 |
| Chironomidae | 0 | 6 | 0 | 9 | 14 | 0 | 14 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropoda | 28 | 35 | 41 | 69 | 219 | 114 | 89 |
| Odonata | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | 0 | 6 | 41 | 41 | 41 | 14 | 18 |

*Cyperus papyrus*: May 1995

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 21 | 89 | 267 | 137 | 0 |
| Chironomidae | 649 | 14 | 7 | 0 | 28 |
| Ephemeroptera | 164 | 7 | 0 | 0 | 0 |
| Gastropoda | 116 | 260 | 779 | 349 | 41 |
| Odonata | 41 | 7 | 7 | 21 | 14 |
| Oligochaeta | 28 | 62 | 14 | 7 | 7 |

*Cyperus papyrus*: July 1995

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 67 | 155 | 192 | 297 | 132 |
| Chironomidae | 73 | 5 | 14 | 31 | 69 |
| Ephemeroptera | 0 | 0 | 0 | 0 | 14 |
| Gastropoda | 0 | 301 | 283 | 151 | 223 |
| Odonata | 16 | 9 | 14 | 0 | 18 |
| Oligochaeta | 5 | 28 | 14 | 21 | 9 |

*Cyperus papyrus*: October 1995

|  | edge | 10 m | 20 m | 40 m | open |
|---|---|---|---|---|---|
| Bivalvia | 50 | 401 | 401 | 497 | 82 |
| Chironomidae | 23 | 14 | 5 | 16 | 12 |
| Ephemeroptera | 55 | 0 | 0 | 0 | 0 |
| Gastropoda | 87 | 328 | 164 | 267 | 98 |
| Odonata | 14 | 14 | 7 | 0 | 0 |
| Oligochaeta | 14 | 28 | 9 | 16 | 12 |

Table 9.   Two-way ANOVA for assessing the significance of two factors
           (vegetation type as habitat dominated by either *Cyperus papyrus* or
           *Eichhornia crassipes*) and distance (from the vegetation edge out
           towards open water) and the interaction of these two on distribution of
           seven benthic macrofauna taxa; four levels of significance àre indicated:
           $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*) and $p > 0.05$
           F = factor ss; E = explain ss, % = a measure of variation explained
           by that factor.

| | vegetation p | F/E (%) | distance p | F/E (%) | interaction p | F/E (%) |
|---|---|---|---|---|---|---|
| Bivalves | 0.000*** | 30 | 0.004** | 38 | 0.009** | 29 |
| Chironomidae | 0.024* | 13 | 0.006** | 45 | 0.003** | 43 |
| Ephemeroptera | 0.078ns | | 0.411ns | | 0.317ns | |
| Gastropoda | 0.000*** | 25 | 0.001** | 37 | 0.001** | 35 |
| Hirudinea | 0.264ns | | 0.460ns | | 0.277ns | |
| Odonata | 0.098ns | | 0.234ns | | 0.128ns | |
| Oligochaeta | 0.035* | 22 | 0.063ns | | 0.475ns | |

Data on abundance of macrofauna associated with the mat of *E. crassipes* at two
sampling sites (Table 10) indicated a marked decline in diversity with distance from
the lakeward edge of the weed into the mats.

A comparison of within *Eichhornia* mat macrofauna patterns showed considerable
differences between roots and the sediments under the weed mats. Roots were
much richer in diversity and abundance of macrofauna in comparison to the
sediments, though more bivalves and gastropods were associated with the
sediments. In contrast to the patterns shown in other sediment samples (Table 5),
Coleoptera, Chironomidae, Gastropoda and the freshwater shrimp *Caridina nilotica*
were recovered as deep as 20 m into the mat. The diversity of macrofauna in the
sediments under *E. crassipes* was about 50 % of that recovered in the weed mat
(roots) but the location into the mat appeared to have no effect on macrofauna
diversity at both sampling sites. The highest diversity and densities in both roots
and sediments were associated with the edges of the plants.

Table 10.    Macrofauna density (ind.m$^{-2}$)in the roots of *Eichhornia crassipes* and the sediments under the weed mats at two shoreline sites in northern Lake Victoria.

| | roots | | | sediments | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | 20 m in | 10 m in | 0 m | 20 m in | 10 m in | 0 m | 10 m off |
| **a. Kakira** | | | | | | | |
| Bivalvia | 0 | 0 | 32 | 34 | 103 | 37 | 37 |
| *Caridina* | 16 | 32 | 192 | 0 | 0 | 0 | 0 |
| Chironomidae | 32 | 32 | 288 | 0 | 0 | 37 | 37 |
| Coleoptera | 32 | 48 | 208 | 0 | 0 | 0 | 0 |
| Ephemeroptera | 0 | 16 | 1424 | 0 | 0 | 74 | 0 |
| Gastropoda | 52 | 66 | 99 | 22 | 46 | 162 | 114 |
| Hemiptera | 0 | 0 | 16 | 0 | 0 | 0 | 0 |
| Hirudinea | 0 | 32 | 160 | 0 | 0 | 37 | 0 |
| Odonata | 0 | 96 | 80 | 0 | 0 | 0 | 0 |
| Oligochaetae | 0 | 0 | 16 | 37 | 37 | 74 | 37 |
| **b. Kiryowa** | | | | | | | |
| Bivalvia | 0 | 15 | 0 | 0 | 35 | 94 | 182 |
| *Caridina* | 0 | 0 | 16 | 0 | 0 | 0 | 0 |
| Chironomidae | 0 | 96 | 16 | 0 | 0 | 147 | 0 |
| Coleoptera | 32 | 32 | 16 | 0 | 0 | 0 | 0 |
| Ephemeroptera | 0 | 0 | 16 | 0 | 0 | 0 | 37 |
| Gastropoda | 0 | 3 | 3 | 7 | 15 | 19 | 160 |
| Hemiptera | 0 | 0 | 16 | 0 | 0 | 0 | 0 |
| Hirudinea | 0 | 32 | 32 | 0 | 0 | 0 | 0 |
| Odonata | 0 | 16 | 48 | 0 | 0 | 37 | 0 |
| Oligochaetae | 0 | 48 | 0 | 37 | 37 | 37 | 0 |

## DISCUSSION

The water hyacinth (*Eichhornia crassipes*) is a recent alien species in the wetlands of Lake Victoria. As often with alien species, the success of *E. crassipes* in Lake Victoria may partly be due to lack of effective competitors, parasites and herbivores. In this lake, the success of water hyacinth could also be due to the eutrophication (Hecky, 1993), a major part of which originates from changed land use, and is mediated through hydrology (Chapter 3). On the other hand, due to the lake's immense size (surface area, c. 68,500 km$^2$, mean depth, 40 m), initial establishment of water hyacinth in most parts of the lake appears to have been due to external factors. These include influx from the Kagera river, and dispersal patterns associated with the regional climatic regime particularly the prevailing winds, hence, the prediction of localities of likely infestation (Twongo, 1991;

Twongo *et al.*, 1993). According to these studies, water hyacinth in Lake Victoria is predominantly associated with *C. papyrus*-fringed shores. Although *C. papyrus* is the most dominant wetland species along the shoreline, recent observations indicate that other types of wetlands such as those dominated by *Typha* and *Vossia* also form associations with the weed (Chapter 3; LVEMP, 1995). In addition, not all papyrus stretches seem equally capable of maintaining water hyacinth associations. Water hyacinth mats tend to accumulate along papyrus stretches which face on-shore winds or, are located deep in indentations within the more sheltered bays where the mats become trapped. In general however, all these shallow areas were associated with other water plants such as the euhydrophytes. Similar localities of water hyacinth infestation to the south of the lake have been identified (Witte *et al.*, 1995). Along other studies on structural aspects of wetlands, it was thus possible to monitor the progress of the water hyacinth and its initial ecological impacts in the lake's wetland zone.

### Successional displacement of indigenous euhydrophytes.

At the start of the observations in 1993 cover abundance of *Eichhornia crassipes* in Lake Victoria was minimal and the weed was widely scattered amongst emergent macrophytes along the shoreline. Vegetations of native euhydrophytes in the wetland ecotones of the study area were intact, dominated by *Nymphaea caerulea*, *Pistia stratiotes* and *Ceratophyllum demersum*. However, after about three years virtually all the beds of indigenous euhydrophytes close to the shore had been smothered by a resident fringe of *E. crassipes* about 10 to 15 m wide. While the resident weed did not cover the shores of all wetland patches, there was a striking similarity in the habitats preferred by native euhydrophytes and *E. crassipes* after a study period of only three years.

However, data from previous studies and observations in this study indicate further transformation of pure stands of resident *E. crassipes* through macrophyte successions which probably changes aspects of the original ecological character even further. For instance, fundamental successional transformation in shoreline vegetation cover following invasion of Lake Kyoga and Lake Victoria by *E. crassipes* has been progressing in the lake since 1992 (Twongo *et al.*, 1992; 1993); pure stands of the water weed in most shore environments of Lake Kyoga were invaded in succession by sedges, ferns and finally by *Vossia cuspidata*, which often eventually overpowered the *E. crassipes* to extend large expanses of the emergent macrophyte into the lake. In Lake Victoria, on the other hand, the succession proceeds largely through direct colonisation of *E. crassipes* by *V. cuspidata*, a process well illustrated in this study by the rapid increase in cover abundance of *V. cuspidata* over a period of about three years.

There was a slight decrease in *E. crassipes* biomass in 1996 which could have been due to seasonality. It may also have been due to mortality in older plants, a feature associated with a reduction in daughter plant production at peak density (Madsen, 1993). This could be the stage when colonisation of water hyacinth mats by other species such as *V. cuspidata* takes place.

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The type of habitat, whether dominated by *C. papyrus* or *E. crassipes* was important in the nutrient content (N, P) of the associated sediments and plants (Table 3; Figs. 4, 5, Appendix 1) even though season was the major influence. Both macrophytes seem to have high nutrient removal efficiencies, a suggestion supported by other observations, though the amounts removed may depend on other factors such as iron and potassium content (Reddy *et al.*, 1990; Michaud *et al.*, 1994; Nogales *et al.*, 1994). Iron in particular, may act as a nutrient in these habitats which lie close to the iron-rich cultivated catchment (Velle and Drichi, 1992). It has to be considered that most variation in water quality and sediment nutrients was explained by seasonality (Chapter 3). Comparing the nutrient content (P, N) of the dominant macrophytes in the two vegetation type, i.e. *C. papyrus* and *E. crassipes*, it is shown that *E. crassipes* has much higher total-N and total-P contents, particularly in the root system. It is possible that this also explains the lower nutrient contents in the water hyacinth sediments compared to the papyrus sediments and could in part be related to the anoxic conditions under the mat.

### Impact on water quality and algal biomass
In a three-way ANOVA (pooled for effects across the two macrophyte-dominated habitats), it initially appeared that vegetation type did not have significant effects on a range of water quality parameters including dissolved oxygen, chlorophyll, conductivity and some nutrients; seasonal effects were more dominant (Table 3). However, from a series of two-way ANOVAS and t-tests for significance, clear differences were obtained in most parameters (Table 4). In a previous study, a clear demonstration of the impact of cover by the water hyacinth on water quality was given by Willoughby *et al.* (1993). The authors measured depressed pH and temperature regimes and a much lower percent oxygen saturation under *E. crassipes*, indicating a changed aquatic environment which would probably contribute to changes in other aspects of the ecological character of the environment under the resident weed. As the present analyzed data indicate (Tables 4 and 5), it is likely that the effects of water hyacinth probably extend to some distance away from the interior of the mats. Apart from biomass cover, depth could be another factor in the extent of *Eichhornia* impacts. Aneija and Singh (1992) found extreme hypoxic conditions in shallow water hyacinth-infested ponds in India where low temperature, pH, dissolved oxygen and $NO_3$-N were recorded. The high level of $NO_3$-N recorded in water hyacinth habitats during the present study in comparison to papyrus habitats (Table 4) could be due to wind-mixing effects at some of the localities. Phytoplankton biomass did not differ much between both vegetation types (Table 4 and 5) except between near shore areas and further away. Of the four seasonal periods investigated, only one of the dry periods (February 1996) showed significantly lower chlorophyll-a contents at the *Eichhornia* sites.

### Influence on macrofauna abundance and diversity
Substrate type has been reported to influence littoral zoobenthic biomass (Rasmussen, 1988). The substrate may be sediment (epifauna or infauna) or the vegetation (epiphytic invertebrates). Considering sediment, both *E. crassipes* and

*C. papyrus* vegetation-dominated habitats had among the lowest diversity and abundance of benthic macrofauna when compared to other vegetation types in the study area (Chapter 3). In contrast to these observations, Wanda (1997) noted the highest abundance of invertebrates in *Eichhornia* habitats but this pattern related more to the epiphytic invertebrates. The present studies show that both abundance and diversity of the macro-invertebrates in sediments associated with *C. papyrus* are slightly higher than in sediments associated with *E. crassipes*. The generally low abundance of macrofauna in the two macrophyte-dominated habitats could be due to less habitat complexity, high predation rates and habitat permanence as implied in several studies (e.g. Cooper and Knight, 1985; Rasmussen, 1990; Hargeby, 1990). In Lake Victoria, an expansion in the submerged macrophyte beds such as *Ceratophyllum* was associated with an increase in the abundance of the *Caridina* shrimp due to lower predation (Goldschmidt *et al.*, 1993) on which Nile tilapia have been shown to feed in some seasons (Chapter 8). It was suggested by Goldschmidt *et al.* (1993) that predation on the shrimps by Nile perch was less on young shrimps due to predator avoidance aided by macrophyte cover. On the other hand, the difference between the two habitat types could be due to a modification of sediment composition under water hyacinth mats. The notable absence of chironomids among water hyacinth sediment samples during this study in comparison to observations by Wanda (1997) could be due to sampling in a period when the mud dwelling stages (Macdonald, 1956) had emerged.

**Extent of change in ecological character**
The results from the studies in northern Lake Victoria presented above indicate a transformation in the physical and chemical environment as well as in the diversity and distribution of the biotic resources in the study habitats. The observed transformations constitute a significant change in aspects of the ecological character along the shore. However, the implications of the observed changes are even more significant when considered in conjunction with information on the global distribution and areal cover of *E. crassipes* in Uganda.

It is noted that were it not for infestations by *E. crassipes*, many areas of the shoreline of Lake Victoria would still be under the influence of papyrus swamps, even though the shallow papyrus-dominated habitats are variable and could further be categorised into definable types on the basis of wind influence (Chapter 3). Therefore, the presence of *E. crassipes* not only simplifies the complexity of habitat type but also leads to alteration of the natural habitat conditions. For example, the accumulated debris under water hyacinth mats off papyrus shores could result into a modification of sediment composition especially towards the shore. The oxygen demand associated with decaying detritus accumulating under the mats (Gopal, 1987), could be responsible for the observed apparent reduction in the abundance and diversity of the benthos associated with *Eichhornia* sediments, a finding corroborated by similar results from observations on water hyacinth impacts in the lake (Willoughby *et al.*, 1993). In contrast, water hyacinth appeared to lead to an increase in invertebrate abundance at the fringes of the weed mats, a pattern similar to the one reported for the Sudd swamps in Sudan (Bailey and Litterick,

1993). Although macrofauna littoral development particularly in *Eichhornia* root mats may be correlated with the vegetation reducing effects of strong winds (Cooper and Knight, 1988), the apparent increase could be misleading considering that in the study area, water hyacinth will have displaced the indigenous euhydrophytes such as *Pistia* and *Ceratophyllum*. These species though not having the same biomass as *Eichhornia* may be more suitable for colonisation of epiphytic invertebrates due to their relatively larger surface areas (Cyr and Downing, 1988) or other factors.

Apart from a modification of the micro-environment under the mats, a potentially major effect of the water hyacinth in Lake Victoria especially where extensive mobile mats are involved, is the dispersal of organisms such as invertebrates and small fishes between habitats. But the same large-sized mats would probably also have the opposite effect of displacing other organisms which may not be associated with large mats.

In an earlier study, fish species diversity among the two vegetation types did not differ much, i.e. 15 taxa in *Eichhornia crassipes* habitats and 13 taxa in *Cyperus papyrus* habitats (chapter 4). *Oreochromis niloticus*, the Nile tilapia, was present in all *Eichhornia* and all *Cyperus* stands; in both vegetation types it was the most frequent species, together with *Lates niloticus*, the Nile perch. It is considered that most fish species would not survive under resident mats of *E. crassipes* due to degraded environmental conditions of, for instance, very low dissolved oxygen. Further away from the vegetation fringes, it appears that water hyacinth presence may drive originally shoreline species out into the open water.

Extensive shoreline habitats such as those traditionally occupied by shoreline euhydrophytes and associated fauna in lakes and rivers in Uganda and elsewhere in eastern Africa, already infested with the weed, have been or would probably be smothered under cover of mats of the weed. Successional vegetation changes in lakes Victoria and Kyoga have driven the transformation even further by creating and facilitating the extension of semi-terrestrial environments into the lake environment. While the stability of such new habitats along the shores of large lakes is unclear, even doubtful, the process constitutes a definite change in the original ecological character of the impacted environments.

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Appendix 1a. Mean plant-nutrient composition (in mg.g DW$^{-1}$) of different sections of papyrus plants in relation to sediment nutrient status. August 1995; n = number of replicates.

*Cyperus papyrus*

|  | N | P | N:P | % AFDW | n |
|---|---|---|---|---|---|
| <u>edge</u> | | | | | |
| roots | 13.2 | 1.6 | 9 | 92 | 2 |
| rhizome | - | - | - | 94 | 3 |
| culm/umbel | 18.7 | 2.0 | 10 | 94 | 3 |
| | | | | | |
| sediment | 21.2 | 0.7 | 30 | 92 | 3 |
| <u>5 m inland</u> | | | | | |
| roots | 17.2 | 0.8 | 22 | 94 | 1 |
| rhizome | 9.5 | 0.8 | 12 | 95 | 2 |
| culm/umbel | 11.3 | 1.7 | 7 | 93 | 3 |
| <u>10 m inland</u> | | | | | |
| roots | 11.5 | 0.7 | 18 | 95 | 1 |
| rhizome | 9.0 | 0.8 | 12 | 95 | 2 |
| culm/umbel | 9.2 | 1.6 | 6 | 93 | 3 |

Appendix 1b.  Mean plant-nutrient composition (in mg.g DW$^{-1}$) of different sections of papyrus plants and the water hyacinth in relation to sediment nutrient status. May 1996; n = number of replicates.

| *Cyperus papyrus* | N | P | N:P | % AFDW | n |
|---|---|---|---|---|---|
| <u>edge</u> | | | | | |
| roots | 15.6 ± 0.5 | 1.4 ± 0.1 | 11 ± 0.5 | 92 ± 1.0 | 5 |
| rhizome | 10.2 ± 0.5 | 1.7 ± 0.2 | 6 ± 0.6 | 92 ± 0.8 | 5 |
| base of culm | 6.7 ± 1.3 | 1.3 ± 0.2 | 5 ± 0.8 | 92 ± 0.8 | 5 |
| apex of culm | 5.1 ± 0.4 | 1.0 ± 0.1 | 5 ± 0.3 | 93 ± 0.3 | 4 |
| umbel/inflor. | 18.6 ± 0.8 | 2.3 ± 0.1 | 8 ± 0.1 | 94 ± 0.4 | 5 |
| | | | | | |
| sediment | 17.4 ± 0.3 | 0.8 ± 0.5 | 24 ± 0.3 | 92 | |
| <u>2 m inland from edge</u> | | | | | |
| roots | 16.2 | 1.2 | 13 | 94 | 1 |
| rhizome | 11.7 | 2.2 | 5 | 94 | 1 |
| base of culm | 10.9 | 3.4 | 3 | 91 | 1 |
| apex of culm | 4.7 | 0.9 | 5 | 94 | 1 |
| umbel/infl. | 21.4 | 2.6 | 8 | 93 | 1 |
| <u>10 m inland from edge</u> | | | | | |
| roots | 15.6 ± 2.4 | 1.1 ± 0.1 | 14 ± 1.8 | 93 ± 1.0 | 5 |
| rhizome | 7.9 ± 1.3 | 2.9 ± 0.2 | 3 ± 0.5 | 94 ± 1.0 | 5 |
| base of culm | 5.0 ± 0.9 | 1.9 ± 0.2 | 3 ± 0.3 | 93 ± 0.8 | 5 |
| apex ofculm | 4.3 ± 0.3 | 1.4 ± 0.1 | 3 ± 0.4 | 95 ± 1.0 | 5 |
| umbel/inflor. | 18.1 ± 1.3 | 2.3 ± 0.1 | 8 ± 0.7 | 93 ± 0.4 | 5 |
| | | | | | |
| *Eichhornia crassipes* | | | | | |
| <u>edge</u> | | | | | |
| roots | 27.3 | 2.6 | 11 | 84 | 3 |
| petiole | 8.1 | 2.9 | 3 | 83 | 3 |
| leaves | 21.9 | 2.8 | 8 | 88 | 3 |
| | | | | | |
| sediment | 12.7 ± 1.5 | 0.3 ± 0.1 | 67 | - | 9 |
| <u>5 m inland from edge</u> | | | | | |
| roots | 26.3 | 2.3 | 12 | 85 | 3 |
| petiole | 7.6 | 2.8 | 3 | 78 | 3 |
| leaves | 20.2 | 2.4 | 8 | 87 | 3 |
| <u>10 m inland from edge</u> | | | | | |
| roots | 24.1 | 2.3 | 11 | 84 | 3 |
| petiole | 6.4 | 2.3 | 3 | 81 | 3 |
| leaves | 24.3 | 2.4 | 10 | 87 | 3 |

Appendix 2.　　Mean seasonal total-N and total-P content (mg.g$^{-1}$) of the sediments from the vegetation types.

| | -5 m | 0 m | 10 m | 20 m | 40 m | open water |
|---|---|---|---|---|---|---|
| **OCTOBER 1994** | | | | | | |
| total-P | | | | | | |
| *Eichhornia* | - | 1.27 ± 0.10 | 1.58 ± 0.16 | 2.23 ± 0.36 | 1.86 ± 0.06 | 1.54 ± 0.20 |
| *Cyperus* | - | 1.46 ± 0.10 | 1.32 ± 0.07 | 1.34 ± 0.07 | 1.75 ± 0.06 | 1.98 ± 0.11 |
| total-N | | | | | | |
| *Eichhornia* | - | 13.24 ± 3.20 | 18.94 ± 1.75 | 11.99 ± 2.53 | 22.50 ± 1.26 | 15.06 ± 1.13 |
| *Cyperus* | - | 24.60 ± 0.85 | 24.42 ± 0.85 | 27.08 ± 1.13 | 26.76 ± 1.45 | 24.54 ± 1.20 |
| **MAY 1995** | | | | | | |
| total-P | | | | | | |
| *Eichhornia* | 0.29 ± 0.06 | 0.41 ± 0.08 | 0.48 ± 0.08 | 0.55 ± 0.11 | 0.54 ± 0.12 | 0.79 ± 0.06 |
| *Cyperus* | - | 0.75 ± 0.05 | 0.66 ± 0.08 | 0.68 ± 0.05 | 0.81 ± 0.08 | 0.95 ± 0.06 |
| total-N | | | | | | |
| *Eichhornia* | 12.67 ± 1.45 | 12.57 ± 1.05 | 11.36 ± 1.78 | 10.40 ± 1.14 | 11.24 ± 1.32 | 10.77 ± 1.54 |
| *Cyperus* | - | 17.44 ± 0.29 | 17.22 ± 0.95 | 15.79 ± 1.71 | 15.14 ± 2.00 | 18.34 ± 1.10 |
| **JULY 1996** | | | | | | |
| total-P | | | | | | |
| *Eichhornia* | 0.87 ± 0.10 | 0.80 ± 0.11 | 0.87 ± 0.10 | 0.97 ± 0.12 | 0.77 ± 0.07 | 1.14 ± 0.12 |
| *Cyperus* | - | 1.07 ± 0.12 | 0.88 ± 0.04 | 0.96 ± 0.05 | 1.01 ± 0.07 | 1.10 ± 0.09 |
| total-N | | | | | | |
| *Eichhornia* | 15.69 ± 2.34 | 15.55 ± 2.65 | 12.25 ± 1.88 | 16.51 ± 1.84 | 16.78 ± 2.49 | 15.76 ± 1.33 |
| *Cyperus* | - | 21.40 ± 0.46 | 19.55 ± 0.78 | 18.90 ± 0.85 | 19.65 ± 1.38 | 19.48 ± 0.86 |

**Appendix 3.** Physical and chemical characteristics of the sampling sites.

**MAY 1995**

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO$_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus papyrus* | | | | | | | | | | |
| edge | 27.4 ± 0.5 | 111 ± 1 | 0.15 ± 0.02 | 8.0 ± 0.2 | 5.2 ± 0.6 | 0.93 ± 0.02 | 517 ± 23 | 5.6 ± 0.2 | 39.4 ± 0.9 | 6.7 ± 0.7 |
| 10-40 m off | 27.5 ± 0.1 | 112 ± 1 | 0.17 ± 0.01 | 8.1 ± 0.1 | 5.2 ± 0.2 | 0.92 ± 0.01 | 509 ± 21 | 6.2 ± 0.2 | 40.0 ± 0.6 | 7.3 ± 0.5 |
| open water | 27.4 ± 0.2 | 107 ± 0 | 0.14 ± 0.01 | 6.7 ± 1.7 | 6.1 ± 1.4 | 0.92 ± 0.01 | 463 ± 40 | 6.8 ± 0.7 | 52.1 ± 10.2 | 5.9 ± 0.6 |
| *Eichhornia crassipes* | | | | | | | | | | |
| 5 m from edge | 27.3 ± 0.2 | 107 ± 2 | 0.38 ± 0.09 | 7.6 ± 0.1 | 6.3 ± 0.4 | - | 505 ± 20 | 7.3 ± 0.7 | 66.0 ± 14.0 | 10.8 ± 4.4 |
| edge | 27.7 ± 0.1 | 104 ± 1 | 0.44 ± 0.11 | 7.7 ± 0.1 | 7.6 ± 0.4 | - | 441 ± 30 | 7.6 ± 1.1 | 36.5 ± 2.8 | 2.7 ± 0.4 |
| 10-40 m off | 27.7 ± 0.0 | 104 ± 1 | 0.15 ± 0.00 | 7.9 ± 0.1 | 7.9 ± 0.2 | 0.90 | 431 ± 19 | 6.9 ± 0.4 | 35.6 ± 2.4 | 2.3 ± 0.2 |
| open water | 27.7 ± 0.1 | 106 ± 2 | 0.52 ± 0.32 | 8.1 ± 0.3 | 8.5 ± 0.7 | 0.87 | 486 ± 47 | 5.4 ± 0.1 | 31.0 ± 6.3 | 2.1 ± 0.9 |

**JULY 1995**

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO$_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus papyrus* | | | | | | | | | | |
| edge | 24.9 ± 0.2 | 119 ± 7 | 0.17 ± 0.00 | 7.5 ± 0.1 | 7.0 ± 0.2 | - | 48 ± 7 | 8.6 ± 0.9 | 40.9 ± 4.8 | 0.8 ± 0.2 |
| 10-40 m off | 25.3 ± 0.1 | 119 ± 4 | 0.17 ± 0.00 | 7.6 ± 0.1 | 7.5 ± 0.8 | - | 43 ± 3 | 8.3 ± 0.5 | 36.9 ± 1.0 | 0.6 ± 0.2 |
| open water | 25.3 ± 0.3 | 104 | 0.18 ± 0.01 | 7.6 ± 0.4 | 7.6 ± 0.3 | - | 77 ± 25 | 7.9 ± 1.2 | 35.1 ± 1.9 | 2.1 ± 1.8 |
| *Eichhornia crassipes* | | | | | | | | | | |
| 5 m from edge | 25.0 ± 0.1 | 119 ± 7 | 0.19 ± 0.01 | 7.0 ± 0.1 | 5.8 ± 0.3 | - | 56 ± 6 | 10.8 ± 0.8 | 89.1 ± 11.8 | 14.5 ± 2.3 |
| edge | 25.1 ± 0.1 | 119 ± 7 | 0.19 ± 0.01 | 7.1 ± 0.1 | 6.5 ± 0.3 | - | 58 ± 4 | 6.5 ± 0.7 | 40.7 ± 2.4 | 3.4 ± 0.1 |
| 10-40 m off | 25.2 ± 0.1 | 119 ± 7 | 0.18 ± 0.01 | 7.4 ± 0.1 | 7.2 ± 0.2 | - | 51 ± 6 | 7.5 ± 0.7 | 36.8 ± 1.2 | 1.2 ± 0.6 |
| open water | 25.2 ± 0.0 | 104 | 0.17 ± 0.01 | 7.5 | 7.3 ± 0.0 | - | 39 ± 5 | 7.4 ± 0.7 | 41.4 ± 0.4 | 0.0 |

# Appendix 3 (continued)

## OCTOBER 1995

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO$_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cyperus papyrus** | | | | | | | | | | |
| edge | 27.1 ± 0.2 | 108 ± 1 | 0.10 ± 0.01 | 8.7 ± 0.1 | 7.5 ± 0.3 | 0.75 ± 0.01 | 266 ± 42 | 10.0 ± 1.2 | 51.2 ± 3.7 | 9.3 ± 0.8 |
| 10-40 m off | 27.1 ± 0.2 | 108 ± 1 | 0.07 ± 0.01 | 8.8 ± 0.1 | 8.2 ± 0.3 | 0.73 ± 0.01 | 234 ± 34 | 9.3 ± 0.8 | 43.0 ± 1.7 | 6.6 ± 0.3 |
| open water | 26.8 ± 0.2 | 108 ± 0 | 0.08 ± 0.01 | 8.9 ± 0.0 | 7.6 ± 0.2 | 0.77 | 228 ± 25 | 8.0 ± 0.7 | 45.5 ± 2.6 | 7.3 ± 0.4 |
| **Eichhornia crassipes** | | | | | | | | | | |
| 5 m from edge | 26.4 ± 0.3 | 107 ± 1 | 0.14 ± 0.02 | 7.4 ± 0.1 | 4.4 ± 0.4 | 0.77 ± 0.00 | 283 ± 15 | 18.3 ± 2.3 | 85.8 ± 9.1 | 26.8 ± 2.4 |
| edge | 26.8 ± 0.2 | 107 ± 1 | 0.13 ± 0.02 | 7.7 ± 0.1 | 5.4 ± 0.4 | 0.72 ± 0.00 | 158 ± 13 | 10.7 ± 1.8 | 52.9 ± 3.0 | 14.2 ± 2.5 |
| 10-40 m off | 26.8 ± 0.2 | 107 ± 1 | 0.11 ± 0.02 | 8.2 ± 0.2 | 6.5 ± 0.3 | 0.73 ± 0.00 | 247 ± 11 | 8.5 ± 0.9 | 49.8 ± 1.9 | 8.9 ± 1.1 |
| open water | 27.5 ± 0.0 | 108 ± 1 | 0.07 | 8.9 ± 0.1 | 8.2 ± 0.1 | - | 152 ± 4 | 8.1 ± 0.5 | 46.6 ± 2.0 | 10.2 ± 2.0 |

## FEBRUARY 1996

| | temp. | EC | redox | pH | oxygen | alkal. | Si | SRP | tot.-P | NO$_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cyperus papyrus** | | | | | | | | | | |
| edge | | | | | | | 910 ± 23 | 5.8 ± 0.6 | 42.5 ± 5.7 | 12.7 ± 3.0 |
| 10-40 m off | | | | | | | 965 ± 19 | 4.0 ± 0.4 | 12.8 ± 1.8 | 5.5 ± 1.4 |
| open water | | | | | | | 999 ± 41 | 2.4 ± 0.4 | 41.4 ± 10.8 | 6.8 ± 1.2 |
| **Eichhornia crassipes** | | | | | | | | | | |
| 5 m from edge | | | | | | | 1034 ± 32 | 10.8 ± 0.8 | 26.5 ± 1.7 | 60.5 ± 4.9 |
| edge | | | | | | | 940 ± 31 | 6.5 ± 0.6 | 24.8 ± 1.7 | 50.8 ± 4.2 |
| 10-40 m off | | | | | | | 972 ± 37 | 5.8 ± 1.3 | 18.4 ± 2.1 | 32.9 ± 3.5 |
| open water | | | | | | | 890 | 1.5 | 14.9 | 3.0 |

# Chapter 9

## Summary and conclusions

Lake Victoria's most direct socio-economic importance traditionally derives from its fisheries and water supply to residents in its densely populated catchment (population growth at an average of 2.4 % annually in comparison to 0.6 % for the developed countries). Hence, to boost the declining fisheries, several species were introduced into the lake in the 1950s, among them, a large predator, the Nile perch (*Lates niloticus*), and a herbivorous tilapine, the Nile tilapia (*Oreochromis niloticus*). Only recently have ecological perturbations in this lake over the years started to be critically examined. The emphasis has been on changes in fish species diversity and water quality in the last two decades, both assumed to be a consequence of exotic fish species introductions (top-down effects), a reflection of the primary interest in fisheries management. Less emphasis has been given to other possibilities such as the phenomenal rise in lake level during 1960s or human population pressure in the adjoining catchment which could produce direct consequences for the fisheries and water quality. An ecological investigation was designed to find out more about the structure of shallow interface habitats in Lake Victoria with particular reference to wetlands and the ecology of the Nile tilapia. This thesis therefore considers that, though less investigated, adjoining wetlands could be important to fish; therefore, human impacts in the catchment could lead to changes in the trophic status of the lake particularly the shallow habitats at the shore.

The first aim of the study was to make an inventory of shoreline wetland plant communities (species composition, distribution and dominance patterns) associated with interface aquatic habitats and to show the extent if any of areal changes in cover which could be attributed to human activity. A second aim was to characterise the structure (plant biomass, water quality, sediments, phytoplankton, macrofauna) of shallow aquatic habitats abutting to dominant plant species at the shore up to the outer limit of the littoral zone, while a third was to elucidate on the relative importance of the different discerned habitats for fish populations (species composition, biomass), also considering reported fish species patterns in other habitats of the lake. A final aim was to study the ecology of the Nile tilapia, in relation to the probable influence of structural elements in the species' distribution, abundance, reproduction and feeding habits, hence to increase general understanding of the Lake Victoria ecosystem.

There were hardly any quantitative data on the structure and diversity of the littoral zone particularly the vegetation dominated habitats, though the extensive papyrus swamps were well known for their inhospitable conditions. In addition, despite its apparent socio-economic importance in small scale fisheries in areas close to the lake, the Nile tilapia was assumed to be restricted to inshore undefined habitats and to follow the same ecological patterns as has been reported for the species in other lakes. In previous studies, inshore could mean depths up to 10 m, bays or distances from the shore within which small boats could be operated without outboard motors. But Nile tilapia which had been stocked in the lake in the 1950s could be caught in a variety of habitats.

In order to achieve the stated aims, this study which was undertaken between 1993 and 1996 consisted of two major parts: (i) literature studies to clarify on the concept of wetlands pertaining to Lake Victoria, and to evaluate the state of knowledge on the Nile tilapia since it was stocked in the lake in the 1950's, and (ii) a series of interrelated field and laboratory studies.

Out of the more than 40 plant species identified along a 110 km shoreline survey, 5 major plant communities could be distinguished according to dominant emergent species at the shore. These were: *Cyperus papyrus* L. (papyrus), *Phragmites mauritianus* Kunth (reeds), *Typha domingensis* Pers (bulrush), *Vossia cuspidata* (Roxb.) (hippo grass) and *Sesbania sesban* (L.) Merrill. The exotic floating *Eichhornia crassipes* (Marts.) Solms-Laubach (water hyacinth) was in early stages of colonisation of the shoreline and quickly gained areal importance to occupy a distinct category of a new wetland type.

Considerable long term changes in the shoreline wetland landscape of Lake Victoria were discerned and appeared to be primarily associated with increasing human activity (agriculture, biomass harvests) which had resulted into a 5 % reduction of wetland cover. However, the study area still contained areas dominated by these macrophytes at the interface with the open lake. In spite of the absence of a well developed euhydrophyte community particularly underwater flora (e.g., *Ceratophyllum* and *Potamogeton*), and increasing infestations with water hyacinth mats, the width of the interface littoral zone was established by secchi transparency as being about 50 - 70 m away from the different emergent macrophytes at the shore. From less than 1 m in depth at the shore, the littoral zone sloped to between 2 m and 4 m at its outer fringe. The diversity of the shallow interface habitats could therefore be identified by the type of dominant macrophyte at the shore. From the outer limit of the littoral platform, depending on the slope from the shore, there was a belt of varying width towards the deeper offshore regions in the lake where bottom sediment composition was dominated by silt.

Excluding *S. sesban* which was considered to have occurred further inland before the lake level rise in 1960s, shallow aquatic habitats off the other five macrophytes were investigated in detail. Apart from the plant biomass at the shore which was highly variable within vegetation types, no significant differences in physico-chemical structural aspects (depth, slope, sediment texture and organic matter, nutrients) within the selected replicate habitat types were detected. Therefore, being singularly dominant and forming discrete patches in particular locations along the shoreline, vegetation types were considered as representing different aquatic habitat conditions on a larger scale in the shallow littoral of the lake. In spite of being defined in terms of the different dominant plant species at the shore, in terms of mean depths, slope and sediment characteristics, the five aquatic habitats could be classified into two major types: Those that were deeper, had more organic matter in sediments (*C. papyrus* and *E. crassipes* - dominated habitats), and those that were more shallow, gently sloping and had more sand in their sediments (*V.*

*cuspidata*, *P. mauritianus* and *T. domingensis* - dominated habitats). As a floating exotic weed, *Eichhornia* had the extra distinction of spreading out in thick mats towards open water and being more strongly associated with papyrus dominated shores which were exposed to on-shore wind patterns. In some locations, it appeared to have become a permanent feature of the coastline. It was therefore observed that apart from water hyacinth presence and wind, additional environmental factors could add to the complexity of the vegetated habitats.

In some structural characteristics (tot.-P, soluble reactive-P, and pH) significant differences between the aquatic habitats were found. They were partly due to the type of the dominant vegetation at the shore. Seasonal effects (hydrology) tended to explain most of the variation in the habitats regarding silica, soluble reactive-P, chlorophyll-a, water temperature and pH. In a few cases, interaction between habitat type and season had distinct horizontal effects on dissolved oxygen and $NO_3$-N differences among and within habitats. Furthermore, distance from the edges of vegetation out towards open water had significant effects on chlorophyll-a, tot.-P, $NO_3$ and pH. Thus, these observations may be considered as being influenced by rainfall and subsequent run-off, which in presence of reduced plant biomass at the shore, would alter the structure of the littoral zone to varying distances towards open water depending on depth, slope and sediment characteristics of the habitats. The hypothesis that human impacts could significantly influence the structure of interface habitats was therefore justified. As an example, concentrations of about 350 $\mu$g.l$^{-1}$ Si, of 50 $\mu$g.l$^{-1}$ tot.-P, 108 $\mu$S.cm$^{-1}$ conductivity and above 20 $\mu$g.l$^{-1}$ chl-a characterised the shallow vegetated aquatic habitats in contrast to about 70 $\mu$g.l$^{-1}$ Si, 1.5 $\mu$g.l$^{-1}$ tot.-P, 94 $\mu$S.cm$^{-1}$ conductivity and below 5 $\mu$g.l$^{-1}$ chl-a in open water regarded in the literature as inshore. Chlorophyll-a and pH were positively correlated with distance from the shore and with rainy seasons.

Four seasons characterise the study area. A long dry season from December to the middle of March is followed by a long wet season which lasts until June. This is followed by a short dry but cool season up to about September. The last part of the year is wet but has less rain than the March - June period. As may be expected, seasonal variations in the water quality of the habitats follow this climatic regime but the timing and magnitude of change may vary on a year to year basis, such as could have happened during exceptionally heavy rains in the period 1960/62.

Among the biotic elements of the littoral zone, phytoplankton composition was dominated by the Cyanobacteria (blue-green algae) genera *Anabaena*, *Lyngbya*, *Merismopedia* and *Microcystis*, but attention is drawn to the filamentous forms in particular, among which specific taxa would have required identification methods which were not available. Of the diatoms, *Nitzschia* was by far the most abundant form while among green algae *Scenedesmus* and *Ankistrodesmus* were commonly identified. Phytoplankton succession between blue-green algae (*Microcystis* and filamentous forms) and diatoms (*Nitzschia*) seemed to follow seasonal changes; it was similar and apparently related to patterns reported in the literature for offshore

stations. The distribution of the invertebrates regarded as macrofauna was less systematic, probably partly due to the small number of samples but also to the strong interaction between vegetation type and distance from the shore. However, gastropods and chironomids were more abundant nearer the vegetation fringes than further away. A secondary pattern reflected in composition and abundance occurred about 400 m away from the edge of the vegetation. This pattern resembled that between the vegetation fringe and 40 m off the fringe and was probably associated with specific differences in taxa or life stages of species found closer to the vegetation. In deeper water, this secondary pattern seemed to be more associated with silty bottom substrata.

From the physico-chemical and biotic characterisation of the study area, it was clear that the littoral zone is spatially structured in two ways: firstly by the vegetation, and secondly by the distance towards the open water. To provide insight into fish populations of the investigated area, species composition, relative abundance (no.ha$^{-1}$) and biomass (kg. fresh weight.ha$^{-1}$) were compared between and among the shallowest regions abutting to specific plant dominants, and patterns further offshore towards the outer fringe of the littoral zone. Of particular concern were: the perceived negative impacts of stocked species on the endemic fish fauna over the whole lake in relation to the stated hypothesis of other causes due to human impacts; the influence of shallow vegetation dominated habitats on fish diversity and abundance and, the position of the socio-economically important Nile tilapia in the fish community structure.

About 30 species of mostly native fish were identified from the five shallow macrophyte (*E. crassipes*, *C. papyrus*, *V. cuspidata*, *T. domingensis*, *P. mauritianus*) dominated habitats in contrast to 10 species in the open water deeper (4 - 8 m) habitats which were at least 300 m away from the vegetated lake's edge. The species inventory would be bigger had identification of the most diverse haplochromine complex not been restricted to trophic categories. Other common endemic species were *Brycinus jacksonii*, *Astatoreochromis alluaudi* and *Protopterus aethiopicus*. Fish biomass in the shallow habitats averaged 46.7 ± 4.0 kg.ha$^{-1}$ in comparison to 6.2 ± 0.1 kg.ha$^{-1}$ in the open water deeper habitats. In spite of a high fish species diversity of the shallow habitats, only three species (*O. niloticus*, *Tilapia zillii* and *L. niloticus*), all stocked, accounted for 90 % of numerical and biomass densities. The type of habitat and distance from the shore explained most of the significant differences in relative abundance patterns among habitats, with *Vossia-Typha-Phragmites* type habitats containing high densities made up of many young fishes; *Cyperus* and *Eichhornia* dominated habitats had few relatively large mostly Nile tilapia fish. Hydrological influences were important in temporal variations in abundance and were reflected in differences in size related patterns according to habitat type. It therefore seemed evident that habitat structural diversity and seasonal effects on differential use of the habitats by different size (age) groups could account for the high species diversity and abundance of fish despite the presence of stocked species. Such habitat complexity could have moderated effects of predation on native species in comparison to the pressure in

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the more open sub-littoral habitats. On this basis, it could be assumed that some native species which were not encountered but were previously abundant, among them, the cyprinids *Barbus* spp. and *Labeo victorianus*, had apart from other impacts (e.g., fishing) experienced the negative impacts of human activity on wetland habitats.

From field studies on fish populations, Nile tilapia was investigated in detail regarding its contribution to the observed patterns. The mean total biomass of the Nile tilapia varied among habitats between 15.3 and 32.5 kg.ha$^{-1}$ corresponding to 45-60 % of the observed biomass of all fish. The *Vossia-Typha-Phragmites* type habitats were the richest in total numbers and numbers of immature fishes; *Eichhornia* dominated habitats had the highest Nile tilapia biomass made up of few large (> 25 cm) fishes. Within individual habitats, the fish biomass was higher closer to the vegetation fringe than only 50 - 70 m away towards open water. These figures have not been corrected for gear selectivity nor for other fish behavioral patterns. However, as the sampling and quantification of biomass were standardised across the investigated spectrum of habitats, the results do provide an approximate but reliable index of the importance of wetland habitats for the Nile tilapia in Lake Victoria.

Fecundity and successful reproduction are among several factors which contribute to successful colonisation of new environments by introduced species. In Lake Victoria Nile tilapia, breeding was observed in all seasons but the two peaks in breeding just after the onset of rainy periods, and an increase in the number of juvenile fishes could be correlated with the hydrological cycle. Maturation size was found to occur when fish are between 18 and 25 cm in length; on average fish could produce 3723 ± 147 eggs.female$^{-1}$. In comparison to the patterns in its natural habitats in some East African lakes, Nile tilapia of Lake Victoria was shown to mature at larger sizes, had a higher body condition index and produced comparatively more eggs. The investigations also showed that maturation size in the Nile tilapia depends on suitability of habitat particularly a stable water level with changes associated with shallow areas depressing size at first maturity. The quality of food resources in Lake Victoria and the possibility of a genetically different Nile tilapia population in Lake Victoria might partly explain the species better condition, higher fecundity and success in this lake in comparison to elsewhere.

Food habits of the Nile tilapia were therefore considered as an ecological parameter to study further in relationship to environmental factors. It had been established that some distribution patterns depended on habitat, others on season and yet, day and night sampling of the littoral zone revealed more activity in the zone during the day than at night. These results therefore indicated that fish start an outward movement from the vegetation fringes early in the morning. Depending on size, some fish move to areas of the littoral zone with silty sediments, while the smaller sizes do not move far away from the vegetated habitats. These patterns were also similar to size related distribution patterns of Nile tilapia across habitats. In relation to feeding in general, fish appeared to reach peak feeding between 11.00 h and

14.00 h and afterwards, a possible movement back to areas nearer the shore may explain the lack of substantial Nile tilapia activity during the night. Considering that many previous studies had relied on samples collected in the night, it was clear that some food items could have been missed in stomach analyses. At least 65 % of stomach contents (i.e. ingested items) consisted of detrital material and chironomid larvae. Some items such as molluscs and *Caridina* shrimps were seasonally important replacing other items as the main contents during the short dry but cool season around July to September. Other items such as Oligochaeta and the Trichoptera were locally important while algae were more associated with older fish. On the basis of these results, Nile tilapia in the investigated area could best be described as omnivorous and opportunistic, in contrast to the widely regarded herbivorous feeding habits in the literature. The mainly flexible feeding habits could account for plasticity in growth, maturation and variations in fecundity and condition among lakes and the species general adaptability to a wide variety of habitats. Hence, reports of the Nile tilapia's occurrence in various other habitats do not show a lesser importance of wetland habitats for the species but offer an explanation of the species' wide ecological range.

*Eichhornia* dominated habitats presented a unique picture. At the beginning of the research, this new wetland type was not a significant factor in the study area. The weed increased in cover abundance by 200 % in the study area over about two years. It rapidly gained areal importance in specific localities where it could have disrupted the original conditions particularly off a special type of papyrus on-shore wind exposed habitats before some of the sampling sites were fully evaluated. A comparison of macrofauna densities between *Eichhornia* and pure *C. papyrus* dominated habitats showed significantly lower densities in some of the fauna associated with *Eichhornia* domianted habitats. However, *Eichhornia* dominance in some areas also revealed that not all papyrus dominated zones were ecologically similar. Two other wetland habitat types (*Vossia* and *Typha*) had also changed in plant species composition, dominance and biomass patterns towards the end of the study. Not only was there an increase in the number of secondary species in *Typha* stands, but the presence of the weed also appeared to lead to an expansion of *Vossia* beds out into open water. The inclusion of this wetland type was therefore opportune as the present results could quickly be used to show the direction of succession in these habitats. The reduction to almost total disappearance of the native underwater plants such as *Nymphaea* spp. and *Ceratophyllum* was correlated with an increase in the spread of water hyacinth mats. Furthermore, it is clear that conditions (e.g., light, phytoplankton production, oxygen) underneath the extensive water hyacinth mats were different from the original hyacinth free habitats and present results could be used to monitor what further changes take place with increasing infestations.

Lake Victoria has an extensive shoreline, most of it including islands bordered by wetlands. A higher diversity and abundance of fish species in these shallow vegetated habitats than occurs in deep open water is strongly correlated with habitat structural diversity. Apart from vegetation types, habitat diversity is clearly

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evident in sediment types, depth profiles, macrofauna species composition and density, and, these patterns are associated with hydrological and horizontal influences. It is concluded that habitat structural diversity plays a major role in the diversity and abundance of fish species despite the presence of stocked fish in the same habitats. For the Nile tilapia, shallow vegetated habitats of the littoral zone play an important role in the biology and ecology of the species for shelter, reproduction and feeding, even though as a stocked fish, these patterns could disrupt part of the assemblage of native species. Different types of wetland habitats seem to play a role in the life cycle of the species. The species presently accounts for between 45 and 60 % of the biomass of all fish in the wetland habitats. However, as all these habitats respond significantly to hydrological influences, it is inferred that human activity (biomass harvests, agriculture, wastewater) could rapidly degrade the complex food webs which currently are responsible for the socio-economically important fisheries. Therefore, the two major hypotheses set out at the begining of this study viz: (1) There are no significant structural differences among or within shoreline vegetated habitats, (2) there are no significant effects of the habitats on the ecology of fish, are rejected. The results presented here also give an indication of the ecological impact of water hyacinth during a transitional state from a pre-*Eichhornia* free littoral zone to what has become a permanent feature of the ecology of the zone.

# Samenvatting en conclusies

Van oudsher is het meest directe sociaal-economische belang van het Victoriameer de visserij en watervoorziening voor de bevolking in dit dicht bevolkte stroomgebied (bevolkingstoename gemiddeld 2,4 % per jaar, vergeleken met 0,6 % voor de ontwikkelingslanden). Om die reden werden in de jaren vijftig verschillende vissoorten in het meer geïntroduceerd, waaronder een grote roofvissoort, de Nijlbaars (*Lates niloticus*) en een herbivore tilapiine, de Nijl tilapia (*Oreochromis niloticus*). Pas recentelijk is men begonnen met het kritisch bestuderen van de ecologische verstoringen die in dit meer de afgelopen decennia zijn opgetreden. De nadruk lag op de veranderingen in de soortsdiversiteit van de visfauna en in de waterkwaliteit gedurende de laatste twee decennia, beide hoogst waarschijnlijk een gevolg van de introductie van exotische vissoorten (top-down effecten). Minder nadruk werd gelegd op andere mogelijkheden, zoals het fenomeen van het stijgen van de waterspiegel in de jaren zestig of de druk van de menselijke bevolking in het aangrenzende stroomgebied. Een ecologisch onderzoek werd opgezet om de struktuur van de ondiepe overgangshabitats in het Victoriameer nader te bestuderen, met speciale nadruk op de wetlands en de ecologie van de Nijl tilapia. Dit proefschrift gaat er daarom vanuit dat, alhoewel weinig onderzocht, aangrenzende wetlands belangrijk voor vissen zouden kunnen zijn; daarom kunnen menselijke invloeden in het stroomgebied leiden tot veranderingen in het trofieniveau van het meer en met name in de ondiepe habitats nabij de oever.

Het eerste doel van de studie was het inventariseren van de wetland vegetaties langs de kustlijn van het Victoriameer (soortensamenstelling, verspreidings- en dominantiepatronen) en om aan te tonen in hoeverre ruimtelijke veranderingen in de bedekking te wijten zijn aan menselijke aktiviteiten. Een tweede doel was het karakteriseren van de struktuur van de ondiepe aquatische habitats in de littorale zone, grenzend aan de wetland vegetaties (plantbiomassa, waterkwaliteit, sediment, fytoplankton, macrofauna) . Een derde doel was het toelichten van het relatieve belang van de verschillende onderscheiden habitats voor vispopulaties (soortensamenstelling, biomassa), waarbij ook gerapporteerde vissoort patronen in ander habitats van het meer beschouwd zijn. Een laatste doel was de ecologie van de Nijl tilapia te bestuderen in relatie tot de waarschijnlijke invloed van strukturele elementen in de soortsverspreiding, abundantie, reproductie en voedingsgewoonten, dus om het algehele inzicht in het Victoriameer ecosysteem te vergroten.

Er waren nauwelijks kwantitatieve gegevens over de struktuur en divesiteit van de littoral zone, speciaal de door vegetatie gedomineerde habitats, alhoewel de uitgebreide papyrusmoerassen uitermate bekend stonden vanwege hun ongastvrije omstandigheden. Bovendien werd verondersteld dat de Nijl tilapia, ondanks zijn klaarblijkelijk sociaal-economisch belang in kleinschalige visserij in gebieden nabij het meer, beperkt was tot niet gedefinieerde habitats nabij de oever en dezelfde ecologische patronen volgt als gerapporteerd is voor de soort in andere meren. In eerdere studies kan onder 'nabij de oever' diepten tot 10 m verstaan worden: baaien of het meer open water, waarbinnen kleine boten zonder buitenboordmotor kunnen opereren. Maar de Nijl tilapia die in het meer sinds de jaren vijftig wordt uitgezet, kan in een hele reeks van habitats gevangen worden.

Teneinde de gestelde doelen te bereiken bestaat deze studie, die tussen 1993 en 1996 is uitgevoerd, uit twee hoofddelen: (1) literatuurstudies om het concept wetland met betrekking tot het Victoriameer duidelijk te krijgen en de huidige kennis omtrent de Nijl tilapia sinds het uitzetten in de vijftiger jaren te evalueren en (2) een reeks van samenhangende veld- en laboratoriumstudies.

De meer dan 40 plantensoorten die bij opnames over een 110 km lange kustlijn werden geïdentificeerd konden in vijf hoofdgemeenschappen worden onderscheiden voor wat betreft de dominante emergente oeversoorten. Deze soorten waren: *Cyperus papyrus* L. (papyrus), *Phragmites mauritianus* Kunth (riet), *Typha domingensis* Pers (lisdodde), *Vossia cuspidata* (Roxb.) (Nijlpaardgras) en *Sesbania sesban* (L.) Merrill. De exotische drijvende *Eichhornia crassipes* (Marts.) Solms-Laubach (waterhyacint) was in zijn beginfase van kolonisatie van de kustlijn en nam snel toe in bedekking, waarbij een nieuw wetlandtype ontstond.

In het wetlandlandschap langs de oevers van het Victoriameer werden aanzienlijke lange termijn veranderingen geconstateerd. Deze veranderingen bleken primair samen te gaan met een toenemende menselijke aktiviteit (landbouw, biomassa oogsten) resulterend in een 5 % reductie van de bedekking met wetlands. Het onderzoeksgebied omvatte echter nog steeds overgangsgebieden naar het open meer, gedomineerd door deze macrofyten. Ondanks de afwezigheid van een goed ontwikkelde euhydrofytengemeenschap van met name submerse vegetatie (zoals *Ceratophyllum* en *Potamogeton*), en de toenemende bedekking met de waterhyacint, kon de breedte van de overgangszone worden vastgesteld, met behulp van meting van de doorzichtdiepte, op 50 - 70 m afstand van de verschillende emergente oeverplanten. De littorale zone liep af vanaf minder dan 1 m diepte nabij de oever tot tussen de 2 m en 4 m aan de buitenste rand. De diversiteit van de ondiepe overgangshabitats kon daarom vastgesteld worden aan de hand van het type dominante oeverplant. Vanaf de buitenste rand van de littorale zone was, afhankelijk van de helling van de oever, een gordel van variabele breedte naar de dieper gelegen gebieden in het meer, waar de sedimentsamenstelling gedomineerd werd door slib.

*S. seban* moet voor de meerspiegelrijzing in de zestiger jaren verder landinwaarts zijn voorgekomen; daarom wordt zij in deze studie niet beschouwd als een apart vegetatietype. De ondiepe aquatische habitats die bij de overige vijf makrofyten behoorden werden in detail bestudeerd. Afgezien van de biomassa van de oevervegetatie, die erg variabel was binnen de vegetatietypen, werden geen significante verschillen vastgesteld in de fysische en chemische strukturele aspecten (diepte, helling, sedimenttextuur en organische stof, nutriënten) binnen de geselecteerde replicate habitats. Daarom werden de vegetatietypen representatief geacht voor de verschillende aquatische hoofdhabitats in het ondiepe littoraal van het meer. Ondanks het feit dat ze gedefiniëerd zijn op basis van verschillende dominante oeverplanten en de gemiddelde diepte, helling en sedimentkarakteristieken, konden de vijf aquatische hoofdhabitats verdeeld worden in twee hoofdtypen: a) diepere habitats met meer organische stof in het sediment

(door *C. papyrus* en *E. crassipes* gedomineerde habitats), en b) ondiepere, geleidelijk aflopende habitats met meer zand in het sediment (door *V. cuspidata*, *P. mauritianus* en *T. domingensis* gedimoneerde habitats). *Eichhornia* onderscheidde zich extra doordat het zich in dikke matten uitstrekte naar het open water toe en dat het sterker geassocieerd was met door papyrus gedomineerde oevers, blootgesteld aan aanlandige wind. Op sommige lokaties bleek de waterhyacint een permanent verschijnsel van de kustlijn te zijn geworden. Daarom werd waargenomen, dat, afgezien van de aanwezigheid van de waterhyacint en de wind, additionele milieufactoren aan de complexiteit van de vegetatiehoudende habitats konden bijdragen.

Voor sommige struktuurkarakteristieken (totaal-P, SRP en pH) zijn significante verschillen tussen de aquatische habitats gevonden. Deze zijn deels te wijten aan het type dominante vegetatie nabij de oever. Seizoenseffecten (hydrologie) leken het grootste deel van de variatie in de habitats te verklaren voor wat betreft silicium, SRP, chlorofyl-a, watertemperatuur en pH. In enkele gevallen had de interaktie tussen habitattype en seizoen duidelijke effecten op verschillen in de horizontale spreiding van opgelost zuurstof en $NO_3$-N tussen en binnen de habitats. Bovendien had de afstand van de rand van de vegetatie tot het open water een significant effect op chlorofyl-a, totaal-P, $NO_3$-N en pH. Waarschijnlijk zijn deze waarnemingen dan ook beïnvloed door regenval en de daarop volgende afspoeling, die in aanwezigheid van verminderde biomassa aan oeverplanten, de struktuur van de littoral zone veranderen tot op verschillende afstanden in het open water, afhankelijk van diepte, helling en sedimentkarakteristieken van de habitats. De hypothese, dat menselijke invloeden de struktuur van de overgangshabitats significant beïnvloeden is daarom gerechtvaardigd. Bijvoorbeeld, de ondiepe aquatische habitats met vegetaties zijn gekenmerkt door concentraties van ongeveer 350 $\mu$g.l$^{-1}$ Si, 50 $\mu$g.l$^{-1}$ tot.-P, 100 $\mu$S.cm$^{-1}$ geleidbaarheid en meer dan 20 $\mu$g.l$^{-1}$ chlorofyl-a, dit in tegenstelling tot ongeveer 70 $\mu$g.l$^{-1}$ Si, 1,5 $\mu$g.l$^{-1}$ tot.-P, 94 $\mu$S.cm$^{-1}$ geleidbaarheid en minder dan 5 $\mu$g.l$^{-1}$ chlorofyl-a in het open water, in de literatuur beschouwd als nabij de oever. Chlorofyl-a en pH waren positief gecorreleerd met de afstand tot de oever en het regenseizoen.

Het studiegebied kent vier seizoenen. Een lang droog seizoen van december tot halverwege maart wordt gevolgd door een lang nat seizoen dat duurt tot juni. Dit wordt gevolgd door een kort droog maar koel seizoen tot ongeveer september. Het laatste deel van het jaar is nat maar heeft minder regen dan de maart-juni periode. Als verwacht mag worden, volgen seizoensvariaties in de waterkwaliteit van de habitats dit klimaatregime, maar optreden en grootte van de verandering kunnen van jaar tot jaar variëren, zoals het geval kan zijn geweest bij dus de uitzonderlijk zware regens in de periode 1960/62.

Voor wat betreft de biotische elementen in de littorale zone werd de fytoplanktonsamenstelling gedomineerd door de Cyanobacteria (blauwalgen), en wel de geslachten *Anabaena*, *Lyngbya*, *Merismopedia* en *Microcystis*. Met name de draadvormige algen waren belangrijk, alhoewel de hiervoor vereiste specifieke

analysemethoden niet voorhanden waren. Onder de diatomeeën was *Nitzschia* veruit de meest abundante vorm, terwijl onder de groenalgen *Scenedesmus* en *Ankistrodesmus* vaak aangetroffen werden. Fytoplanktonsuccessie van blauwalgen (*Microcystis* en draadvormige algen) naar diatomeeën (*Nitzschia*) leek seizoensveranderingen te volgen; het leek sterk op en was waarschijnlijk verwant aan patronen die in de literatuur vermeld zijn van lokaties ver uit de kust.

De verspreiding van evertebraten (makrofauna) was minder systematisch, waarschijnlijk als gevolg van een te klein aantal monsters, maar ook door de sterke interaktie tussen vegetatietype en afstand van de oever. Gastropoden en chironomiden waren echter talrijker nabij de rand van de vegetatie dan verder weg. Een tweede patroon, weerspiegeld in de samenstelling en abundantie, trad op ongeveer 400 m van de rand van de vegetatie. Dit patroon leek op dat tussen de rand van de vegetatie en 40 m vanaf de rand en hing waarschijnlijk samen met specifieke verschillen in taxa of levensstadia van soorten die dichter bij de vegetatie zijn gevonden. Alhoewel in dieper water, lijkt dit secundaire patroon meer samen te hangen met slibrijke bodemsubstraten.

Gezien de fysische en chemische karakteristieken van onderzoeksgebied, was het duidelijk dat de littorale zone ruimtelijk langs twee assen gestruktureerd is: één gedefinieerd door de vegetatie en één door de afstand naar het open water. Om inzicht te verkrijgen in de vispopulaties van het onderzoeksgebied, zijn soortensamenstelling, relatieve abundantie $(no.ha^{-1})$ en biomassa $(kg.ha^{-1}$ natgewicht) vergeleken tussen gebieden die horen bij specifieke dominante planten, en patronen verder naar de buitenste rand van de littorale zone. Belangrijk hierbij waren a) de waargenomen negatieve effecten van uitgezette soorten op de endemische visfauna over het gehele meer in relatie tot de gestelde hypothese van andere oorzaken ten gevolge van menselijke invloeden, b) de invloed van ondiepe, door makrofyten gedomineerde habitats op de visdiversiteit en -abundantie en c) de plaats van de sociaal-economisch belangrijke Nijl tilapia in de visgemeenschapsstruktuur.

Ongeveer 30 soorten, voornamelijk inheemse vis, zijn aangetroffen in de vijf vegetatietypen (*E. crassipes, C. papyrus, V. cuspidata, T. domingensis, P. mauritianus*), en 10 soorten in diepere (4-8 m) open water habitats, op minstens 300 m van de oever. Wanneer de determinatie van het meest diverse haplochromine complex niet beperkt was gebleven tot trofische categorieën, was het aantal onderscheiden soorten groter geweest. Andere algemene endemische soorten waren *Brycinus jacksonii, Astatoreochromis alluaudi* en *Protopterus aethiopicus*. De visbiomassa in de ondiepe habitats was gemiddeld $46,7 \pm 4,0$ $kg.ha^{-1}$ vergeleken met $6,2 \pm 0,1$ $kg.ha^{-1}$ in het diepere open water. Ondanks de hoge soortsdiversiteit in de ondiepe habitats maken slechts drie soorten (*O. niloticus, Tilapia zillii* en *L. niloticus*), alle uitgezet, 90 % uit van zowel aantal als biomassa. Het type habitat en de afstand van de kust verklaarde de meeste van de significante verschillen in relatieve abundantiepatronen tussen de habitats, waarbij *Vossia-Typha-Phragmites* type habitats de hoogste dichtheden hadden, vooral veel jonge vis; *Cyperus* en

*Eichhornia* gedomineerde habitats hadden weinig, relatief grote vis, meestal Nijl tilapia. Hydrologische invloeden waren belangrijk voor temporele variaties in abundantie en werden weerspiegeld in verschillen in grootte-gerelateerde patronen overeenkomstig het habitattype. Daarom leek het evident dat de diversiteit in struktuur van de habitats en seizoenseffecten op verschillend gebruik van de habitats door verschillende grootte (leeftijds)groepen verantwoordelijk kunnen zijn voor de hoge soortsdiversiteit en abundantie van vissen, ondanks de aanwezigheid van geïntroduceerde soorten. Een dergelijke complexiteit van de habitat zou dempende effecten kunnen hebben op de predatie van inheemse soorten vergeleken met de druk in de meer open water habitats. Op deze gronden kan worden aangenomen, dat sommige inheemse soorten, die niet aangetroffen zijn, maar voorheen talrijk waren, zoals de cypriniden *Barbus* spp. en *Labeo victorianus*, naast andere invloeden (zoals visserij) negatieve effecten van menselijke aktiviteit op wetland habitats ervaren hebben.

Middels veldstudies aan vispopulaties werd de Nijl tilapia in detail bestudeerd voor wat betreft zijn bijdrage aan de waargenomen patronen. De gemiddelde totale biomassa vande Nijl tilapia variëerde tussen de verschillende habitats van 15,3 tot 32,5 kg.ha$^{-1}$, hetgeen overeenkomt met 45 - 60 % van de totale visbiomassa. De *Vossia-Typha-Phragmites* type habitats waren het rijkst in totale aantallen een aantal onvolwassen vissen; *Eichhornia* gedomineerde habitats hadden de hoogste biomassa Nijl tilapia, bestaande uit een paar grote (> 25 cm) vissen. Binnen de individuele habitats was de visbiomassa hoger nabij de rand van de vegetatie dan slechts 50 - 70 m verder in het open water. Deze cijfers zijn niet gecorrigeerd voor selectie door de gebruikte netten, noch voor andere gedragspatronen van de vis. Echter, aangezien de bemonstering en kwantificering van de biomassa gestandaardiseerd waren over het onderzochte spectrum van habitats, geven de resultaten een dicht benaderde, maar betrouwbare indicatie van het belang van wetland habitats voor de Nijl tilapia in het Victoriameer.

Fecunditeit en succesvolle reproductie zijn factoren die bijdragen aan een geslaagde kolonisatie van nieuwe milieus door geïntroduceerde soorten. De Nijl tilapia in het Victoriameer broedt in alle seizoenen, maar de twee pieken in broeden vlak na het begin van de regenperiodes en een toename van het aantal juveniele vissen konden gecorreleerd worden met de hydrologische cyclus. De grootte waarop de vissen rijp worden lag tussen 18 en 25 cm lengte; gemiddeld kon de vis 3723 ± 147 eieren.vrouwtje$^{-1}$ produceren. Vergeleken met de patronen in zijn oorspronkelijke habitats in bepaalde Oostafrikaanse meren, bleek de Nijl tilapia in het Victoriameer bij grotere lengten rijp te worden, een hogere lichaamsconditie index te hebben en meer eieren te produceren. Het onderzoek toonde ook aan dat de rijpingsgrootte van de Nijl tilapia afhangt van de geschiktheid van de habitat, in het bijzonder een stabiel waterniveau, waarbij veranderingen in de ondiepe delen de grootte bij de eerste rijping verlagen. De kwaliteit van het voedsel in het Victoriameer en de mogelijk genetisch verschillende populatie van de Nijl tilapia in het Victoriameer kunnen deels een verklaring zijn voor de betere conditie van de soorten, de hogere fecunditeit en het succes in dit meer vergeleken met elders.

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Het fourageergedrag van de Nijl tilapia werd daarom beschouwd als een ecologische parameter die verder bestudeerd moest worden in relatie tot omgevingsfactoren. Er werd vastgesteld dat sommige verspreidingspatronen afhingen van de habitat, andere van het seizoen. Niettemin toonden dag- en nachtbemonsteringen van de littorale zone aan dat er overdag meer aktiviteit was dan 's nachts. Deze resultaten geven dan ook aan dat de vis 's morgens begint met een migratie vanuit de vegetatieranden. Afhankelijk van de grootte verplaatsen sommige vissen zich naar gebieden met slibrijke sedimenten in de littorale zone, terwijl de kleinere vissen zich niet ver van de habitats met vegetatie verwijderen. Deze patronen kwamen ook overeen met grootte gerelateerde verspreidingspatronen van de Nijl tilapia over de habitats heen. Ten aanzien van het fourageren in het algemeen leken de vissen een maximum in het fourageren te bereiken tussen 11.00 en 14.00 uur en later; een mogelijke beweging terug naar gebieden nabij de oever kan het gebrek aan substantiële activiteit van de Nijl tilapia gedurende de nacht verklaren. In gedachten houdend dat veel van de eerdere studies gebaseerd zijn op monsters, die gedurende de nacht verzameld zijn, is het duidelijk dat bepaalde soorten voedsel in de maaganalyses gemist zijn. Minstens 65 % van de maaginhoud (d.w.z. opgenomen voedsel) bestond uit detritus en chironomidenlarven. Sommige soorten voedsel, zoals molluscen en *Cardina*-garnalen waren in bepaalde seizoenen belangrijk, waarbij zij andere soorten voedsel vervingen, zoals in het korte droge, maar koele seizoen rond juli tot september. Andere voedselsoorten zoals Oligochaeta en Trichoptera waren plaatselijk belangrijk, terwijl algen meer geassocieerd waren met oudere vis. Op basis van deze resultaten kon de Nijl tilapia in het onderzochte gebied het best omschreven worden als omnivoor en opportunistisch, in tegenstelling tot het in de literatuur breed aanvaarde herbivore voedingsgedrag. Het zeer plooibare fourageergedrag kan de reden zijn voor de plasticiteit in groei, rijping en variaties in fecunditeit en conditie tussen de verschillende meren en het algehele aanpassingsvermogen van de soort aan een grote variatie in habitats. Bijgevolg tonen vermeldingen van het voorkomen van de Nijl tilapia in allerlei andere habitats niet een minder belang van wetland habitats voor de soort aan, maar geven zij een verklaring voor het brede ecologische spectrum van de soort.

*Eichhornia* gedomineerde habitats geven een uniek beeld. Aan het begin van het onderzoek was dit nieuwe wetland type geen significante factor in het onderzoeksgebied. De waterplant nam in het onderzoeksgebied echter in twee jaar met 200 % bedekking toe. Nog voordat alle monsterplaatsen volledig geëvalueerd waren, nam de bedekking met de waterhyacint op bepaalde plaatsen snel toe, waarbij het de oorspronkelijke omstandigheden kon hebben verstoord, met name bij sommige papyrus habitats op plekken met aanlandige wind. Een vergelijking van de makrofaunadichtheden tussen *Eichhornia* en pure *C. papyrus* gedomineerde habitats gaf significant lagere dichtheden van sommige fauna-elementen in de *Eichhornia* gedomineerde habitats. De *Eichhornia* dominantie in sommige gebieden toonde echter ook aan dat niet alle papyrus gedomineerde zones ecologisch gelijk waren. Twee andere wetland habitat typen (*Vossia* en *Typha*) waren tegen het eind van de studie ook veranderd qua soortensamenstelling, dominantie en biomassapatronen van de planten. Er was niet alleen een toename in het aantal

secundaire soorten in *Typha* vegetaties, maar de aanwezigheid van de waterhyacint bleek tevens te leiden tot een expansie van *Vossia*-velden naar het open water toe. Het opnemen van dit wetland type was daarom belangrijk omdat de huidige resultaten snel gebruikt konden worden om de richting aan te tonen waarin de successie van deze habitats verloopt. De reductie tot bijna volledig verdwijnen van de oorspronkelijk drijvende en submerse planten zoals *Nymphaea* spp. en *Ceratophyllum* was gecorreleerd met een toename in de verspreiding van de waterhyacint. Bovendien is het duidelijk dat omstandigheden onder de uitgestrekte waterhyacint matten (zoals licht, fytoplankton productie, zuurstof) verschillen van de oorspronkelijk waterhyacint-vrije habitats en de huidige resultaten zouden gebruikt kunnen worden om vast te leggen welke veranderingen in de toekomst optreden bij een toenemende bedekking met waterhyacint.

Het Victoriameer heeft een uitgebreide kustlijn, voor het grootste deel met eilanden die door werlands omzoomd zijn. Een hogere diversiteit en abundantie van vissoorten in deze ondiepe wetland habitats vergeleken met het diepe open water is sterk gecorreleerd met de diversiteit in de struktuur van de habitats. Habitatdiversiteit is, afgezien van vegetatietype, duidelijk aantoonbaar in sediment type, diepteprofielen, soortensamenstelling van de makrofauna en dichtheid en deze patronen hangen samen met hydrologische en horizontale invloeden. Het is vastgesteld dat de strukturele diversiteit in de habitats een belangrijke rol speelt bij de diversiteit en abundantie van vissoorten, ondanks de aanwezigheid van uitgezette vis in dezelfde habitats. Voor de Nijl tilapia spelen ondiepe habitats met vegetatie een belangrijke rol in de biologie en ecologie van de soort voor wat betreft schuilplaats, reproductie en voeding, zelfs, aangezien het een uitgezette vis is, wanneer deze patronen een deel van de samenstelling van de oorspronkelijke soorten kan verstoren. Verschillende typen wetland habitats lijken een rol te spelen in de levenscyclus van de soort. De soort bepaalt op dit moment 45 tot 60 % van de biomassa van alle vissen in de wetland habitats. Aangezien al deze habitats echter significant reageren op hydrologische invloeden, is hieruit afgeleid dat menselijke aktiviteit (oogsten van biomassa, landbouw, afvalwater) snel de complexe voedselwebben, die op dit moment verantwoordelijk zijn voor de sociaal-economisch belangrijke visserij, kunnen afbreken. Daarom worden de twee balngrijkste hypothesen, die aan het begin van dit onderzoek zijn gesteld, zijnde (1) er is geen significant verschil tussen of binnen de oeverhabitats met vegetatie en (2) er zijn geen significante effecten van de habitats op de ecologie van vissen, verworpen. De hier gepresenteerde resultaten geven ook een indicatie van de ecologische invloed van de waterhyacint tijdens een overgangsfase van een pre-*Eichhornia* vrije littoral zone naar wat een permanent verschijnsel voor de ecologie van de zone is geworden.

# Curriculum Vitae

John Stephen Balirwa was born in Kamuli district, Uganda on 24 December 1950. He attended and finished ordinary and advanced secondary education at Busoga College Mwiri in 1971. In 1975, he obtained a Bachelor of Science (BSc) honours degree of the University of Dar es Salaam, Tanzania. He worked briefly with the Uganda Government Tsetse Control Department before joining the present Fisheries Research Institute (FIRI) at Jinja in Uganda as a research officer. With a fellowship from the Commonwealth Fund for Technical Cooperation (CFTC), he finished his Master of Science (MSc) degree in fisheries and aquatic sciences, specialising in "Ecological separation among the *Barbus* species of Lake Victoria" at the University of Dar es Salaam in 1984. While at FIRI, he received an EU fellowship to undertake a post-graduate diploma course in Environmental Science and Technology at the International Institute for Infrastructural, Hydraulic and Environmental Engineering (IHE) at Delft, The Netherlands. In 1992, he received an IHE fellowship to follow the IHE M.Sc programme in Environmental Science and carried out his research on "Nutrient and hydrological balances in the Province of North-West Overijssel", The Netherlands. From 1993, he started his PhD research studies under the sponsorship of the Cooperation in Environmental Ecotechnology (CEEDC) Project initiated by the Wageningen Agricultural University (WAU) and IHE. His PhD research, carried out in Lake Victoria, concerned structural aspects of shallow aquatic habitats bordered by wetland vegetation and their influence on species diversity and ecology, with special emphasis on fish and the ecology of the Nile tilapia, *Oreochromis niloticus*. John S. Balirwa has published a number of articles in international journals mainly in the fields of aquatic ecology and fisheries.