Shifts in the food of Nile tilapia, *Oreochromis niloticus* (L.) in Lake Victoria, Kenya

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Abstract

Studies of the food of introduced Nile tilapia, *Oreochromis niloticus* (L.) with respect to size, habitat and season were conducted between November 1998 and October 2000 in Kenyan waters of Lake Victoria. Stomach contents of 1980 specimens collected by demersal trawl and seining were analysed. Nile tilapia originally known to be herbivorous, feeding mostly on algae has diversified its diet to include insects, fish, algae and plant materials. The major diet of fish <5 cm total length was zooplankton whereas bigger fish included a wider range of food items in their diet. There was spatial variation in diet with insects and algae dominating in the gulf and open water habitats respectively. There was no seasonal variation in the food items ingested and diel feeding regime indicated that *O. niloticus* is a diurnal feeder. The shift in diet could be due to ecological and environmental changes in Lake Victoria, which have been associated with changes in composition and diversity of fish and invertebrate fauna, emergence and dominance of different flora including water hyacinth *Eichhornia crassipes* (Mart.) Solms-Laub., and algae communities. The feeding habit of *O. niloticus* is discussed in the context of changes occurring in the lake.

Key words: diet, ecosystem changes, insectivorous, Nile perch, haplochromines, herbivorous

Résumé

Entre novembre 1998 et octobre 2000, on a réalisé des études sur la nourriture des tilapias, *Oreochromis niloticus* (L.), introduits dans les eaux kenyanes du lac Victoria, en fonction de leur taille, de l'habitat et de la saison. Les contenus stomacaux de 1980 spécimens récoltés par la pêche du fond au chalut et à la senne ont été analysés. Le tilapia, connu au départ comme un herbivore, se nourrissant principalement d'algues, a diversifié son régime alimentaire pour y inclure des insectes, des poissons, des algues et d'autres matières végétales. La plus grande partie du régime des poissons de moins de 5 cm de longueur totale se composait de zooplancton, alors que les plus gros poissons y incluaient une gamme plus variée d'aliments. Il y avait une variation spatiale du régime, les insectes et les algues dominant respectivement dans le golfe et dans les eaux ouvertes. Il n'y avait pas de variation saisonnière des aliments ingérés, et le régime quotidien indique qu' *O. niloticus* se nourrit de jour. Les changements de régime alimentaire pourraient être dus à des changements écologiques et environnementaux dans le lac Victoria, qui pourraient eux-mêmes avoir été associés à des changements de la composition et de la diversité de la faune piscicole et invertébrée, à l'émergence et à la dominance d'une certaine flore, y compris la jacinthe d'eau, *Eichhornia crassipes* (Mart.) Solms-Laub., et de communautés d'algues. Les habitudes alimentaires d' *O. niloticus* sont discutées dans le contexte des changements survenus dans le lac.

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Introduction

Nile tilapia, *Oreochromis niloticus* (L.) is widely distributed in Africa and many parts of the world (Trewavas, 1983). It was introduced into Lake Victoria in the 1950s together with other tilapiines like *O. leucostictus* (Graham), *Tilapia zillii* (Gervais) and *T. rendalii* (Boulenger) (Welcomme, 1967; Trewavas, 1983). In 1960, *O. niloticus* constituted <1% of commercial catch landings (Welcomme, 1967), rising to 7% by 1999 (Othina & Tweddle, 1999). Currently *O. niloticus* is the most important tilapiine, whereas the native species of *O. variabilis* (Boulenger) and *O. esculentus* (Graham) have largely disappeared (Witte & Van densen, 1995). Nile tilapia now constitutes the third most important commercial fishery in the Kenyan portion of Lake Victoria, after Nile perch, *Lates niloticus* (L.) and a native cyprinid, *Rastrineobola*

argentea (Pellegrin) (Njiru *et al.*, 2002). The dominance of *O. niloticus* over other tilapiines in the lake is attributed to several factors including high fecundity and fast growth rates (Welcomme, 1967; Balirwa, 1998).

Observations made in lakes and rivers where *O. niloticus* occurs shows the species to prefer algae and plant material in its diet, but it ingests a great variety of foods (Lowe-McConnell, 1958; Moriarty & Moriarty, 1973; Ochumba & Manyala, 1992; Getabu, 1994; Balirwa, 1998). The species tends to feed on bottom deposits derived from the planktonic rain and other sources, and gains nutritive value from organic particles and other organisms, which cover their surface (Moriarty & Moriarty, 1973). In the Nyanza Gulf of Lake Victoria, *O. niloticus* was observed to feed primarily on blue green algae and diatoms, desmids and green algae (Getabu, 1994).

In recent years, the fish community structure and ecosystem dynamics of the lake have changed, but no studies have been carried out to assess whether the fishes have altered their diets in the Kenyan waters of Lake Victoria. The aim of this study was to determine whether *O. niloticus* has changed its feeding habits with ecosystem and fish community structure changes in the lake.

Materials and methods

Study area

The Kenyan part of Lake Victoria comprises the main lake (open waters) and semi-enclosed Nyanza Gulf also known as Kavirondo or Winam Gulf (Fig. 1). The main geographical, hydrological and physical characteristics of Lake Victoria and Nyanza Gulf have been summarized by Crul (1995). Nyanza Gulf lies within the equatorial region. The water temperature and solar radiation are relatively constant throughout the year (mean value of 22 ± 3°C and

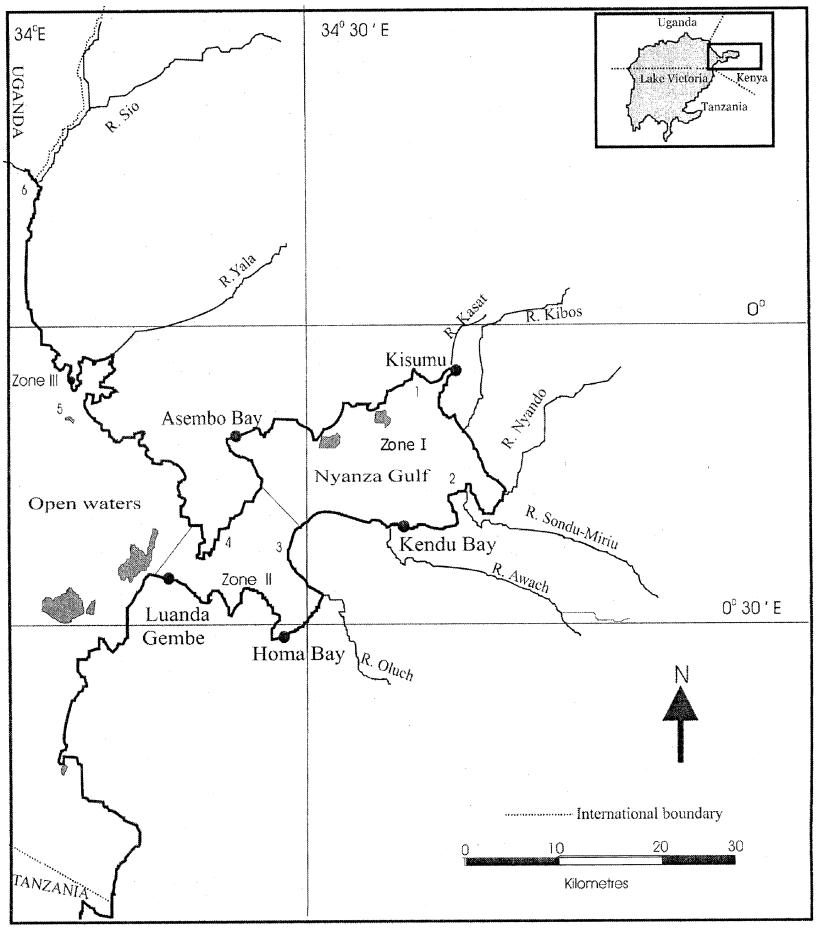


Fig 1 Map of Lake Victoria, Kenya, showing sampling areas

1200 ± 140 ME M^{-1} S^{-1}). There are two main rainy seasons, the long rains occurring from March to May and short rains from November to December.

Sampling procedures

The Kenyan part of Lake Victoria was divided into three zones (Fig. 1). Zone I is shallow (3–4 m), has the highest number of rivers and covers the inshore Nyanza Gulf waters. Zone II is deep (10–20 m) and covers the offshore Nyanza Gulf waters. Zone III is shallow (5–6 m) covering the inshore open lake. Samples of *O. niloticus* were obtained by bottom trawl (head rope 22.6 m, codend mesh size 24.5 mm) and mosquito seine (5 mm) during November 1998 to October 2000. Trawls were conducted monthly except when circumstances could not permit. Seining caught most fish below 10 cm. Immediately after capture total length (TL, cm) of fish was measured to the nearest centimetre and gut contents removed and preserved in 4% formalin. The gut contents were analysed using a modified point method according to Hynes (1950) as reviewed by Hyslop (1980). Each stomach was awarded an index of fullness from 0 to 20; empty stomach scored 0; a quarter full 5; half full 10; three-quarter full 15 and full 20. In the laboratory, stomach contents were emptied into a Petri dish and food items were sorted into categories using a binocular (×50) microscope. Each category was assigned a number of points proportional to the estimated contribution. The importance of each food category was expressed as a percentage by dividing the total points awarded to all food types into number of points awarded to the food type in question. Stomach contents for each 5 cm length class were assessed separately.

To establish when the fish fed, a 24-h sampling regime was conducted every 2 h by seining. Individual fish caught were weighed (g) and measured (TL, cm). The stomachs were opened up and the contents weighed (g) using an electronic balance. Stomach fullness (SF) were expressed as percentage of fish viz.

$$SF = SC/\text{fish weight (g)} \times 100,$$

where SC = stomach contents (g).

Results

Diet composition

During the period November 1998 to October 2000 the gut contents of 1980 Nile tilapia, *O. niloticus*, were analyzed. The fish examined ranged from 1.6 to 55.5 cm TL. Insects, particularly *Povilla adusta* (Návas), fish (*R. argentea*), algae and plant material were the most important food types, with fish of all sizes including them in their diet (Fig. 2). Insect constituted 42.6%, of which unidentified insect remains were 21.5%, *P. adusta* 10.8%, Trichoptera 8.1%, Odonata 1.1% and Chironomid 1.1%. Fish constituted 18.1%, of which unidentified fish remains were 11.9%, *R. argentea* 4.7%, haplochromines 0.9% and juvenile Nile perch 0.5%. Algae and plant constituted 14.3% and 12.5%, respectively, of the entire diet fed upon by *O. niloticus*. Other invertebrates included zooplankton (Cladocera, Copepoda), which constituted 4.8%, *Caridina nilotica* (Roux) 0.6%, and oligochaetes 0.3% of the total food items ingested by *O. niloticus*. Bivalves and detritus contributed 3.6% and 3.1%, respectively, of the food items in the tilapia gut.

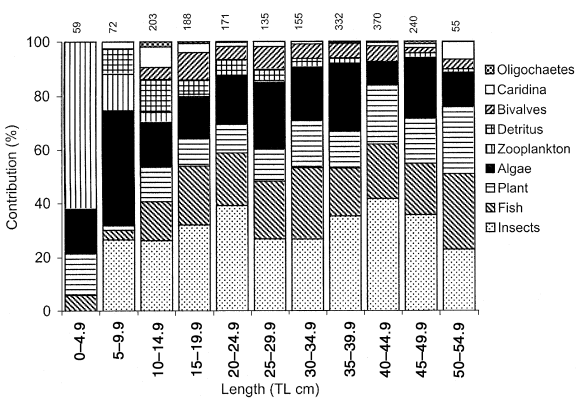


Fig 2 Food of *Oreochromis niloticus* of different length from Lake Victoria, Kenya. Numbers above columns indicate sample size

Food in relation to fish size

A change in the diet with increasing size was apparent, with all size classes consuming all the important food items (Fig. 2). Zooplankton was the major food of *O. niloticus* under 5 cm TL, and was of little importance to fish larger than 10 cm TL. Insects were also of little importance to the diet of small Nile tilapia (<5 cm), but were major food items of larger fish. Algae, fish and plant material were consistently important to all size groups. Fish <10 cm did not consume bivalves, *C. nilotica* or oligochaetes. Only one fish of 55.5 cm TL was caught with gut full of *P. adusta*.

Spatial variation in diet composition

There was spatial variation in the composition of the food items consumed by Nile tilapia in Lake Victoria, Kenya. Insects dominated tilapia diet in the inshore (51.1%) and offshore gulf (42.8%) of the lake. The other important food items in the gulf were fish and plant material. In the inshore open waters zone, the important food item was algae (32.7%) followed by fish (26.8%) and insects (24.4%). Detritus (6.0%) constituted a significant proportion of tilapia food in the inshore gulf and bivalves (6.8%) featured more in the offshore zone. Zooplankton was consumed more in the inshore zone while oligochaetes and Huridinea were rarely ingested in any of the zones. Chi-square test revealed significant difference between the ingested insects ($\chi^2 = 9.47$, $P < 0.05$), plant ($\chi^2 = 7.00$, $P < 0.05$), algae ($\chi^2 = 19.3$, $P < 0.05$), detritus ($\chi^2 = 6.21$, $P < 0.05$) and zooplankton ($\chi^2 = 10.3$, $P < 0.05$) in the three zones. No significant spatial variation was detected between the other food items.

Further analyses by station revealed that insects were the most important food items except in station 6 where algae dominated (Table 1). Fish ingested in all the stations was dominated by *R. argentea* with tilapia at stations 5 and 6 having no haplochromines and Nile perch in its diet. Plant and detritus were consumed more in the gulf stations, while *Caridina* was frequently eaten at stations 2 and 5. Bivalves featured more in stations 3 and 4 while oligochaetes and Huridinea were rarely consumed.

Seasonal variation in diet composition

The monthly variation in the composition of the food ingested by *O. niloticus* by zones showed insects to be the most important annually in the inshore (51.1%) and offshore (42.8%) gulf while algae dominated in the inshore (32.7%) open waters. The other important food items annually in all the zones were fish and plant material. Fish contributed 17%, 16.1% and 26.8% of the total diet of Nile tilapia in zones I, II and III respectively. Contribution of plant material to the diet of *O. niloticus* varied from 12.3%, 15.1% to 3.6% in zones I, II and III respectively. Bivalves were ingested by tilapia in all the months in zone II and occasionally taken in the other zones. Zooplankton, *Cari-*

Table 1 Percentage contribution of various food items in the gut of *O. niloticus* from various zones in Lake Victoria

	Zone I		Zone II		Zone III	
Food item	1*	2	3	4	5	6
Insect remains	8.2	34.3	26.1	19.4	23.5	0.6
Chironomid		0.2	0.1	2.3	4.5	
Trichoptera	10.2	14.4	6.4	8.3	3.6	0.6
Povilla	28.6	6.7	8.0	11.1		3.3
Odonata	0.1		3.1	0.1		
Total insects	47.1	55.6	43.7	41.2	31.6	4.5
Fish remains	13.8	10.4	9.9	10.6	17.4	19.1
R. argentea	0.9	5.8	5.0	3.3	8.2	11.0
Haplochromines	1.8	1.5	0.7	1.1		
Nile Perch		0.5	1.0	0.2		
Total fish	16.5	18.2	16.6	15.2	25.6	30.1
Plant	17.5	6.2	11.8	20.4	1.3	9.8
Algae	6.3	9.9	13.0	12.5	25.8	51.6
Detritus	8.0	3.9	3.6			0.8
Cladocera	1.9	0.1	0.4	1.0	0.2	
Copepoda	0.4			0.1	8.7	
Zooplankton	2.3	0.1	0.4	1.1	8.9	
Bivalves			7.9	5.0	0.4	
Caridina	2.3	6.0	3.0	3.0	6.4	2.4
Oligochaetes				1.3		
Huridinea		0.2				0.7

*Station number.

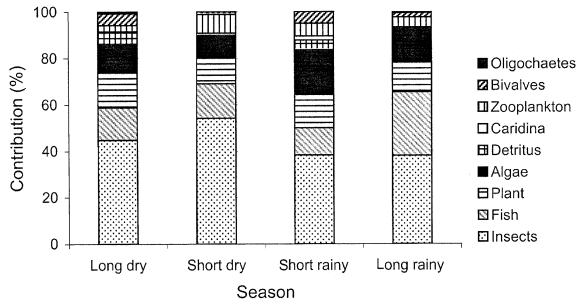


Fig 3 Seasonal variation of food items ingested by *O. niloticus* in Lake Victoria, Kenya

dina, oligochaetes and Huridinea were sporadically taken in all the zones annually.

The seasonal variation in the diet of *O. niloticus* shows the highest (54.3%) consumption of insects occurred in the short dry season (Fig. 3). Nile tilapia ingested more plant, detritus, bivalves and oligochaetes in the long dry season whereas fish was mainly consumed in the long rainy season. Most algae and *Caridina* were ingested during the short rainy season while zooplankton was mainly consumed in the short dry season. A chi-square test detected no significant seasonal differences between the food items ingested by *O. niloticus*.

Diel feeding rhythm

A 24-h feeding study showed *O. niloticus* feeds mostly during the day and very little food is ingested at night (Fig. 4). The daily feeding regime has two peaks, one around 11.00 and the other around 17.00 hours. Food ingested starts declining after dusk (19.00 hours) reaching the lowest level at 02.00 hours in the morning. The stomach contents start to increase again at 05.00 hours.

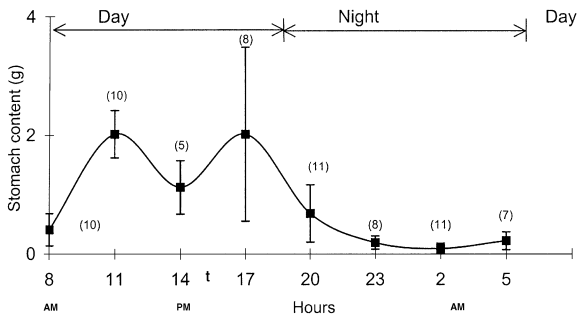


Fig 4 Diel feeding regime of *O. niloticus* from Lake Victoria, Kenya. Vertical lines indicate the mean ± SD. Figures in parentheses indicate sample size

Discussion

Despite its wide ecological tolerance (Lowe-McConnell, 1958; Balirwa, 1992), Nile tilapia in Lake Victoria is depicted as retaining food habits similar to those of the indigenous tilapiine (*O. esculentus* and *O. variabilis*), which it replaced (Trewavas, 1983; Witte & Van densen, 1995). Nile tilapia is described as primarily herbivorous, feeding mostly on phytoplankton (Moriarty & Moriarty, 1973; Getabu, 1994).

Nile tilapia exhibited a trophic shift between 1994 and 1998–2000 from predominantly herbivorous (mainly algae) to a more diversified diet (Fig. 5). Getabu (1994) observed *O. niloticus* to feed mainly on algae (87%) and aquatic invertebrates (13%) in the Kenyan waters of Lake Victoria. The invertebrates consumed in 1994 included mainly Copepoda, Cladocera and Rotifera. Overall the most notable change in *O. niloticus* diet was the dramatic decrease in the importance of algae and the increased importance of fish, plants and invertebrates (mainly insects and bivalves). The dietary shift in Kenyan waters of Lake Victoria was coincident with a decline of non-cichlids (cat fishes, lungfish) and cichlids (haplochromines) (Ogutu-Ohwayo, 1990; Othina & Tweddle, 1999; Njiru *et al.*, 2002). The reduction in fish species in Lake Victoria is attributed to various factors, among them, invasion of predatory *L. niloticus* and overexploitation. The change in *O. niloticus* feeding behaviour could be attributed to its

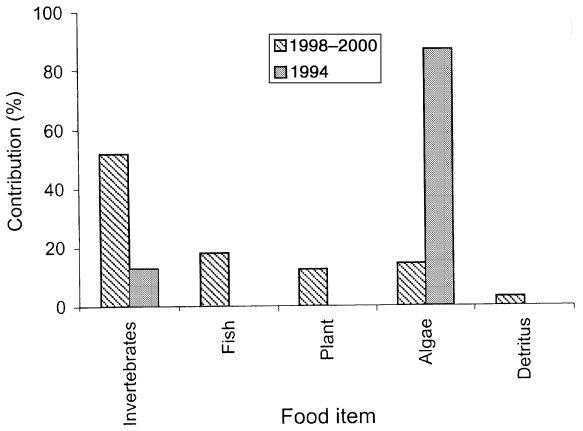


Fig 5 Contribution of the main food items in the gut of *O. niloticus* in Kenyan waters of Lake Victoria in 1994 and 1998–2000

niche breadth. The species is filling niches previously occupied by various cichlids and non-cichlids which no longer exist in the lake (Ogutu-Ohwayo, 1990; Witte & Van densen, 1995; Balirwa, 1998). The reduction in fish groups previously occurring in the lake may have led to an increase in food resources and a reduction in competition, an opportunity that has been utilized by *O. niloticus*.

The dominance of insects in the diet of *O. niloticus* could be attributed to infestation of the lake by floating macrophytes especially water hyacinth, which provides more habitats for insects (Muli, Mavuti & Ntiba, 2000). Except for a fringe of papyrus and reeds, floating and submerged macrophytes are rare in Lake Victoria (Balirwa, 1998). Insects were more important in the Nyanza Gulf compared with inshore open waters. Nyanza Gulf sheltered from strong winds had more floating macrophyte infestation. The inshore open water stations experience stronger waves making it difficult for floating macrophytes to be stationary in the area for a long time. The availability of more macrophytes in the gulf may account for more insects being ingested here than in the inshore open waters. The dietary importance of algae in the inshore open waters may be due to low availability of invertebrates (due to fewer macrophytes).

Bivalves (which were not reported in the diet of tilapia in 1994) composed a significant proportion of tilapia diet in 1998–2000 with the highest ingestion in the offshore gulf (6.8%) and inshore open waters (5.3%) in this study. The high consumption of molluscs in the tilapia diet could be the result of the increase of molluscs in the lake, coincident with loss of several molluscivorous haplochromines, which were more abundant in the deeper waters of Lake Victoria (Olowo & Chapman, 1999).

The increase in fish (mainly *R. argentea*) in *O. niloticus* diet could be attributed to a reduction of in numbers its main predator the Nile perch. In contrast to most of the native species the pelagic cyprinid *R. argentea* has increased in Lake Victoria (Witte *et al.*, 1992; Othina & Tweddle, 1999). The *R. argentea* habitat overlap with Nile perch is small and the predation pressure exerted by the perch was more on zooplanktivorous haplochromines than *R. argentea*. Higher predation pressure on haplochromines could have led to competitive release (food) and this might have benefited *R. argentea*. Thus the increase in *R. argentea* in tilapia diet could have been due to its availability compared with haplochromines and juvenile perch.

The monthly variation in the feeding pattern of *O. niloticus* showed no obvious trends. The abundance of most food items fluctuated between months, probably in response to changes in availability of food items in the environment. The monthly change in diet observed may also be related to relative abundance and convenient size of food items in the lake. When the monthly data was grouped into seasons no variation was detected in the diet ingested by *O. niloticus*. Coulter (1977) reported that in many fishes selection of prey is governed by availability rather than preference for a particular species, which could be the case for *O. niloticus* in Lake Victoria. Ogari & Dadzie (1988) noted a similar pattern in *L. niloticus* an introduced species in Lake Victoria, which switched from haplochromine cichlids to more abundant zooplankton crustacean (*C. niloticus*) when the former declined.

Predators are also known to maximize the overall rate of uptake of nutrients if they eat the most profitable food and they tend to ignore less valuable food when more profitable ones are abundant (Krebs, 1979). The optimal diet model predicts specialization on the more profitable prey when they are abundant, and selectivity increases as the more valuable prey become more abundant (Krebs, 1979). Satiated predators become less selective than somewhat less well fed ones. To predators that take both animal and plant material a balanced diet may be more valuable. In comparison with other food items, algae are low in energy and other nutrients, and difficult to digest due to their strong cell walls and high content of indigestible material (Hay, Kappel & Fenical, 1994). The Nile tilapia could be opting for the more profitable animal protein source for nutrition in invertebrates and fish remains instead of algae. The fish could also be maximizing nutritional sources by taking both plant and animal materials.

The dominance of zooplankton in *O. niloticus* <5 cm TL is in agreement with Moriarty & Moriarty (1973). Small fish (0–4.9 cm) did not ingest insects, *C. nilotica*, bivalves or oligochaetes probably because of their smaller mouth gape. Getabu (1994) made similar observations, whereby the percentage occurrence of invertebrates in *O. niloticus* diet increased with increase in fish size. A variety of the diet consumed by *O. niloticus* within various size groups could be due to reduced competition for food. It has also been hypothesized that because juvenile fish have higher mass specific protein demand as a consequence of higher specific growth rate and greater mass specific metabolism, they may not satisfy their demand by consuming a herbivorous diet. Small fish may be forced to consume animal prey, which have greater content of protein and energy per unit weight (Benavides, Cancino & Ojeda, 1994).

Diet shift has been recorded for several fish species in Lake Victoria. Wanik & Witte (2000) report that *R. argentea*, a zooplanktivorous fish, feed on a variety of food items including prawns and chironomids. The diet of Nile perch, which was originally piscivorous now consists of *C. nilotica*, juvenile Nile perch and *R. argentea* (Ogutu-Ohwayo, 1990). *Bagrus docmak* (Forsskåll) has exhibited a shift from primarily piscivorous diet dominated by haplochromines to a broader diet of invertebrates and *R. argentea* while *Schilbe intermedius* (L.), also previously piscivorous, is now insectivorous (Olowo & Chapman, 1999). The shift in diet of Lake Victoria fish is being attributed to the impact of *Lates* predation and overexploitation of native fish species, which have been virtually wiped out and the subsequent ecological changes in the lake. This flexibility in diet may permit existence, albeit in reduced numbers, of Lake Victoria fishes in the rapid changing ecosystem.

From the wet weight of stomach contents, it is clear that Nile tilapia follows a diurnal feeding regime. These results concur, with Trewavas (1983) who found that feeding of *O. niloticus* in Lake George is a daytime activity, beginning a little before dawn and ending at sunset, and digestion is usually completed about 2 h after midnight. Moriarty & Moriarty (1973) found *O. niloticus* in Lake George to have empty stomachs between 02.00 and 05.00 hours. After fish start to feed there was a steady increase in the average dry weight of stomach contents. This continues until the fish stops feeding (usually shortly before sunset), after which there is a steady decrease in the average dry weight of the stomach contents. The diurnal feeding activity could be attributed to the fact that *O. niloticus* feeds by sight.

Findings from this study are of considerable ecological significance. Nile tilapia is a highly adaptable species able to exploit new opportunities and expand its realized niche to successfully colonize new habitats (Cowx, 1998; Njiru *et al.*, 2002). In Lake Victoria the species has widened its traditional niche exploiting algal food resources towards an insectivorous feeding mode. These niches were probably vacated by the disappearance of the haplochromines. These results are comparable with Balirwa (1998) who found *O. niloticus* to feed on a variety of food items, with plant material and insects dominating. The sampling (1995–97) was during water hyacinth invasion in Ugandan waters of Lake Victoria. The results also suggest that *O. niloticus* may continue to expand its niche until the lake ecosystem stabilizes, although overfishing and ecosystem degradation may lead to further instability in the lake ecology with unknown consequences. It could also be important to use stable isotope technique to discern the proportions of the food items ingested by tilapia if they are assimilated and utilized for energy and growth.

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