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Changes in population characteristics and diet of Nile tilapia *Oreochromis niloticus* (L.) from Nyanza Gulf of Lake Victoria, Kenya: what are the management options?

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Length frequency data collected from 1998 to 2001 from commercial landings was used to estimate asymptotic length (L_∞), growth coefficient (K), mortality (Z, F, M), growth performance index (ϕ') and exploitation rate (E) of Oreochromis niloticus *from the Nyanza Gulf of Lake Victoria, Kenya. Studies on the diet of* O. niloticus *collected by demersal trawl and seining between 1998 and 2000 were also conducted.*

Length frequency data were analyzed using the FISAT software (an FAO-ICLARM Stock Assessment Tool package). The L_∞ had a mean value (±S.D) of 58.78 ± 2.42 cm TL, K of 0.59 ± 0.05 yr^{-1}, Z of 2.16 ± 0.40 yr^{-1}, M of 1.00 ± 0.06 yr^{-1}, F of 1.12 ± 0.34 yr^{-1}, E of 0.48 ± 0.11 and ϕ' of 3.31 ± 0.04. Length at first entry into the fishery (L_{50}) was observed at 26.18 ± 12.50 cm TL. Recruitment occurred throughout the year, with two peaks corresponding with the rainy seasons.

A comparison with previous studies in the gulf indicates that O. niloticus *is now caught at a smaller mean size, whereas K, Z, and M have increased. Fish appeared to become sexually mature at a smaller size.*

Nile tilapia originally known to be herbivorous, feeding mostly on algae, has diversified its diet to include insects, fish, algae and plant materials, all being important food items. The changes in population characteristics and diet of O. niloticus *are discussed in context of changes occurring in the lake and its surroundings.*

Keywords: Growth parameters, mortality, ecosystem changes, Nile perch

Introduction

The Nile tilapia, *Oreochromis niloticus* (L.), was introduced into Lake Victoria in the 1950's, together with other tilapiines like *Oreochromis leucostictus* (Trewavas), *Tilapia zillii* (Gervais) and *Tilapia rendallii* (Boulenger) (Welcomme, 1967). In 1960, *O. niloticus* constituted less than 1% of commercial catch landings and by 1965 it featured prominently in commercial fish catches (Welcomme, 1967).

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Currently, *O. niloticus* is the most important tilapiine; whereas the native species of *Oreochromis variabilis* (Boulenger) and *Oreochromis esculentus* (Graham) have largely disappeared (Witte and Van Densen, 1995; Cowx et al., 2003). 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).

The dominance of *O. niloticus* over other tilapiines in the lake is attributed to several factors including fast growth rates and over-fishing of endemic tilapiines, thus reducing competition while clearing of swamps could have increased its spawning areas (Welcomme, 1967). Nile tilapia can also survive a wide range of pH values; it resists low levels of dissolved oxygen and feeds on a variety of food items (Getabu, 1994; Njiru et al., 2004).

Studies further show that the fishery is operating beyond its maximum sustainable yield, indicating overfishing (Cowx et al., 2003). In recent years, fishing pressure, the fish community structure and ecosystem dynamics of the lake have changed, but studies have not been carried out to assess whether population characteristics and diet have changed. This study was designed to study population parameters and diet of *O. niloticus* in Lake Victoria, Kenya. The results are compared with previous studies to provide management strategies for the fishery.

Materials and methods

Study area

The Nyanza Gulf constitutes the major portion of the Kenyan part of Lake Victoria, with an area of 1920 km^2, a length of 60 km and a width varying from 6 to 30 km (Figure 1). The Gulf is shallow with a mean depth of 6 m and lies at an altitude of 1134 m above sea level. The air temperature ranges between 17.1°C and 34.8°C. The hottest months are from December to March. The water temperature and solar radiation are relatively constant throughout the year (mean values of 22 ± 3° and 1200 ± 140 ME M^{-1} S^{-1}). The annual rainfall ranges from 400 to 800 mm with long rains occurring from March to May and the short rains in November and December. A detailed description of the physical and hydrological characteristics of Nyanza Gulf is given by Crul (1995).

Growth parameters

Monthly length frequency data on *O. niloticus* were collected from July, 1998 to April, 2001 from commercial catches at five landing sites in the Nyanza Gulf of Lake Victoria (Figure 1). The samples were representative of the stock from the outer, mid, and inner Gulf, *or* Dunga, Kendu Bay, Asembo Bay, Homa Bay and Luanda Gembe. Approximately two hundred specimens were randomly selected from commercial catches every month at each station and the total length (TL) was measured to the nearest cm. The temperature of the surface water was recorded for each station every month to contribute the estimation of the natural mortality coefficient.

Data analysis was based on length frequency distribution analysis (Pauly et al., 1984; Sparre and Venema, 1998). The Electronic Length Frequency Analysis (ELEFAN I and II) computer programs incorporated in the FAO-ICLARM Stock Assessment Tool (FISAT) (Ganyanilo et al., 1996) were used to estimate population parameters. Parameters of the Von Bertalanffy growth formula (VBGF) (Sparre and Venema, 1998) were estimated from:

$$L_t = L_\infty(1 - exp(-K * (t - t_o))),$$

where L_t is the predicted length at age t, L_∞ is the asymptotic length, K is a growth constant, t is the age, and t_o is the age of the fish at zero length. Preliminary estimation of L_∞ was done by the Powell-Wetherall method and FISAT was further used to improve the accuracy of the L_∞ and K estimates. The growth performance index (ϕ') was computed according to Pauly and Munro (1984): $ø' = \log_{10} K + 2\log_{10} L_\infty$, where K is the growth constant (yr^{-1}) and L_∞ is the asymptotic length. Age at time zero or the birthday of the fish was computed using Pauly's (1979) empirical formula: $t_o = -0.3922 - 0.2752 \log L_\infty - 1.038 \log K$.

Total mortality coefficient (Z) was estimated by using a length-converted catch curve (Pauly et al., 1984). This method consists of plotting of the natural logarithm of the number of fish in various age groups against their corresponding age. A regression analysis is done on the descending right hand arm of the catch curve, and Z estimated as the negative slope. The natural mortality coefficient (M) was estimated following Pauly's empirical formula (Pauly, 1980), linking natural mortality with the Von Bertalanffy parameters, K(yr^{-1}), L_∞ (cm) and the mean annual

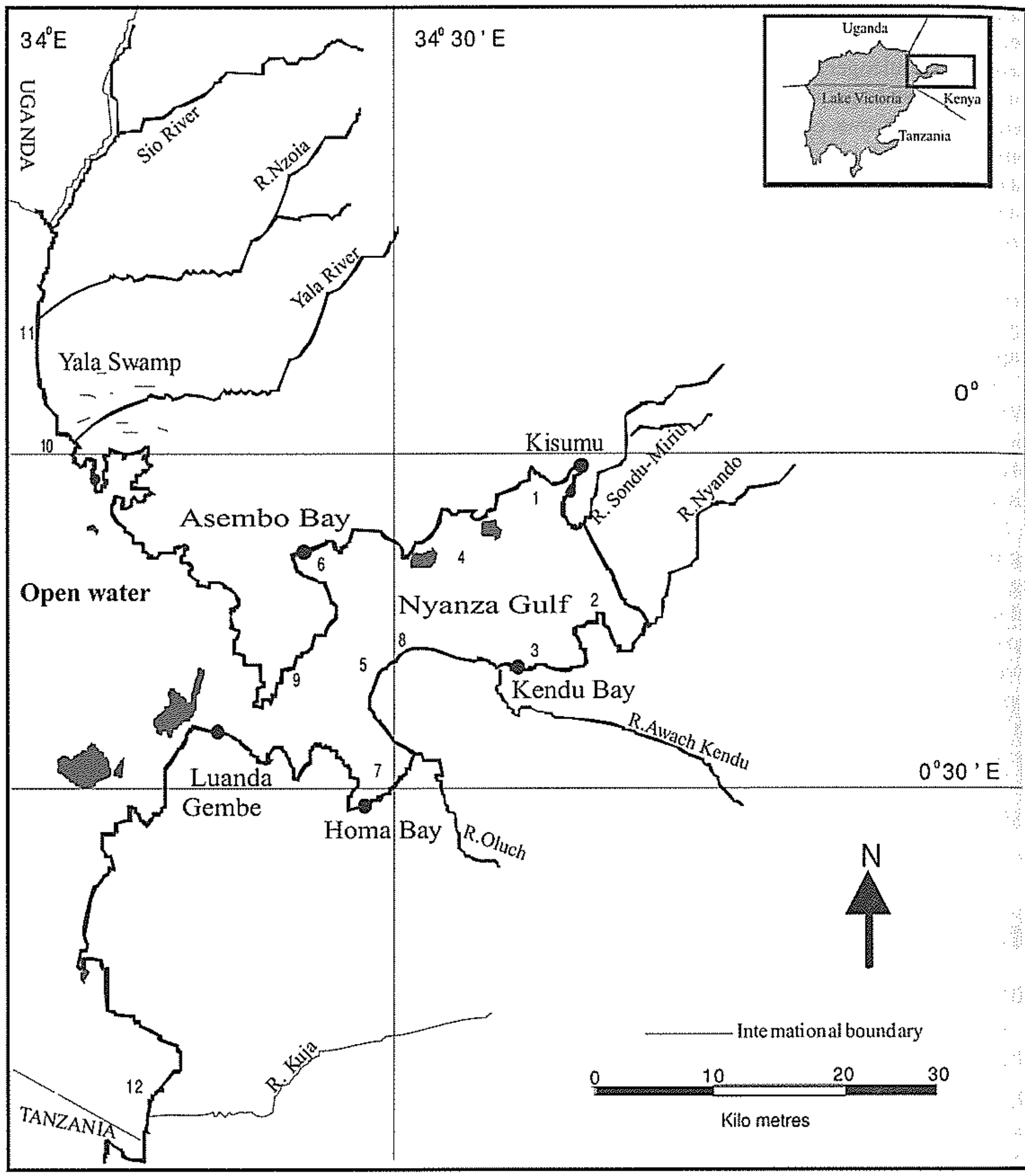

Figure 1. Map of Nyanza Gulf, Lake Victoria Kenya, showing sampling sites.

temperature (T°C) of the water in which the fish live (in this case 25°C):

$$\log_{10}(M) = -0.0152 - 0.279 * \log_{10} L_\infty + 0.6543 \log_{10} K + 0.463 \log_{10} T$$

Fishing mortality (F) was computed from the relationship $F = Z–M$, while the exploitation rate (E) was calculated from the relationship $E = F/Z = F/(F + M)$.

Gear selection was estimated by backward extrapolation of the catch curve, thus estimating the number of juveniles which would have been caught, had it not been for incomplete selection and recruitment (Pauly et al., 1984).

Diet studies

Samples of *O. niloticus* were obtained from bottom trawl catches (headrope 22.4 m, cod-end mesh size 24.5 mm) and mosquito seining (mesh size 5 mm, length 50 m) in the Kenyan part of Lake Victoria (Figure 1) during November, 1998 – October, 2000. Trawl hauls were conducted monthly except when circumstances could not permit operations. Seine nets caught most fish below 10 cm TL. Stations were chosen to cover near shore waters (3–4 m depth) and offshore (10–20 m depth) waters of the Gulf, and near shore waters (5–6 m depth) of the open lake. Immediately after capture, total length (TL cm) of fish was measured to the nearest cm and gut contents removed and preserved in 4% formalin. The gut contents were analysed using a modified point method (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.

Results

Population characteristics

The mean (±SD) L_∞ was 58.33 ± 1.79 cm TL and 58.78 ± 2.42 cm TL for Powell-Wetherall and FISAT methods, respectively (Table 1). Luanda Gembe (62.50 cm) had the highest L_∞ and Homa Bay (56.60 cm) the lowest. The growth coefficient (K) had a mean (± SD) of 0.59 ± 0.05 yr^{-1} with Homa Bay (0.68 yr^{-1}) and Kendu Bay (0.55 yr^{-1}) with the highest and the lowest values respectively (Table 2). The growth performance index (ϕ') had a mean (±SD) of 3.31 ± 0.04, with Luanda Gembe (3.36) achieving the highest and Dunga (3.26) the lowest (Table 1). Estimated mean (±SD) age at zero length was −0.64 ± 0.04 years with Homa Bay (−0.70 yr) having the lowest and Kendu Bay (−0.61 yr) the highest value (Table 1). The estimated total mortality coefficient (Z) had a mean (± SD) of 2.12 ± 0.40 yr^{-1}, natural mortality coefficient (M) of 1.00 ± 0.06 yr^{-1}, fishing mortality coefficient (F) of 1.12 ± 0.34 and exploitation rate (E) of 0.49 ± 0.11 (Table 2). Mean (± SD) length at entry into the fishery at L_{25}, L_{50}, and L_{75} was 20.96 ± 15.75, 26.18 ± 12.50 and 28.54 ± 12.19 cm TL, respectively (Table 2). Recruitment of *O. niloticus* occurs throughout the year with peaks from May to July and in November and December.

Diet composition

Insects, particularly *Povilla adusta* (Navas), fish (*R. argentea*), algae and plant material were the most important food types (Figure 2). Other ingested food items include bivalves and detritus. Zooplankton (Cladocerans and Copepods) was the major food of *O. niloticus* smaller than 5 cm TL, and was of little importance to fish larger than 10 cm TL (Figure 3). 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.

Table 1. Asymptotic length L_∞ (cm), growth curvature (K yr^{-1}), growth performance index (ø') and time at zero (t_0 yr) of *O. niloticus* artisanal catches from Nyanza Gulf, Lake Victoria, Kenya.

Station	L_∞ (cm) Powell-Wetherall	L_∞ (cm) ELEFAN	K	(ø')	t_0
Dunga	56.07	57.00	0.56	3.26	−0.62
Kendu Bay	58.83	58.00	0.55	3.27	−0.61
Asembo Bay	58.59	59.80	0.59	3.32	−0.64
Homa Bay	57.31	56.60	0.68	3.34	−0.70
Luanda Gembe	60.86	62.50	0.58	3.36	−0.64
Mean	58.33	58.78	0.59	3.31	−0.64
±SD	±1.79	±2.42	±0.05	±0.04	±0.04

Table 2. Total mortality (Z yr^{-1}), natural mortality (M yr^{-1}), fishing mortality (F yr^{-1}) coefficient, exploitation rate (E) and probability of capture and sizes (cm) at which 25, 50 and 75% of the encountered *O. niloticus* were retained by commercial gears from Nyanza Gulf of Lake Victoria.

Station	Z	M	F	E	L_{25}	L_{50}	L_{75}
Dunga	2.06	0.97	1.09	0.53	35.80	38.21	40.19
Kendu Bay	1.77	0.95	0.82	0.46	32.35	35.74	38.30
Asembo Bay	2.02	0.99	1.03	0.51	28.74	31.45	31.31
Homa Bay	2.81	1.10	1.71	0.61	5.17	13.25	15.31
Luanda Gembe	1.93	0.97	0.96	0.32	2.74	12.24	15.38
Mean	2.12	1.00	1.12	0.48	20.96	26.18	28.54
±SD	±0.40	±0.06	±0.34	±0.11	±15.75	±12.50	±12.19

Bivalves, *Caridina nilotica* and oligochaetes were not found in fish smaller than 10 cm TL.

Nile tilapia ingested mainly insects (39.8%), plant material (21.4%) and fish remains (19.2%) in the near shore Gulf stations (Figure 4). At the off-shore Gulf stations insects (36.3%), algae (24.0%) and fish (19.6%) dominated the diet. The major food items in the near-shore open water stations were algae (33.7%), insects (25.9%) and fish (23.3%). A

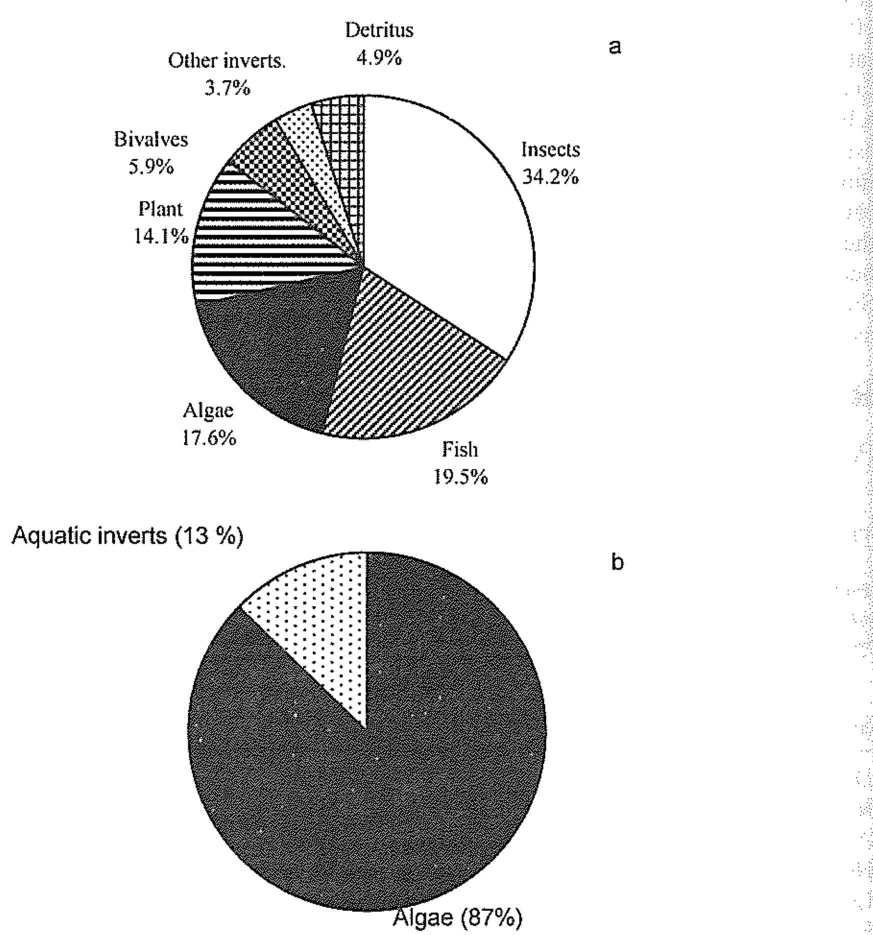

Figure 2. Percentage contribution of different food items ingested by *O. niloticus* in Lake Victoria, Kenya, a) 1998–2000, b) late 1980s. Adapted from Getabu (1994). (inverts. = invertebrates, i.e. *Caridina*, Oligochaetes, Huridinea).

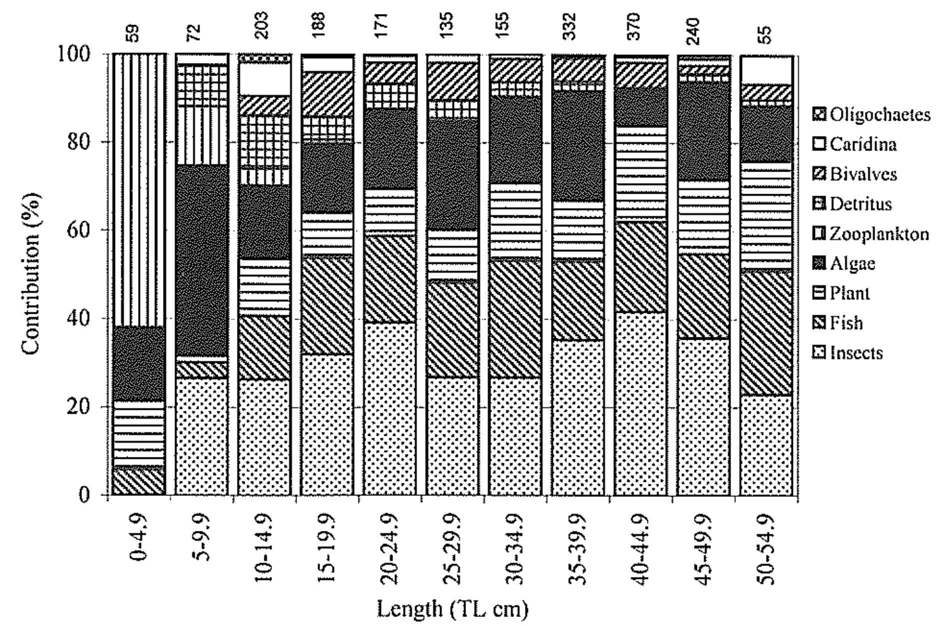

Figure 3. Food of *Oreochromis niloticus* of different size length from Lake Victoria, Kenya. Numbers above columns indicate sample size.

chi square test revealed a significant difference between plant ($\chi^2 = 10.40$, $P < 0.05$) and algae ($\chi^2 = 10.33$, $P < 0.05$) ingested at all the stations.

Discussion

Previous studies show that the L_∞ of *O. niloticus* has decreased from 64.60 cm TL in 1985/1986 to 56.78 cm TL in the present study, K increased from 0.25 yr^{-1} to 0.59 yr^{-1}, while ϕ' has increased from 3.02 to 3.31 at the same time (Table 3). The food types and their digestibility have been found to determine the different growth patterns of Nile tilapia in natural waters. Bowen (1982) indicated that tilapia consumes food material of high calorific value, which is suitable for growth. Nile tilapia exhibited a trophic shift between 1994 (Getabu, 1994) and 1998–2000 from predominantly herbivorous (mainly algae) to a more nutritious diversified diet (Figure 2a, b), and this could be contributing to a higher growth rate (K) and thus a higher ϕ' (Table 3).

Overexploitation results in reduction of average size of fish in a stock and a faster growth rate (Sparre and Venema, 1998). The Kenyan portion of Lake Victoria constitutes only 6% of the entire lake, but it has the highest concentration of boats (8,000) and fishers (30,000) (Asila, 2000). The fishery is

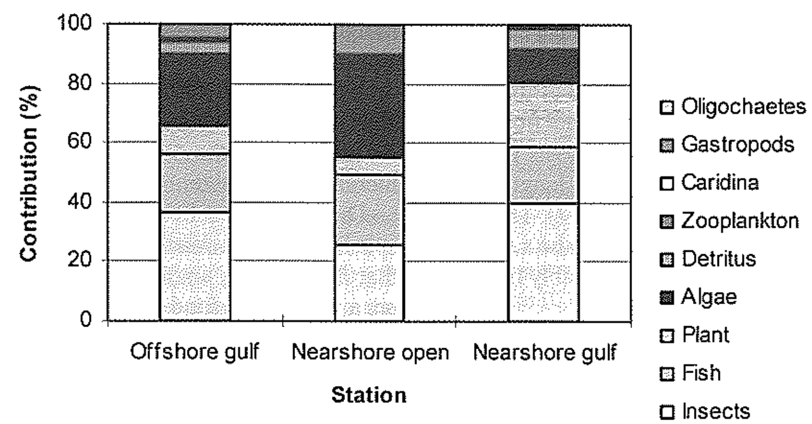

Figure 4. Contribution by station of the major food items ingested by *O. niloticus* in Lake Victoria, Kenya.

Table 3. Growth parameters (K yr^{-1}, L_∞ cm), mortality (Z, M, Fyr^{-1}), exploitation (E), and growth performance (Ø′) estimates of *O. niloticus* from Nyanza Gulf of Lake Victoria, Kenya.

L_∞	K	Ø′	Z	M	F	E	Data collection and source
64.60	0.25	3.02	0.82	0.54	0.28	0.34	1985–1986 (Getabu, 1992)
63.10	0.35	3.14	1.71	0.72	0.99	0.58	1989–1990 (Dache, 1994)
58.78	0.59	3.31	2.12	1.00	1.12	0.53	1998–2001 (Present study)

characterised by an open access and there is no limit to the number of boats and gears used. The recommended gillnet mesh size for the *O. niloticus* fishery is ≥5 inches (127 mm), although 2–3 inch mesh sizes (50.8–76.2 mm) were commonly encountered. Destructive beach seines, although illegal in the lake, were still operational during the study. The fishing mortality (F) of 1.12 yr^{-1} is higher than previously reported in the lake indicating increased exploitation (Table 3). Tilapia caught at sites where mainly mosquito seines and beach seines are operated, like Homa Bay, exhibited higher F, K, E and lower L_∞ values as compared to Kendu Bay where mainly gill nets are operated (≥127 mm mesh size).

Natural mortality has increased from 0.54 yr^{-1} in 1985/1986 to 1.00 yr^{-1} in the present study (Table 3). Faster growing fish have higher natural mortalities (Sparre and Venema, 1998), and the warmer the ambient temperature the higher the natural mortality. Increase in K in *O. niloticus* and ambient temperatures from 22°C (Crul, 1995) to 25°C could be contributing to this increased mortality.

The length at first capture (L_{50}) for *O. niloticus* with the present commercial fishing gears varied from 12.2 cm TL at Luanda Gembe to 38.2 cm TL at Dunga. In Kenyan waters of the lake, the smallest ripe *O. niloticus* male was 26.2 cm TL and female 23. 3 cm TL, fifty percent maturity for males was at 30 cm TL and females 33 cm TL. Therefore, the present commercial gears in Kenyan waters of Lake Victoria are catching high proportions of immature *O. niloticus*. There has also been a reduction in the size at first maturity since the early 1990s when *O. niloticus* was maturing at an average length of 35 cm TL in Kenyan waters (Getabu, 1992). This maturation of tilapia at smaller sizes could be a strategy to maximize reproductive success possibly linked to population response to over-fishing.

The dietary shift in Nile tilapia could be due to decline of non-cichlids (catfish, lungfish) and cichlids (haplochromines) mainly due to the invasion of predatory *L. niloticus*. Nile tilapia could be filling niches previously occupied by these fish species (Ogutu-Ohwayo, 1990).

The dominance of insects in the diet of *O. niloticus* could be attributed to invasion of the lake by floating macrophytes, especially water hyacinth (1996–1998), which provided more habitats for insects. Bivalves had not been reported in the diet of tilapia earlier and were first encountered in this study. The appearance of molluscs in the tilapia diet could be attributed to the increased occurrence of molluscs in the lake, which possibly coincided with loss of several mollusc-feeding haplochromines (Wanink, 1998; Olowo and Chapman, 1999). The increase in fish (mainly *R. argentea*) in *O. niloticus* diet could be due to its increased availability attributed to the reduction of its main predator, the Nile perch.

Nile tilapia could be maximizing the overall rate of uptake of nutrients by eating the most profitable food consisting of insects and fish. In comparison with other food items, algae are low in nitrogen and other nutrients, and difficult to digest due to their strong cell walls and high content of indigestible material (Hay et al., 1994).

The dominance of zooplankton in *O. niloticus* of less than 5 cm TL is in agreement with Getabu's findings (1994). Adult tilapia take less zooplankton as they change their mode of feeding to gulping water, and zooplankton detect the feeding current and move away. Small fish (0 – 4.9 cm) did not ingest insects, *C. nilotica,* bivalves or oligochaetes probably due to their smaller mouth. Getabu (1994) made similar observations, whereby the percentage occurrence of invertebrates in the *O. niloticus* diet increased with increase in fish size.

Diet shift has been recorded for several fish species in Lake Victoria. Wanink (1998) reports that *R. argentea*, a zooplanktivorous species, feeds on a variety of food items including prawns and chironomids. The diet of the Nile perch which was originally piscivorous now consists of *C. nilotica*, juvenile Nile perch and *R. argentea* (Ogutu-Ohwayo, 1990). *Bagrus docmak* (Forsskåll) exhibits a shift from a primarily piscivorous diet dominated by haplochromines to a broader diet of invertebrates and *R. argentea,* while *Schilbe intermedius* (L.), also piscivorous, has become insectivorous (Olowo and Chapman, 1999). The shift in diet of Lake Victoria fishes is being attributed to the impact of *Lates* predation, and overexploitation of native fish species, some of which have been virtually wiped out, and the subsequent ecological changes in the lake. This flexibility in diet may allow survival, albeit in reduced numbers of Lake Victoria fish species in a rapidly changing ecosystem.

Conclusions and recommendations

Continued use of mesh size smaller than recommended and the destruction of breeding grounds through the application of illegal fishing gears may lead to a further reduction of the size of *O. niloticus* at first capture. The fishers in turn will further reduce their mesh size and resort to illegal fishing methods to target the smaller fish. This could result in a long-term decline of the size and catches of the species. However, even under these stressful conditions, *O. niloticus* shows a high growth performance index and attains a large size.

Attainment of this condition could be due to the protein-rich diet the fish is consuming and if well managed, production could be increased. Higher production would provide more protein and income to people living around the lake, who depend so much on fishing as farming is not well developed due to poor soils and unpredictable rains. In order to sustain the fishery, imposing the existing ban on beach seining, use of illegal mesh sizes and other destructive fishing methods needs to be urgently addressed by the relevant authorities. Entry into the fishery, which is now open, should be limited. In addition to the registration of boats, licensing of nets should be introduced to help in monitoring the effort exerted on the fishery resources. Fishers should be provided with cold storage to avoid wastage and the landed fish should be sold through co-operative societies to improve returns. Law enforcers should increase their efforts and political interference in the running of the fishing industry should be reduced. The fisheries management should incorporate a co-management system to better enforce laws and regulations. Alternative sources of livelihood, such as aquaculture and farming, should be encouraged to reduce pressures on the fishery.

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The effect of overfishing on the life-history strategies of Nile tilapia, *Oreochromis niloticus* (L.) in the Nyanza Gulf of Lake Victoria, Kenya

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Studies were conducted on reproductive characteristics of Oreochromis niloticus *from 1998 to 2000. The results were combined with published work on growth parameters of* O. niloticus *from 1985 to 1999 in order to establish the current survival strategies exhibited by* O. niloticus *in the Nyanza Gulf of Lake Victoria. The study revealed that size at maturity had decreased concurrently with increasing fishing mortality. Observations on reproductive effort point to a fish species under stress. It is observed that the behavioural change in* O. niloticus *is not due to size selective predation but due to size selective exploitation. Indications that* O. niloticus *in the Nyanza Gulf of Lake Victoria allocates more energy for reproduction than for somatic growth (i.e. increased turnover rate) are multiple. It is concluded that* O. niloticus *in the Nyanza Gulf exhibits an 'r'-selected life history strategy in order to survive stressful conditions.*

Keywords: Maturity, population parameters, reproductive strategy

Introduction

The Nile tilapia, *O. niloticus* (L.), is the most important cichlid of commercial interest in Lake Victoria. Introduced in the 1950s, together with other tilapiines such as *O. leucostictus* (Graham), *Tilapia zillii* (Gervais) and *Tilapia melanopleura* (Dumeril), it then quickly out competed the other endemic tilapiines, namely: *O. esculentus* (Graham) and *O. variabilis* (Boulenger). It subsequently became the dominant tilapiine in Lake Victoria (Welcomme, 1967; Trewavas, 1983). The success of this species has been attributed to, among other factors, its mouth-brooding reproduction system, feeding flexibility and its tolerance to a wide range of physico-chemical variables (Balirwa, 1998).

In the recent past, *O. niloticus* in the Nyanza Gulf of Lake Victoria has been under intense pressure as a result of over–fishing and other environmental factors (Getabu, 1992; Ojuok, 1999). Earlier studies also show that this species is not under predation pressure from the introduced Nile perch, *Lates niloticus* (L.) (Ogutu–Ohwayo, 1985; Mkumbo and Ligtvoet, 1992).The breeding characteristics of *O. niloticus* have changed in the recent past (Ojuok, 1999). The adaptability and plasticity of tilapias are well–known but, despite enormous research efforts (Fryer and Iles, 1972; Balarin, 1979), a clear understanding of their life histories still remains elusive. In stable lacustrine environments the selective pressures are normally associated with density–dependent mortalities. Intensive intra-specific and inter–specific competition, highly

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