Causes and effects of the Lake Victoria ecological revolution

Goudswaard, Pleun Cornelis

CHAPTER 8

The tilapiine fish stock of Lake Victoria before and after the Nile perch upsuge

Kees (P.C.) Goudswaard[1], Frans Witte[1] & Egid F.B. Katunzi[2]

[1]Institute of Biology, University of Leiden, P.O. Box 9516,

2300 RA Leiden, The Netherlands

[2]Tanzania Fisheries Research Institute, P.O. Box 475, Mwanza, Tanzania.

Published in: Journal of Fish Biology 60: 838-858, 2002

Abstract

Since the beginning of fisheries in Lake Victoria, two native tilapiine species, *Oreochromis esculentus* and *Oreochromis variabilis*, were the main target of the local fishermen. A continuous increase in fishing pressure led initially to a declining catch per unit of effort, and a smaller average fish size; eventually, there was a reduced landing of tilapiines. To boost the fisheries, three alien tilapiine species and the Nile perch *Lates niloticus* were introduced. Thirty years after its introduction, *Oreochromis niloticus* appeared to be the most successful tilapiine species. It replaced the indigenous tilapiines almost completely before the Nile perch came to dominate the ecosystem of Lake Victoria. Reduced fishing pressure on the tilapiines in the 1980s, due to the shift of the local fishery towards the Nile perch, resulted in an increase in the stock of *O. niloticus* and an increase in average fish size. Subsequently, the total mass of *O. niloticus* landed increased. The stocks of the indigenous tilapiines did not recover but declined to extremely low levels, or vanished from the main lake. Currently, these species still occur in satellite lakes of Lake Victoria, from which *O. niloticus* is absent. Nile perch feed on *O. niloticus*; however, the limited overlap in distribution between piscivorous Nile perch and *O. niloticus* of consumable sizes is probably an important factor in explaining the coexistence of the two species. The main cause of the disappearance of the native tilapiine species is presumed to be competitive dominance by *O. niloticus*.

Introduction

Only two species of tilapiine cichlids are indigenous to the Lake Victoria basin (East Africa): *Oreochromis variabilis* (Boulenger) and *Oreochromis esculentus* (Graham). Both species have a geographical distribution which is limited to the Lakes Victoria and Kyoga, including the satellite lakes and all the tributary rivers (Trewavas, 1983), as well as the small lakes in the Kagera River Basin below the Rusumu Falls (Fig. 8.1; Plisnier et al., 1988). Both species are ecologically complementary with little

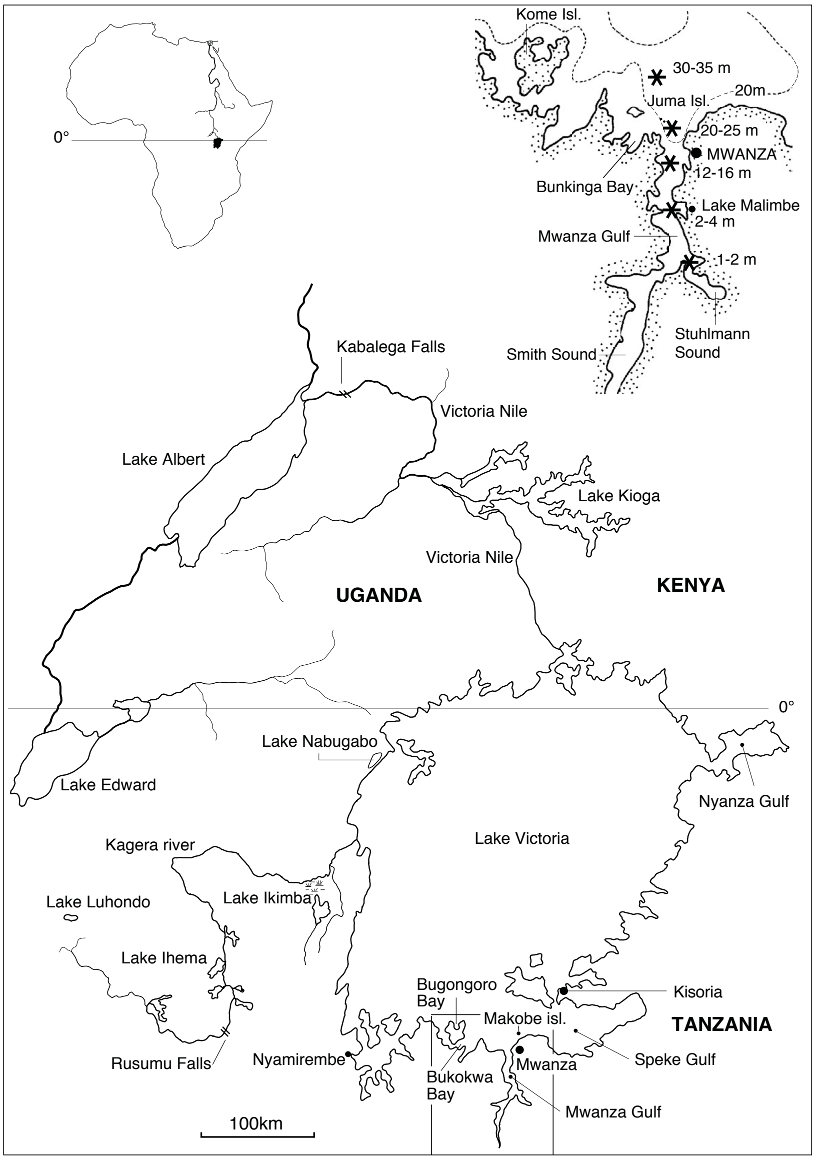

Fig. 8.1. *Map of a part of the Victoria Nile basin with Lake Victoria and its satellite lakes mentioned in the text. Inset: details of the Mwanza gulf. The five study sites in the Mwanza Gulf area are indicated with asterisks.*

or no competition between them (Lowe-McConnell, 1982). They occur in shallow areas, but *O. esculentus* prefers land-locked bays where the bottom consists of soft flocculent mud, while *O. variabilis* is most abundant off more exposed shores and in water-lily lagoons (Lowe-McConnell, 1956, 1982; Fryer, 1961).

After 1905, when gillnets were introduced to Lake Victoria, both species became the main targets of the local fishermen (Graham, 1929). Fishing pressure was negligible around 1900, but rose constantly afterwards. This was because the number of fishermen increased almost annually, as did the number of nets that each of them used. The catch per unit of effort (CPUE) declined accordingly, as may be expected in a newly developing fishery (Graham, 1929; Beverton, 1959; Fryer & Iles, 1972).

To augment the native species, four exotic tilapiine species were introduced during 1951–1954 (Beauchamp, 1958; Welcomme, 1968, 1988; Lever, 1996). These were: *Oreochromis leucostictus* (Trewavas), *Oreochromis niloticus* (L.), *Tilapia zillii* (Gervais) and *Tilapia rendalli* (Boulenger). These species were thought to be able to coexist with the native species and to boost the fisheries. Moreover, the existence of a large stock of small, under-exploited haplochromine cichlids led to the idea of introducing a large predatory fish into the lake. Graham (1929) had already discussed the possibility of introducing Nile perch *Lates niloticus* (L.), but warned of possible negative effects on the indigenous tilapiines. In 1954, Nile perch were actually released into Lake Victoria (J. O. Amaras, pers. com.). There was a sudden increase in the numbers of Nile perch in the 1980s and, at the same time, the catches of haplochromine cichlids and several other fish species strongly declined; native tilapiines also continued to decline (Ogutu-Ohwayo, 1990a; Witte et al., 1992a; Goudswaard & Witte, 1997). In contrast, catches of the introduced *O. niloticus* increased during the same period (Ogutu-Ohwayo, 1990a; Ligtvoet et al., 1995). Apart from local over-exploitation, predation by Nile perch was thought to be the major cause of the decline of the haplochromine cichlids (Ogutu-Ohwayo, 1990a; Witte et al., 1992a; Kaufman & Ochumba, 1993). The decline of the tilapiine cichlids, however, has been attributed to a wider range of factors, including fisheries, predation by Nile perch, competition and hybridization with introduced tilapiines, and effects of eutrophication (Welcomme, 1968; Ogutu-Ohwayo, 1990a; Kaufman & Ochumba, 1993; Bundy & Pitcher, 1995; Twongo, 1995; Batjakas et al., 1997; Balirwa, 1998).

In this paper the changes in the tilapiine fish stocks in the Tanzanian waters of the lake are described, and the possible factors in the decline of the native tilapiines and the increase of introduced *O. niloticus* evaluated.

Materials and methods

The following sources of information were analysed: (1) Landing statistics and records of fishing effort from the Fisheries Departments of Tanzania and Kenya (Beverton, 1959; CIFA, 1985,1988,1990). Though the reliability of these statistics is arguable (CIFA, 1988), it is assumed that they reflect general trends in landings. Annual summaries for Kenya from 1968–1987 and for Tanzania from 1958 until 1992 were used. Tanzanian data from 1971–1974 could not be obtained; (2) trawl records from MV Mdiria (120 hp, trawl headrope 25 m, codend mesh 20 or 90 mm) operating in the Mwanza Gulf (Fig. 8.1) from 1973–1986. Records were also collected during 1982–1983 from fishmeal factory boats (170 hp, trawl headrope 21 m, codend mesh 20 mm) targeting haplochromine cichlids at the entrance of the Mwanza Gulf. Commercial vessels generally made trawl shots of 2 h; (3) data from research vessel MV Kiboko (105 hp, bottom trawl headrope 18 m, codend mesh 20 mm) of the Haplochromis Ecology Survey Team (HEST) and the Tanzania Fisheries Research Institute (TAFIRI). This vessel made trawl shots of 30 min. The period of sampling was from October 1984 until July 1990. Most frequently fished was the Mwanza Gulf. Here, five stations, with a soft mud bottom and a depth range from 1.5 m in the south to 35 m in the north, were sampled on a monthly basis. On a less frequent basis the distant areas, Bukokwa Bay and Bugongoro Bay (Fig. 8.1), were fished as well. All data used here were collected by day, except for the station at 12–16 m depth in the Mwanza Gulf. For this station 18 h of trawling during nighttime, in addition to 110 h of trawling during daytime, were available and used. These night-time records confirm the daylight data; (4) data collected with gillnets (3.5 and 4 inch mesh) by the East African Freshwater Fisheries Research Organization (EAFFRO) during the period 1973–1975 in the Tanzanian part of Lake Victoria; (5) data from beach seines, mosquito seines, gillnets and angling that were collected from commercial fishermen, as well as from other fishing activities in the Mwanza Gulf area (unpubl. data).

The total length (TL) of tilapiine species was measured to the nearest cm below. Fishes measured in standard length (SL) were converted to TL (all units in cm): TL (*O. niloticus*) = 1.23 SL+3.91 (N= 415, R^2 = 0.9990), TL (*O. variabilis*) = 1.31 SL+0·01 (N= 60, R^2 = 0.9980), TL (*O. esculentus*) = 1.16 SL+1.27 (N = 38, R^2 = 0.9953). For calculation of the average size of the tilapiines in Table I, all fishes <20 cm TL were excluded from the analysis. This was because different fishing methods and mesh sizes had been used. The differences in selectivity lead to significant bias in the retention of smaller length classes. To make the average size of the fishes from the trawl catches from 1987 to 1989 of MV Kiboko comparable to those of the other vessels, the data of the 1–2 m deep station were excluded, because only MV Kiboko fished in such shallow areas.

The vulnerability of *O. niloticus* to Nile perch predation was estimated by relating maximum body depth of *O. niloticus* to the mouth gape of Nile perch. Body depth (BD) and TL of *O. niloticus* are related as BD= 0.377 TL -0·07 (N= 305, R^2=0.9916). The mouth gape (MG) in Nile perch is related to the TL as follows: MG= 0.112 TL+0·43 (Ligtvoet & Mkumbo, 1990, transformed to cm). Matching these data gives the maximum size ($TL_{(max)}$) of *O. niloticus* that can be swallowed by Nile perch as: $TL_{(max)}$ (*O. niloticus*)= 0.295 TL (Nile perch)+1.51. To calculate the fraction of Nile perch able to swallow *O. niloticus* of a certain size Nile perch >25 cm TL were used. This was because fishes generally constitute a major part of the diet, in individuals that have attained that size (Hamblyn, 1966; Ogari & Dadzie, 1988; Ogutu-Ohwayuo, 1990b).

The data did not meet the assumptions of analysis of variance, and so the Kruskall-Wallis test was used for differences in average fish size and in catch rates at different depths. To test if catch rates decreased significantly over time, the Jonckheere-Terpstra test for ordered alternatives (SPSS 9.0 for Windows) was used.

Results

Species composition

In Lake Victoria, the indigenous species dominated the tilapiine catches until the middle of the 1970s. The introduced species were caught in increasing numbers after that time and from 1986 onwards *O. niloticus* dominated the tilapiine catches (Fig. 8.2).

In the period from 1973 to 1975, *O. esculentus* was still common in the Tanzanian part of Lake Victoria (Table 8.1).

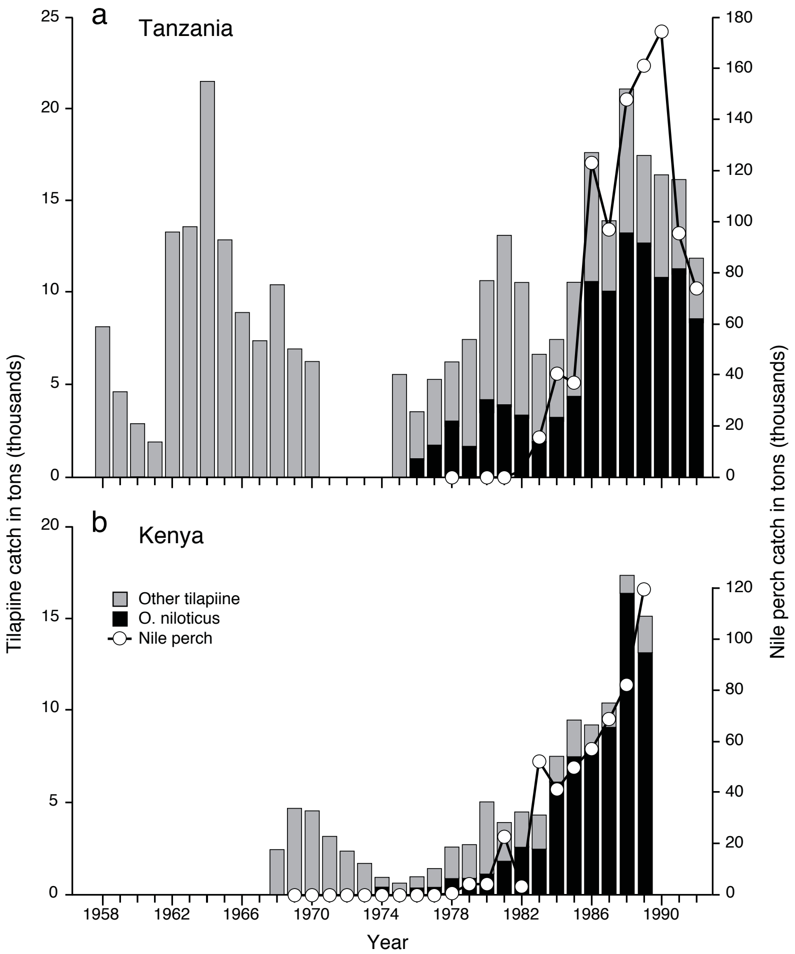

Fig. 8.2. *Composition of commercial landings of tilapiine fishes and Nile perch from Lake Victoria.*
a) Landings in Tanzanian waters during the period 1958-92 (data for 1971-74 are missing).
b) Landings in Kenyan waters during 1968-89. (sources: CIFA 1985,1988, 1990, Ministry of Tourism, Natural Resources and Environment in Tanzania).

Intensive trawl surveys from 1982 to 1990, in the Tanzanian part of the lake, together with the examination of many catches of local fishermen during this period, revealed only two *O. esculentus*. They came from an artisanal gillnet catch in the Mwanza Gulf in 1982. During the same period, *O. esculentus* was encountered at four locations in the vicinity of the Tanzanian part of the lake (Fig. 8.1). The locations were as follows: (i) in 1985, a fisherman caught 60 *O. esculentus* in a pool inside a papyrus swamp near Nyamirembe; (ii) in 1986 a fisherman caught a few *O. esculentus* in a pool near Kisoria; (iii) in May 1990, local fishermen using gillnets and angling rods caught 315 *O. esculentus*, but no other tilapiines, in Lake Malimbe. Experimental fishing with gillnets in this lake in 1993 and in 1999–2000 gave similar results (Seehausen et al., 1997b; EFBK, unpubl. data); (iv) in June 1990, 671 *O. esculentus*, two *O. leucostictus* and one fish which was tentatively identified as *Oreochromis macrochir* (Boulenger) were found in artisanal gillnet catches from Lake Ikimba. In 1999, only *O. niloticus* and *O. macrochir* were caught in this lake. The lakes mentioned above are water bodies isolated from the main lake by a form of barrier. Lake Ikimba is connected with the Kagera River that flows into Lake Victoria, but is separated from the main river by papyrus swamps of many kilometers. Lake Malimbe, a swamp lagoon near Nyegezi, and the pools near Nyamirembe and Kisoria are water bodies that are separated from the main waters of Lake Victoria by extensive papyrus swamps.

In contrast to *O. esculentus*, *O. variabilis* was still common in Lake Victoria at the beginning of the 1980s. In 1982–1983, commercial vessels targeting small sized haplochromines in the northern part of the Mwanza Gulf, and in the Bukinga Bay (2–18 m deep), caught 978 *O. variabilis* in 18 h trawling. Other tilapiine species in these

Table 8.1. *Mean and maximum size (TL in cm) of endemic and introduced Oreochromis species in the Tanzanian part of Lake Victoria.*

Period/ Species	*O. esculentus*			*O. variabilis*			*O. niloticus*		
	mean ± std	max	n	mean ± std	max	n	mean ± std	max	n
1973-74[a]	24.3 ± 2.6	36	952	24.0 ± 2.8	33	1206	29.4 ± 5.7	46	74
1974[b]	25.1 ± 3.6	35	64	24.5 ± 4.0	33	22	30.2 ± 4.9	45	44
1982-83[c]				22.4 ± 2.1	31	587	29.4 ± 5.3	39	222
1987 89[d]							39.5 ± 9.2	54	160
1987-89[e]							38.0 ± 10.3	56	1084

[a] Gill nets.
[b] Bottom trawling with 90 mm codend (MV Mdiria).
[c] Bottom trawling with 20 mm codend (commercial vessels).
[d] Bottom trawling with 20 mm codend (MV Mdiria).
[e] Pair trawling with 60 mm codend.

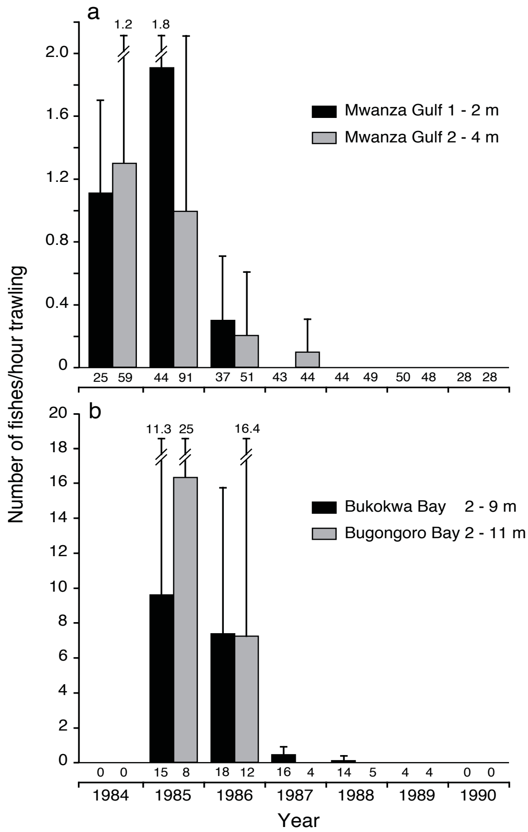

Fig. 8.3. *Mean catch rate (number h*[-1]*) and standard deviation of Oreochromis variabilis by MV Kiboko. a) Two shallow stations in the Mwanza Gulf. b) Two shallow bays west of the Mwanza Gulf. Numbers at bottom of bars indicate the number of trawl shots.*

catches comprised *O. niloticus* (N= 1498) and *T. zilli* (N=10). Bottom trawl catches of MV Kiboko between October 1984 and July 1990 in the Mwanza Gulf at the shallow (1–4 m) stations, revealed a strong decline in *O. variabilis* (Fig. 8.3a; Jonckheere-Terpstra test: 1–2 m, P= 0.000; 2–4 m, P= 0.000). From February 1987 until July 1990 not a single *O. variabilis* was caught. A similar decline was observed in the catches of this vessel in Bukokwa and Bugongoro Bays, where only a small number of local fishermen were active (Fig. 8.3b; Jonckheere-Terpstra test: Bukokwa, P= 0.00; Bugongoro, P= 0.01) After 1988, *O. variabilis* was no longer caught in these bays.

Species and size distribution

In 1973–1974, the mean total lengths of *O. esculentus* and *O. variabilis* (>20 cm TL) in both gillnets and bottom trawls ranged from 24 to 25 cm. The largest fishes caught were respectively 36 and 33 cm (Table 8.1). In 1973–1974, *O. niloticus*, from gillnets and bottom trawls, had average sizes ranging from 29 to 30 cm, and a maximum size of 46 cm. Bottom trawling in 1982–1983 revealed the same average size. In 1987–1989 the mean size of *O. niloticus* in both the catches of MV Kiboko and the pair trawlers, however, had increased to *c.* 39 cm, while the maximum size increased to 56 cm (Table 8.1). The difference in average fish size

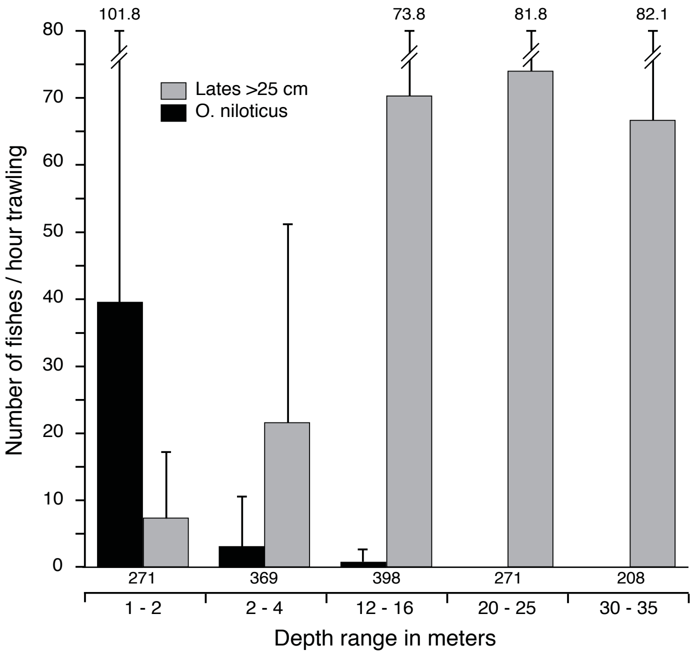

Fig. 8.4. *Mean catch rate (number h^{-1}) and standard deviation of Oreochromis niloticus and large (>25 cm) Nile perch in bottom trawl catches of MV Kiboko at different depths in the Mwanza Gulf area. Numbers at bottom of bars indicate the number of trawl shots.*

over the period 1973–1989 was significant (Kruskall-Wallis P = 0.000). The largest *O. niloticus*, a fish of 72 cm TL, was found in 1990 at a trading site near Mwanza town. At localities in the Mwanza Gulf, outside the regular sampling stations, 10 more fish >60 cm were caught by trawling; the largest of these was 68 cm TL.

The major distribution of *O. niloticus* is limited to the shallow littoral zone (<2 m deep) along the shores of Lake Victoria. In trawl catches from 1984–1990 at all stations in the Mwanza Gulf, 88% of the total number (N = 6033) and 67% of the total mass (2494 kg), were caught at Buzumu station. During 230 h trawling between September 1984 and July 1990 no *O. niloticus* were caught at stations >20 m deep. The mean numbers of *O. niloticus* decreased with increasing depth (Fig. 8.4; Kruskall-Wallis, P= 0.000). The densities of piscivorous (>25 cm) Nile perch in shallow water (<4 m) were significantly lower than in deeper water (Fig. 8.4; Kruskall-Wallis, P= 0.000).

The largest (>20 cm) *O. niloticus*, caught by angling, came from the most offshore sites. Fish <15 cm were caught between the fringing vegetation and fish of 15–25 cm were caught near the shore (Fig. 8.5a,b). In trawl catches, *O. niloticus* <20 cm were mainly caught in water of 1–2 m depth (Fig. 8.5d). Larger fish occurred in both shallow and deeper water (Fig. 8.5d,e,f). At depths of 12–16 m, most fish caught were >40 cm (Fig. 8.5f). A similar correlation between length frequency distributions, and distance from the shore (including depth), was obtained using three different fishing methods (Fig. 8.5g,h,i). The mosquito seines of fishermen targeting the small (circa 5 cm TL), pelagic, cyprinid dagaa *Rastrineobola*

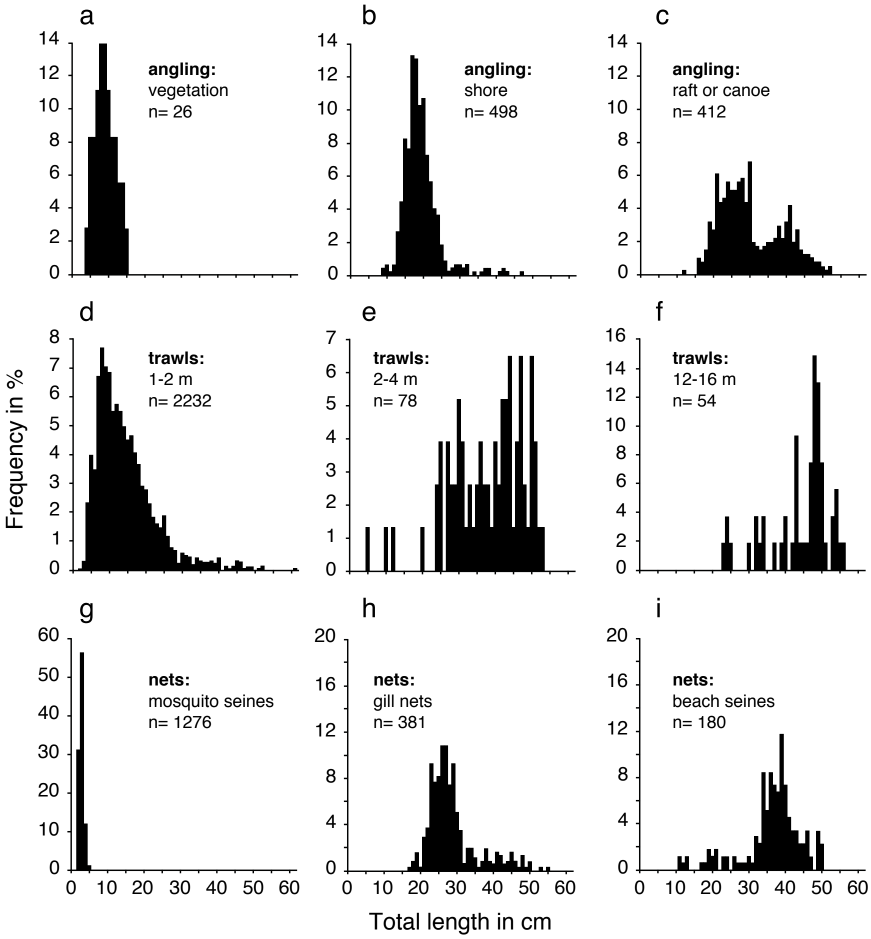

Fig. 8.5. *Length frequencies of Oreochromis niloticus collected with different fishing techniques in the Mwanza Gulf during the period 1988-90. From left to right: increasing depths and distances from the shore. a,b,c) angling at different sites different net types, d,e,f) bottom trawls of MV Kiboko at different depths, g,h,i) different net types.*

argentea (Pellegrin) are used near the beach only. Beach seines, catching *O. niloticus* of mainly 30–50 cm, reach hundreds of meters into the lake. Gillnet fishermen place their nets in the intermediate zone and accordingly catch intermediate sizes (20–30 cm) of *O. niloticus*.

Changes in the fishery

The numbers of boats and fishing licenses for the Nyanza Gulf between 1933 and 1957 indicate an increase of fishing effort (Fig. 8.6a; Beverton 1959). Over the same period the CPUE for tilapiines, mainly *O. esculentus* in a 5 inch (c. 125 mm) gillnet, decreased. In the Tanzanian part of the lake, the number of fishermen and canoes continuously increased between 1958 and 1990 (Fig. 8.6b). On top of this increase in effort, the replacement of flax and cotton gillnets by more efficient nylon nets, during the 1950s, also increased fishing pressure.

After 1985, the total fishing effort further increased, as people were attracted

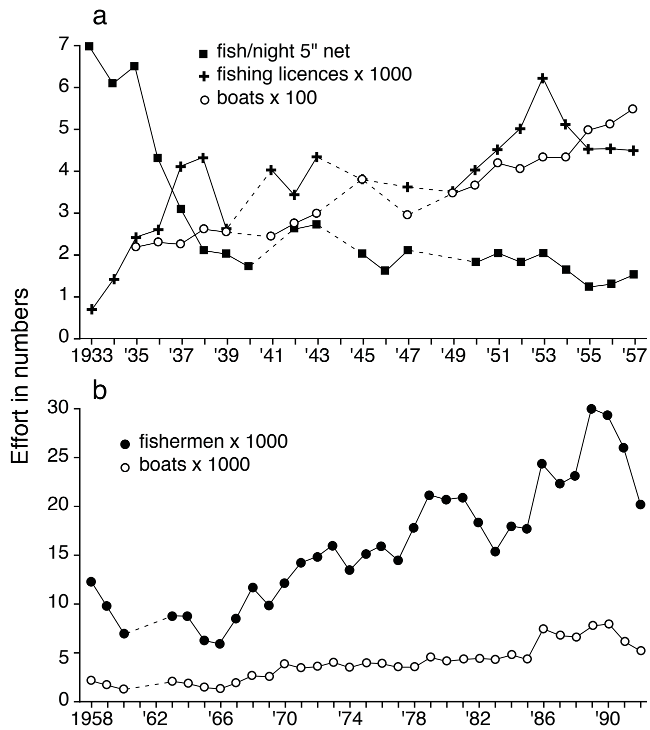

Fig. 8.6. *Catch per unit of effort and effort increase in Lake Victoria.*
a) In Kenyan waters during the period 1933-1957 (source: Beverton 1959).
b) In Tanzanian waters during the period 1958-1992 (source: Ministry of Tourism, Natural Resources and Environment of Tanzania).

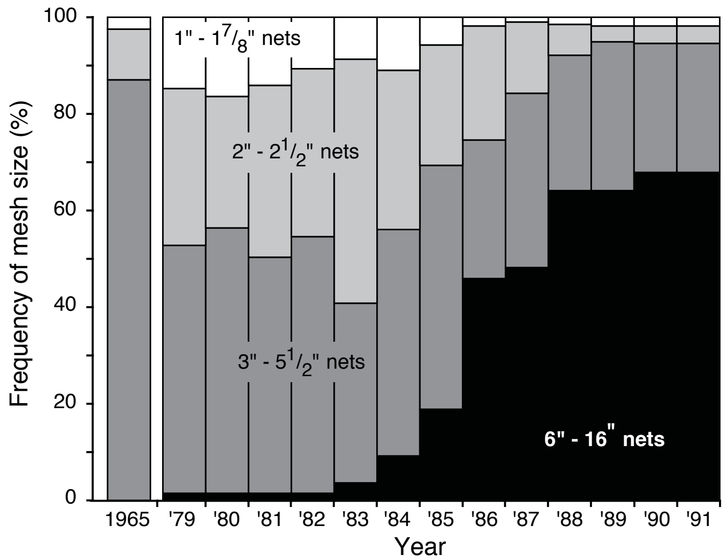

Fig. 8.7. *Mesh size distribution in gill nets of artisanal fishermen in the Tanzanian part of Lake Victoria. (source: Ministry of Tourism, Natural Resources and Environment of Tanzania).*

to the fisheries by the Nile perch boom (Fig. 8.6b; Reynolds et al., 1995). Almost all newly starting fishermen, however, targeted Nile perch. Gillnet fishermen that previously had been targeting tilapiines and haplochromines also switched to the more profitable Nile perch (Ligtvoet et al., 1988). This is reflected in a shift to mesh sizes >6 inches (*c*. 150 mm) (Fig. 8.7).

Discussion

The data indicate a decline of indigenous tilapiines in Lake Victoria and an increase of the introduced *O. niloticus*. As has been suggested by other authors (Ogutu-Ohwayo, 1990a; Twongo, 1995; Lowe-McConnell, 2000), the decline of the native tilapiines may reflect the impacts of fisheries, Nile perch predation, eutrophication, hybridization and competition with introduced tilapiines, or a combination of these.

Impact of the fisheries on tilapiines

Based on the decline of CPUE of *O. esculentus* in 5 inch gillnets from 1933 to 1957, Beverton (1959) and Fryer & Iles (1972) suggested over-exploitation of the tilapiine stock. During the same period, however, the total fishing effort in the lake increased, and the use of 3 inch and 4 inch nets increased (Fryer & Iles, 1972). These developments made it unavoidable that the catch rate per 5 inch gillnet decreased. As Garrod (1960) already suggested, such a decrease does not imply that the total landings of the tilapiines decreased or that the tilapiines could not resist the increased fishing pressure. As far as is known, there are no data that unequivocally show that the total mass of native tilapiines harvested from Lake Victoria had declined before 1950. Although there is circumstantial evidence of local over-exploitation in the heavily fished areas in the 1950s (Garrod, 1960), this does not indicate over-exploitation for the whole lake.

In spite of the continued steady increase of fishing effort during the second half of the century, strong fluctuations occurred in the total landings of tilapiine fishes. The increase in the early 1960s has been attributed to the sudden rise in lake level (Welcomme, 1970). The decline in landings between the mid 1960s and the mid 1970s in Tanzania and Kenya may indicate over-exploitation. The total landings, however, increased again in both countries after 1975. This increase may be partly explained by the entry and subsequent increase of *O. niloticus* in the landings.

A strong increase in the landings of *O. niloticus* in the 1980s, occurred after the Nile perch boom, when many fishermen switched from a tilapiine to a Nile perch fishery (Ligtvoet er al., 1988). They replaced their 3 and 4 inch gillnets with 6 inch and larger nets. As commercially sized Nile perch mainly occur outside the shallow littoral zone, these fishermen moved towards deeper waters. This implies that the fisheries for Nile perch and tilapiines are spatially segregated (Wanink et al., 1999). As a result, fishing pressure on the tilapiine stock, in particular on the inshore dwelling juvenile tilapiines, was reduced. In Tanzania, fishing pressure in the early 1980s was also reduced by a shortage of gillnets suitable for the tilapiine fishery. The effect of this reduced fishing pressure may have led to the increased stock and an increased average size of *O. niloticus*.

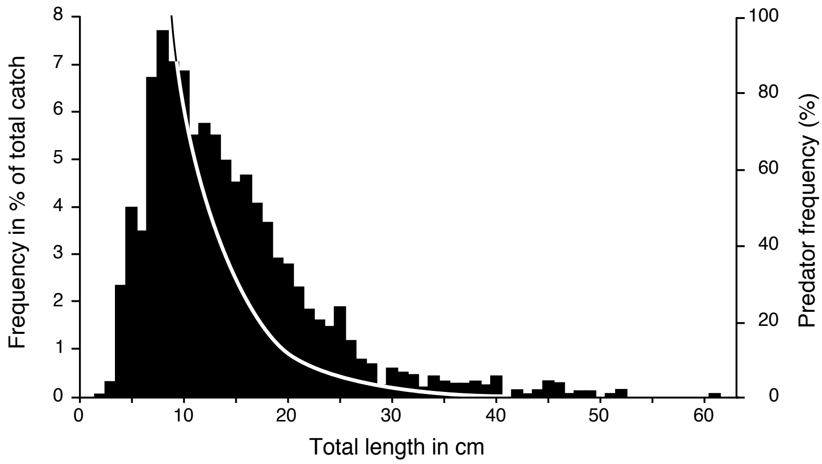

Fig. 8.8. *Length frequency distribution of O. niloticus (bar) and fraction of piscivorous Nile perch (>25 cm) that can prey upon O. niloticus of a certain length at the 1-2 m station. See text for further explanation.*

This subsequently led to increased landings. In contrast, in the Ugandan Lakes Wamala and George, the average size of *O. niloticus* decreased due to increased exploitation (Gwahaba, 1973; Okaronon, 1995). As in these lakes, it is to be expected that stock and fish size in Lake Victoria will decline again when the exploitation level of *O. niloticus* increases.

There can be no doubt that fishing had a strong influence on the tilapiine stocks of Lake Victoria (Bundy & Pitcher, 1995). It does not seem realistic, however, to blame the fishery for the complete disappearance of the native tilapiine species. Over-exploitation alone has rarely been responsible for the eradication of a fish species (Beverton, 1992). Moreover, the observed increase in density and individual mass of *O. niloticus* in the 1980s does not suggest that, at that time, the tilapiine stocks were over-exploited.

Impact of the Nile perch

In Lakes Victoria and Kyoga, Nile perch do feed on *O. niloticus*, though tilapiines constitute only a minor part of their diet (Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b; Mkumbo & Ligtvoet, 1992). There are two possible explanations for this relatively low contribution of *O. niloticus* to the Nile perch diet: (i) Experiments in captivity with *O. niloticus*, common carp *Cyprinus carpio* L. and grey mullet *Mugil cephalus* L. revealed that *O. niloticus* was the least vulnerable to predation by Nile perch (El Gamel, 1992). It is suggested that the relatively deep body of *O. niloticus* makes the species more difficult for Nile perch to swallow; (ii) most *O. niloticus* live in inshore waters (<2 m deep) while piscivorous Nile perch (>25 cm LT) prefer deeper water, thus reducing the overlap between prey and predator. A similar preference of *O. niloticus* for shallow water was already found in a lake-wide survey long before the Nile perch upsurge (Kudhongania & Cordone, 1974a, b). Therefore the reversed distribution pattern cannot be the result of predation by Nile perch in the deeper water.

Assuming that the mouth gape of predators determines the maximum prey length, as a function of body depth (Hambright 1991; Dennerline & Van Den Avyle, 2000), Nile perch can feed on *O. niloticus* of *c*. 33% of their own length. This implies that Nile perch of 25 cm LT, which are mainly piscivorous, can feed on *O. niloticus* <9 cm. Cumulative frequency distributions of piscivorous Nile perch with a mouth gape that could swallow an *O. niloticus* of a certain length, show that the fraction of Nile perch that can prey upon the larger tilapiines, in the 1–2 m deep station in the Mwanza Gulf, quickly drops with increasing prey size (Fig. 8.8). This is because larger Nile perch mainly live in deeper water. For example, only 10% of the Nile perch (>25 cm) at the 1–2 m deep station are large enough to prey upon *O. niloticus* of 20 cm. The actual fraction is probably lower as piscivorous fishes tend to feed on prey that are smaller than the maximum size possible (Gillen et al., 1981; Hambright, 1991). Also other littoral fish species were relatively little affected by Nile perch predation (Witte et al., 1992a; Kaufman & Ochumba, 1993; Goudswaard & Witte, 1997; Seehausen et al., 1997a). This was especially the case when they lived near vegetation and rocks, the habitats where the smallest tilapiines occur.

Like *O. niloticus*, the two native tilapiines, *O. esculentus* and *O. variabilis* were most common in shallow areas (Kudhongania & Cordone, 1974a, b). Their habitat overlap with Nile perch was small, indicating that Nile perch is unlikely to be responsible for the decline of the indigenous species. *Oreochromis esculentus* used to be the most abundant native tilapiine species in the Mwanza Gulf (Kudhongania & Cordone 1974a). Nevertheless, this species vanished before the Nile perch boom.

In conclusion, although Nile perch may have had some effect on the tilapiine stock, it cannot be held responsible for the almost complete disappearance of the native tilapiines of Lake Victoria.

Impact of environmental changes

Due to human activities, eutrophication of Lake Victoria has been increasing since the 1920s (Hecky, 1993). In particular during the last decades, algae blooms have been observed, together with a shift from large filamentous diatoms to smaller colonial cyanobacteria and green algae (Ochumba & Kibaraa, 1989; Witte et al., 1992b; Hecky, 1993; Mugidde, 1993; Verschuren et al., 1998). The disappearance of phytoplanktivorous fishes may also have contributed to these algae blooms, through reduced phytoplankton consumption (Kilham & Kilham, 1990; Goldschmidt et al., 1993; Ogutu-Ohwayo, 1990). Decomposition of algae that sank to the bottom has caused a serious decrease in dissolved oxygen concentration at depths >40 m, subsequently resulting in occasional mass fish kills (Ochumba& Kibaara, 1989; Kaufman, 1992; Hecky et al., 1994). Nile perch, the catfish *Bagrus docmak* (Forsskåll) and deepwater haplochromines were most abundant in these mass mortalities (PCG, pers. obs.). Tilapiine fishes are found in shallow waters and are, for this reason, unlikely to be affected by these mass kills. Moreover, it has been demonstrated that juvenile tilapiines can survive under relatively low oxygen concentrations. Juveniles of a tilapiine hybrid (*O. niloticus x O. mossambicus* Peters) have been raised in the laboratory for >12 months at 10% air saturation (W. Abbink, S. Baecke,

F. Witte & G. van den Thillart, pers. com.). In the field, *O. esculentus* was even found in areas with lower oxygen concentrations (<1 ppm) than *O. niloticus* (Welcomme, 1964).

Batjakas et al. (1997) demonstrated that *O. niloticus* is a more efficient suspension feeder which utilizes a broader range of particle sizes compared to *O. esculentus*. They concluded that the disappearance of *O. esculentus* and the dominance of *O. niloticus* in Lake Victoria might be explained by the shift from large filamentous diatoms to small cyanobacteria and green algae, which are more beneficial for *O. niloticus*.

In some artificial and eutrophic lakes near the towns of Singida and Shinyanga, south of Lake Victoria, *O. esculentus* was found in 1986–1987 while *O. niloticus* was absent. These lakes were green with algae, especially during the dry season. Nevertheless, *O. esculentus* was abundant, which indicates that the species can survive in a eutrophic lake. In the satellite Lake Malimbe, *O. esculentus* was found to feed predominantly on blue-green algae in 1999 (E. F. B. Katunzi, pers. obs.). In conclusion, a strong impact of deoxygenation on the native tilapiines seems unlikely, whereas the impact of eutrophication and the related shift in phytoplankton composition is not clear.

Impact of hybridization

Hybridization has been suggested as a possible factor concerning the disappearance of *O. variabilis* and *O. esculentus* (Ogutu-Ohwayo, 1990a). A hybrid between *O. variabilis* and *O. niloticus* has been observed in Lake Victoria (Welcomme, 1968). Five years after the introduction of *O. esculentus* into Lake Nkugute, which already contained *O. niloticus*, suspected hybrids between these species were found, although the fish all had the general appearance of *O. niloticus* (Lowe-McConnell, 1958).

The contribution of hybridization with *O. niloticus* to the disappearance of *O. esculentus* and *O. variabilis* remains unclear. A molecular study by J. F. Agnèse (pers. com.) revealed no evidence for the presence of genetic material of *O. esculentus* in *O. niloticus* from the Nyanza Gulf. Molecular work by Mwanja & Kaufman (1995) revealed evidence of *O. niloticus* in *O. esculentus* populations from satellite lakes, but Lake Victoria *O. niloticus* showed little evidence of *O. eculentus* alleles. Individuals were rarely observed that could have been hybrids between the native tilapiine species and *O. niloticus* (unpubl. obs). The general appearance of the last individuals of *O. esculentus* and *O. variabilis*, did not suggest that they were intermediate forms. It should be noted, however, that there are cases in which hybrids between *O. niloticus* and other species came to resemble *O. niloticus* in later generations (Lowe-McConnell, 1958, 2000).

Impact of interspecific competition

It was expected that the introduced tilapiine species would be able to coexist with the native tilapiines in Lake Victoria. Already in the early 1960s, however, there were indications of competition for breeding and nursery grounds between the introduced *T. zillii* and *O. variabilis* (Fryer, 1961; Lever, 1996; Lowe-McConnell, 2000). The suggestion that lack of suitable spawning and nursery grounds limit population expansion is supported by the dramatic increase in *O. esculentus* catches in 1964–1965, following the strong increase in lake level in 1961–

1962. The lagoons that were flooded at that time extended the nursery areas (Welcomme, 1970; Lowe-McConnell, 1982). Almost 20 years after its introduction and well before the Nile perch boom, *O. niloticus* had become important in the commercial catches and gradually replaced the indigenous *O. esculentus* and *O. variabilis*.

Observations in Lake Ikimba provide an additional example of replacement of native tilapiines by *O. niloticus* and *O. macrochir*. Here *O. esculentus* was replaced within a period of 10 years, but it is not known when exactly *O. niloticus* had found its way into the lake. Similar observations were made in Lake Ihema. In 1972, *O. variabilis* and *O. esculentus* were the only tilapiines in this lake (Kiss. 1976). Ten years later only *O. niloticus* was found and *O. esculentus* and *O. variabilis* had vanished (Plisnier et al., 1988). As *L. niloticus* was not found in these lakes, these examples show that the disappearance of the native tilapiines in Lake Victoria is more likely to be the result of the introduction of *O. niloticus* than of the introduction of Nile perch.

Oreochromis niloticus may be regarded as a dominant competitor, a view which is supported by the following observations: (i) In Lake Luhondo, a source of the Kagera River, the colonization of *O. niloticus* coincided with the disappearance of some cyprinid fish species (De Vos et al., 1990); (ii) in the Kafue River, a tributary of the Zambezi River in Zambia, *O. macrochir* and the native *Oreochromis andersonii* (Castelnau) are gradually declining, while the introduced *O. niloticus* increases in number (Schwank, 1995); (iii) the natural distribution of *O. esculentus* and *O. variabilis* within the Nile basin, down stream of lakes Victoria and Kyoga is restricted to the Victoria Nile above the Kabalega Falls (formerly called Murchison Falls). In Lake Albert, below these falls, *O. niloticus* is present. It is likely that the Kabalega Falls are an insurmountable obstacle for fishes migrating upstream but not for those migrating downstream. Consequently, both *O. esculentus* and *O. variabilis* must have been able to enter Lake Albert. Apparently neither one of these species could establish itself in this lake where *O. niloticus* occurs naturally.

The main features which make *O. niloticus* a more successful species than *O. variabilis* and *O. esculentus* are: (i) Its opportunistic feeding behaviour. Recent observations suggest that it has presently a more diverse diet than shortly after its introduction (Balirwa, 1992; Gophen et al., 1993); (ii) the supposed higher reproductive success of *O. niloticus* due to its wider habitat tolerance for spawning and nursery purposes (Twongo, 1995) and its higher fecundity (Lowe- McConnell, 1995); (iii) its ability to grow to a larger size and its, assumed, aggressiveness towards other species on the breeding grounds (Plisnier et al., 1988; Lever, 1996; Lowe-McConnell, 2000). Its mating places are found in a shallow zone of the lake (Welcomme, 1968: Fryer & Iles 1972), and are tightly packed with dominant territorial males leaving no space, or only inferior places, to subordinate fish (Welcomme, 1970).

Restoration of the original species flock

The two native tilapiines of Lake Victoria did not disappear completely. Small populations of *O. esculentus* can still be found in satellite lakes which are isolated from the main lake and where *O. niloticus* and Nile perch are not present. In 1992, a small population of *O. variabilis* was still found in coexistence with *O. niloticus* at Makobe Island in the Speke Gulf, isolated by deep water (30 m) from the mainland shore (Seehausen et al., 1997b).

The disappearance of several indigenous species from Lake Victoria has caused a general awareness concerning reduced biodiversity in African Lakes (Pitcher & Hart, 1995). The present situation in Lake Victoria does not seem to be reversible as the introduced Nile perch and *O. niloticus* cannot be eliminated. Moreover, given the importance of these species in the present day fishery, this may not be desirable for economic reasons. Besides other objections, e.g. loss of genetic integrity (Muli, 1996), against reintroduction of native tilapiines into Lake Victoria, reintroductions will be doomed to fail due to competition with *O. niloticus*, which caused their disappearance in the past.

Acknowledgements

Thanks go to the staff of the Tanzania Fisheries Research Institute. The crew of MV Kiboko collected many data under difficult circumstances. The director of the Freshwater Fisheries Training Institute, R. Mapunda, provided the catchdata of MV Mdiria. W. igtvoet provided additional data. J. Balirwa, J. H. Wanink and R. H. Lowe-McConnell commented on earlier drafts of this paper. The HEST-project was financially supported by the section for Research and Technology of the Netherlands Minister of Development Co-operation and the by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).


SALTER
TAFIRI N'EGEZI