Chapter 4
Fish Biology and Life History Indicators

E.F.B. Katunzi, Yunus D. Mgaya, O.C. Mkumbo, and S.M. Limbu

Abstract Life history traits like growth, reproduction, food and mortality are principal factors in the survival of the fish. This chapter examines the life history indicators of three commercial fish species in Lake Victoria, namely Nile perch (*Lates niloticus*), Nile tilapia (*Oreochromis niloticus*) and the cyprinid known as 'Dagaa' (*Rastrineobola argentea*). The size at first maturity for Nile perch has been declining due to stress in the population caused by heavy exploitation, changes in food availability and deteriorating water quality parameters, particularly dissolved oxygen concentration. The fish exhibits ontogenic shifts in food. *R. argentea* has an offshore surface dwelling behaviour with about 68% found distributed in waters of more than 40 m depth. Its size at first maturity varies from place to place. *R. argentea* breeds throughout the year but with distinct peaks during the rainy season. An increase in fecundity has been observed in Nile tilapia and it is considered a mechanism to compensate for the intensive fishing pressure in the lake. Studies indicate an increase in size and growth parameters for Nile tilapia despite the heavy fishing pressure as a result of increased demand in local and foreign markets. The success of the species could be due to the ability of the species to expand their niche. It has diversified its food to include *Caridina nilotica*, chironomids, chaoborids, molluscs and bottom detrital matter. An ecosystem approach guided by a precautionary principle is required in order to manage the fishery resources in Lake Victoria and to ensure their sustainability.

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4.1 Introduction

Life history parameters, when monitored over time, can give an indication of the performance of a species in an ecosystem. They give a direction of success or failure, in which case, appropriate measures can be devised accordingly. Life history traits like growth, reproduction, and mortality are regarded as principal factors in the survival of fish (Stearns 1992; Matsuishi et al. 2006; Murua 2014). The fish will be forced to increase the growth rate and switch to early reproduction when under pressure due to exploitation and other environmental changes (Heino and Godø 2002). Due to a compromise between reproduction and somatic growth, this early maturation can cause stunted growth (Stearns 1992; Tsikliras et al. 2007). However, for the larger fishes, the reaction could be an increase in fecundity. This chapter examines life history indicators of three commercial species in Lake Victoria, namely, the Nile perch, the Nile tilapia and the cyprinid dagaa (*R. argentea*).

4.2 The Nile Perch

The Nile perch (*L. niloticus* Linnaeus) is a predatory fish of high commercial and recreational value. It can grow to a length of two meters and a weight of 200 kg (Geheb et al. 2008). It was introduced into lakes Kyoga, Nabugabo and Victoria in Uganda from Lake Albert during the 1950s and early 1960s (Hamblyn 1961; Geheb et al. 2008). Eight specimens from Lake Turkana were introduced in the Kenyan part of Lake Victoria at Kisumu in 1963 (Odero 1979). The fish was introduced to feed on the small-sized haplochromine cichlids, which were at that time abundant and relatively unexploited for conversion into larger fish of greater commercial and recreational value (Anderson 1961; Downing et al. 2014).

4.2.1 Reproduction

Size at First Maturity

The length at first maturity (Lm_{50}) is often used as an indicator in relation to changes in the mean length of the population being fished. Lm_{50} is the point on the curve where 50% of the fish are mature (Fontoura et al. 2009). A research carried out by LVFRP (Cowx 2005) revealed that about 20% of the fish captured in trawl surveys were mature, and of these, females represented about 30%.

Soon after the Nile perch introduction, the size at first maturity of male Nile perch was between 30–34 cm total length for males, and 33–35 cm for females (Okedi 1974). The length at first maturity of 54 cm for males and 69 cm for females was recorded by Acere (1985). The trend of events changed to males maturing at

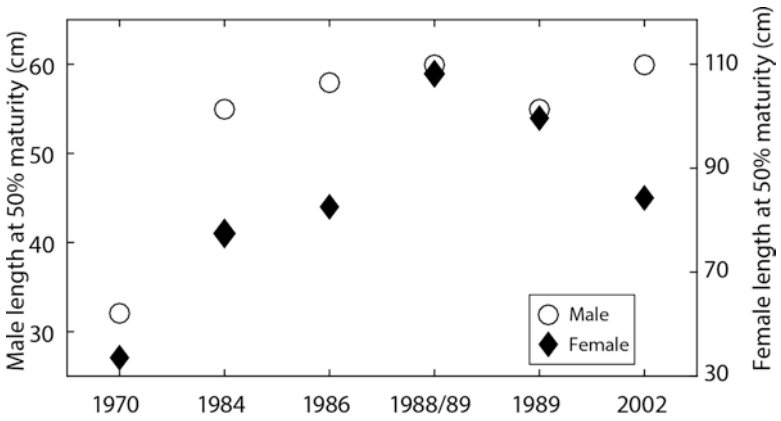


Fig. 4.1 Trends in size at 50% maturity for *L. niloticus* (Sources: 1970: Okedi (1971); 1984: Acere (1985); 1986: Ogutu-Ohwayo (1988); 1988/89: Ligtvoet and Mkumbo (1990); 2002: Mkumbo (2002)). Note: The low Lm50 values in 1970 and 1984 could be attributed to the various authors using a different (maturity) assessment method

50–65 cm and females at 60–95 cm as per Ogutu-Ohwayo (1988). In Tanzania, the size at first maturity for females and males in the Mwanza Gulf, Tanzania (1988–1989) was at 110 cm and 60 cm TL, respectively (Ligtvoet and Mkumbo 1990). In 2002, Mkumbo (2002) recorded a decrease in size when she noted the lengths at maturity for males and females to be 54 cm and 77 cm respectively (Fig. 4.1). The declining trend in the size of maturity points to stress in the population, which could be a result of heavy exploitation, changes in food availability and deteriorating water qualityparameters in the lake environment (Njiru et al. 2007; Hecky et al. 2010).

Generally, males of *L. niloticus* attain maturity at a smaller size than females based on the available growth rate data (Hughes 1992; Mkumbo 2002). Using the parameters of the von Bertalanffy growth function and the relationship of $t_m = t_0 - \ln(1 - L_m/L_\infty)/K$ (Froese et al. 2000), where t_m is the age at first maturity and L_m is the size at first maturity, Mkumbo (2002) calculated the age at first maturity for males and females of *L. niloticus* at 1.6 years and 2.5 years respectively.

Breeding Cycle

Mature fish (ripe and running condition) were found throughout the year (Ligtvoet and Mkumbo 1990; Mkumbo 2002) with a peak in the proportion of individuals in advanced stages of maturation occurring in November and December and a smaller peak in May/June. The former and latter peaks coincide with the start and end of the rainy season, respectively (Acere 1985). It should be pointed out that since the patterns of dry and wet seasons do not run concurrently in all parts of the lake, the breeding cycle of the Nile perch is not expected to be identical over the whole lake. Ligtvoet and Mkumbo (1990) reported that the Nile perch preferred to spawn in shallow sheltered areas, and nursery grounds are located at a wide range of 2–57 m depth.

4.2.2 Length Frequencies

The length frequency trends over the years and proportion of fish larger than 80 cm total length (TL) are depicted in Figs. 4.2 and 4.3. The length frequency data presented in Fig. 4.2 were collected using different trawls (in different zones) and hence should be interpreted with caution. The data collected in 1985–1990 on the Tanzanian side with bottom trawls has confirmed a sharp fall in percentage compositions of fishes larger than 80 cm total length (Fig. 4.3). For the years after 1999, there is a progressive increase in the quantity of larger fishes. Increased fishing effort could be the main cause of the observed changes. However, environmental factors such as the lake's limnochemistry could also explain the observed fluctuations in fish populations.

4.2.3 Growth

From Lake Victoria, specimens could grow up to 190 cm TL (Acere, 1985) and 200 cm TL (Okemwa 1984). Females grow to a much larger size than males. Ligtvoet and Mkumbo (1990) reported the growth increments of 28, 28 and 21 cm $yr.^{-1}$ for three fishes that were tagged in the Mwanza area at lengths of 32, 47 and 51 cm respectively. Asila and Okemwa (1999) reported a growth increment within that range (29 cm $yearr^{-1}$) from tagged fishes. The differences and inconsistencies observed in the estimated growth parameters could possibly be explained by the differences in the size of the catch populations. With bigger sizes in the sample, the higher the L, the lower the K (Fig. 4.4).

4.2.4 Distribution

L. niloticus is endemic in lakes Albert, Rudolf, Turkana, Tana, Chad, and the Nile River basin; but introduced in lakes Victoria and Kyoga. The Nile perch has a lake-wide distribution, which depends on dissolved oxygen concentration and depth ranging from 0 to 60 m. However, juveniles of the length <30 cm in lakes Chad, Turkana and Albert are mainly distributed in the shallow inshore waters (Hamblyn 1962; Gee 1966). The littoral rocky habitat is possibly one of the few habitats in Lake Victoria that has not been invaded by *L. niloticus* (Witte et al. 1991). This habitat has a spectacular assemblage of haplochromines not known to exist elsewhere in the lake. The highest catch rates of the Nile perch in the Tanzanian area in 1985 were obtained from waters between 16 and 50 m deep (Goudswaard and Witte 1985).

The batho-spatial distribution pattern exhibited a decline in *L. niloticus* stock abundance with depth, similar to that observed in 1969/1970 (Kudhongania and Cordone 1974), but with differences in the depth ranges of high abundances (Mkumbo 2002). Results of bottom trawl surveys conducted under LVFRP (1999–

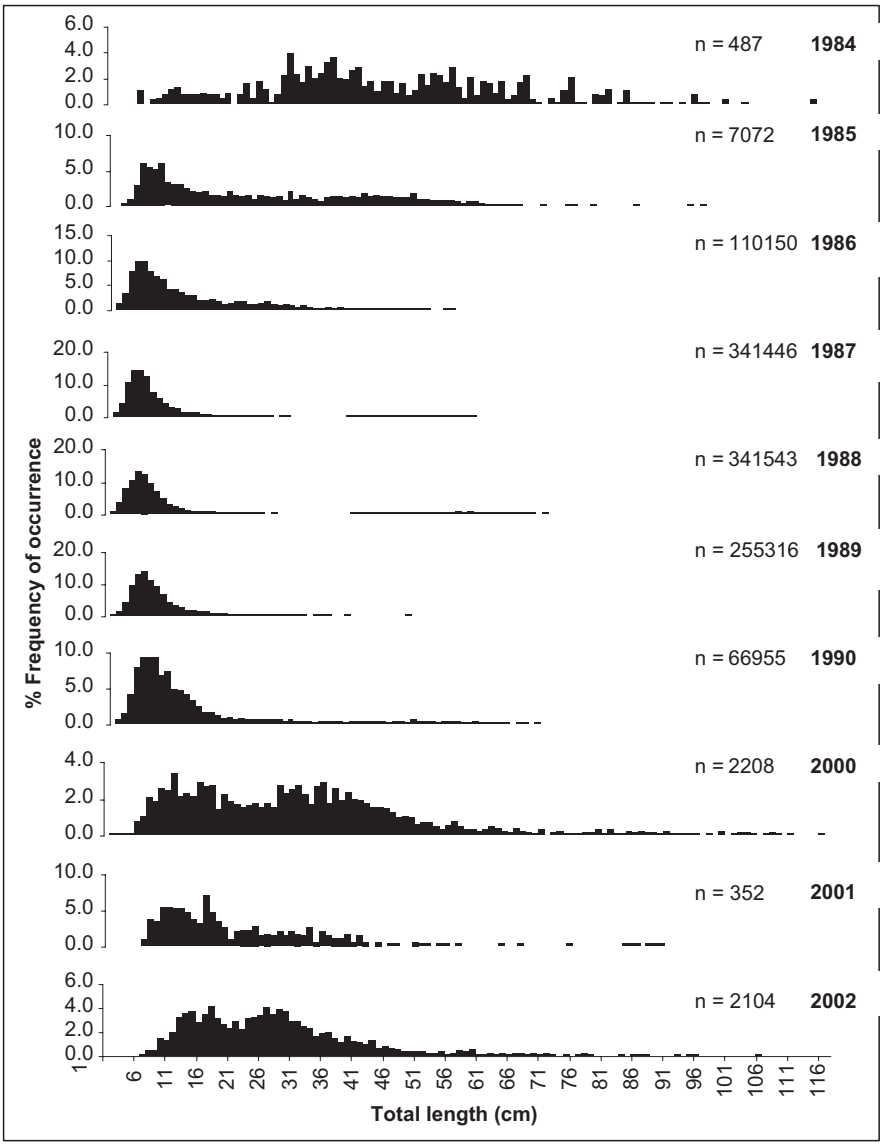


Fig. 4.2 Length frequency distribution for *L. niloticus* in the experimental catches from the Tanzanian part of Lake Victoria (Data from TAFIRI Unpublished Reports)

2001) recorded the highest catch rates at depths of 4 m to 20 m with a remarkable decline in catch rates at depths below 50 m. Unlike the 1960–1970 surveys, which recorded a drop in catch rates below 70 m, the mean catch rates dropped abruptly below 50 m during the LVFRP survey (Mkumbo 2002). This is probably linked to changes in the physico-chemical characteristics of the lake and the presence of a

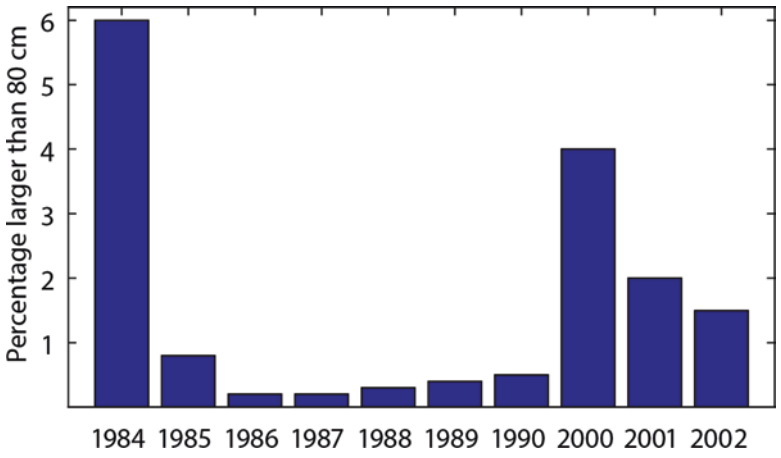


Fig. 4.3 Proportion of fish larger than 80 cm TL for *L. niloticus* (Data from TAFIRI, Unpublished Reports)

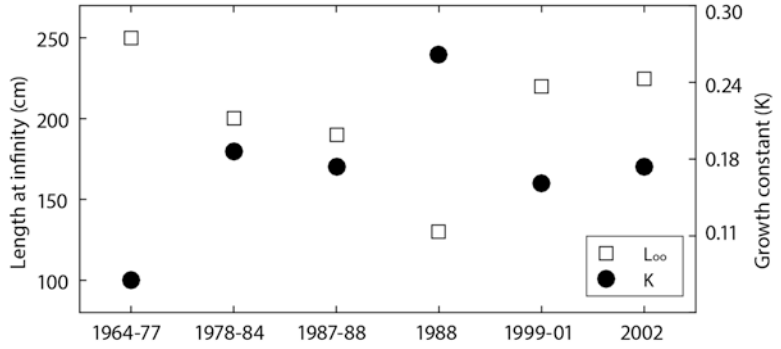


Fig. 4.4 von Bertalanffy growth parameters, length at infinity (L∞) and growth constant (K) for *L. niloticus* (Sources: 1964–1977: Acere (1985); 1978–1984: (Asila and Ogari 1988); 1987–1988: Ligtvoet and Mkumbo (1990); 1998: Asila and Okemwa (1999); 1999–2001: Mkumbo (2002); 2002: (Muhoozi 2002))

low dissolved oxygen (hypoxic) layer below 50 m (Hecky et al. 1994; Wanink et al. 2001; Sitoki et al. 2010). The hypoxic layer in deeper waters is not a permanent feature since oxygen concentrations as high as 6.67 mg/L at 67-m depth in August, 5.7 mg/L at a depth of 55 m in September 2000 and 5.8 mg/L at 50 m deep in February 2001 have been reported (Mkumbo 2002).

4.2.5 Food and Feeding

Feeding Habits and Adaptations

Between 1968 and 1977, haplochromines were the dominant prey of most sizes of the Nile perch in Lake Victoria. By 1988, the major types of prey eaten by the perch in Lake Victoria had changed to *Caridina nilotica*, anisopteran nymphs, Nile perch juveniles, *R. argentea* and tilapiines with very few haplochromines (Ogari and Dadzie 1988; Mkumbo and Ligtvoet 1992). These remained the major types of prey of the Nile perch in Lake Victoria between 1995 and 2000 with proportions of haplochromines increasing significantly (Fig. 4.5).

A decline in the importance of haplochromines in Lake Victoria was accompanied by a relative increase in *R. argentea* (Mkumbo and Ligtvoet 1992). However, as haplochromine stocks improved, the Nile perch reverted to feeding more on haplochromines (Mkumbo 2002) suggesting that the fish shifts to *R. argentea* in the absence of haplochromines. It also suggests that *R. argentea* may be a less preferred prey than haplochromines (Kishe-Machumu et al. 2012; van de Wolfshaar et al. 2014).

Ontogenic Shifts in Diet

Nile perch exhibits a clear ontogenic shift in diet at various sizes (Downing et al. 2013; Nyboer and Chapman 2013; Nkalubo et al. 2014). For example, while Nile perch individuals with less than 20 cm total length (TL) fed on *C. nilotica, R. argentea*, anisopteran nymphs and chironomids; individuals with TL from 20 cm to 60 cm mainly ingested *R. argentea*, anisopteran nymphs, *C. nilotica*, tilapiines, juvenile Nile perch and to a lesser extent haplochromines. Nile perch with 60–100 cm TL mainly ate *R. argentea,* Nile perch juveniles, tilapiines and haplochromines, while individuals with >100 cm TL depended almost solely on tilapiines and Nile perch juveniles (Nkalubo et al. 2014). The ontogenic shift in the diet of the Nile perch is further illustrated by studies done in Tanzania and Kenya (Ogari and Dadzie 1988; Kishe-Machumu et al. 2012). The diets of the Nile perch with total lengths <20 cm were dominated by *C. nilotica*, which contributed more than 70% of the prey items (Mkumbo 2002).

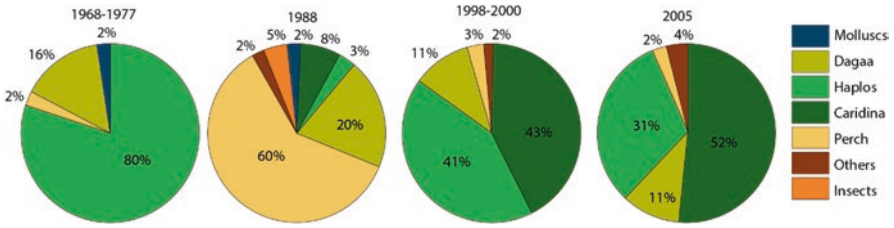


Fig. 4.5 Shifts in feeding habits of the Nile perch in Lake Victoria for the period of 1968–2005 (Data from Unpublished IFMP Report 2005)

Between 20 cm and 60 cm TL, *C. nilotica* dominance decreased from 48% to about 30%, as the Nile perch switched to feeding on haplochromines, which contributed more than 70% of their diet. In large fish (>90 cm TL), the Nile perch became cannibalistic, feeding on its own juveniles, which contributed about 30% of the diet. Other fish prey such as *Clarias gariepinus* (7%), *Oreochromis* species (8%) and *Barbus profundus* (7%), also became important, and the contribution of haplochromines declined to about 50%. The contribution of dagaa was low (<16%) in all sizes of Nile perch <100 cm TL, and absent in the stomachs of larger fish (Mkumbo 2002).

4.3 The Silver Cyprinid (*Rastrineobola argentea*)

4.3.1 Introduction

R. argentea (locally known as dagaa) is endemic to the Victoria Nile and lakes Kyoga, Nabugabo and Victoria (Corbet 1961; Greenwood 1966). The species has been able to survive alongside the voracious Nile perch *L. niloticus* (Ogutu-Ohwayo 1995; Taabu-Munyaho et al. 2016). Over a long period of time the fish has not attracted the attention of both scientists and investors. This could probably have been due to its small size and low abundance especially before the decline of the haplochromines. The exploitation of dagaa is first reported as a light fishery in the mid-1960s (Okedi 1981). The fishing is reported to have flourished after the reduction of the haplochromines due to overfishing and predation (Barel et al. 1991; Reynolds et al. 1995). Currently the species is second to the Nile perch in abundance and importance in the lake's fisheries.

4.3.2 Distribution

R. argentea has been described as an offshore surface dweller (Greenwood 1974). The majority of the biomass of *R. argentea* (an average of 68%) is distributed in waters of more than 40 m depth (Tumwebaze et al. 2007). However, *R. argentea* was later found in the pelagic waters probably because of displacement by the more competitive zooplanktivorous haplochromines while following the downward movement of the zooplankton (Getabu et al. 2003). Further colonization of the species followed the disappearance of the demersal haplochromines. Parasitism also was known to have an impact on the distribution of the fish. For example, juveniles and parasitized adults stay near the surface throughout the day (Wanink 1992). Physical environmental factors like light and oxygen also have an impact on the distribution of fishes. *R. argentea* also migrates diurnally within the water column. It occupies the surface waters at night and deep waters during the day.

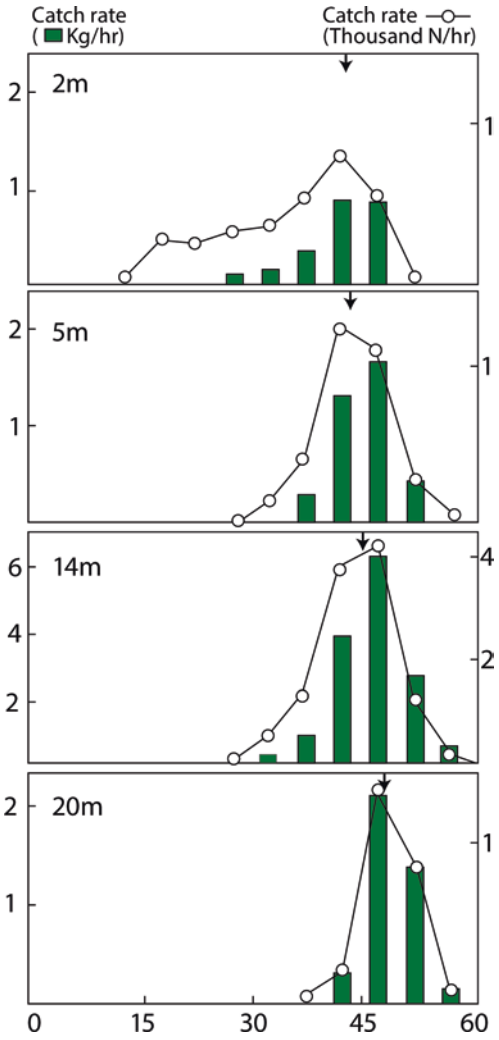


Fig. 4.6 Horizontal distribution of *R. argentea* over five stations in the Mwanza Gulf (Redrawn from Wanink 1998)

Wanink (1992) observed majority of the adult fishes to be concentrated in the upper part of the water column in the night but during daytime they were found close to the bottom with a smallpopulation at the surface but mostly parasitized by *Ligula intestinalis* (Oyoo-Okoth et al. 2010). Juvenile dagaa >35 mm SL were abundant in daytime surface trawls but could not be caught at night, which may indicate that they occupy intermediate depths. Night catches from the surface trawl show that the size of adult dagaa increases with water depths and distance from the shore (Wanink 1998) (Fig. 4.6).

4.3.3 Reproduction

Size at First Maturity

Size at first maturity of *R. argentea* has been reported to vary from place to place. Wanink (1998) reported that females from the Mwanza Gulf mature at 36 mm standard length. Outside the gulf, *R. argentea* has been found to mature at 39 mm SL for females and 44 mm SL for males (Bayona et al. 2003).

Absolute Fecundity

The absolute fecundity (± SD) of dagaa in 1987 was 1073 ± 313 eggs (n = 22). However, Okedi (1974) reported fecundity of 2282 ± 1065 (n = 36) for the period between 1970 and 1974. The difference was significant (Mann-Whitney U-test; $p < 0.01$). This could be a result of dwarfism since a positive correlation exists between the size of dagaa and absolute fecundity.

Breeding

R. argentea breeds throughout the year but with distinct peaks. The peak was reported in March in the Mwanza Gulf (Wanink 1998). Protracted breeding indicates that the species has a high capacity to replace itself.

4.3.4 Length Frequency Distributions

The modal lengths have been changing since 1970–2005 from 7 cm to 4.2 cm (Fig. 4.7). The decrease has been a result of increased fishing pressure, and reduction in somatic growth at the expense of reproductive expansion (Wanink 1998). A further decrease in the mean modal length of the population for the years 2002 and 2005 has also been observed (Nsinda Unpublished data).

4.4 The Nile Tilapia

4.4.1 Introduction

The Nile tilapia, *Oreochromis niloticus*, was introduced into Lake Victoria in the 1950s together with other non-indigenous tilapiines, including *Oreochromis leucostictus* Trewavas, *Tilapia zillii* Gervais and *Tilapia rendalii* Boulenger from Lake

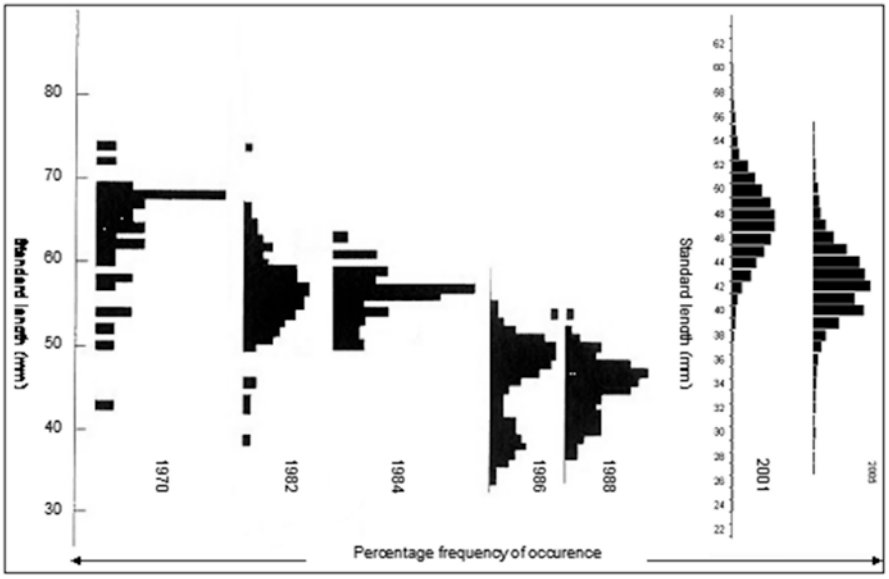


Fig. 4.7 Length frequency distributions of *R. argentea* (Source: Wanink (1991); for 1970–1988 data; Nsinda, unpublished data 2005). Dagaa were caught by gillnets in earlier years (1970–1988) and by fishers' nets in the years between 2001 and 2005

Albert (Welcomme 1968). The fish, however, had been introduced into the lake as early as 1930s (Lowe-McConnell 1958; Fryer and Iles 1972), but only established in the late 1960s (Welcomme 1968) along with the voracious predator Nile perch, *L. niloticus* Linnaeus. *O. niloticus* appeared in commercial catches in 1960 constituting less than 1% of the landings (Welcomme 1968). By 1965, it featured prominently in the commercial catches and currently it is the most commercially important tilapiine, whereas the native species of *O. variabilis* and *O. esculentus* have largely disappeared (Witte and van Densen 1995; Othina and Tweddle 1999). Currently, *O. niloticus* constitutes the third most commercially important fishery in Lake Victoria (Nunan 2014), after the introduced *L. niloticus* and the endemic cyprinid *R. argentea* Pellegrin.

4.4.2 Food

O. niloticus was predominantly a phytoplanktivorous and bottom feeder during the earlier stages of its colonisation of the lake (Welcomme 1968). However, later observations indicated that in Lake Victoria, the food of *O. niloticus* became more diversified and including *C. nilotica*, chironomids, chaoborids, molluscs and bottom detrital matter (Kaggwa et al. 2009) (Fig. 4.8).

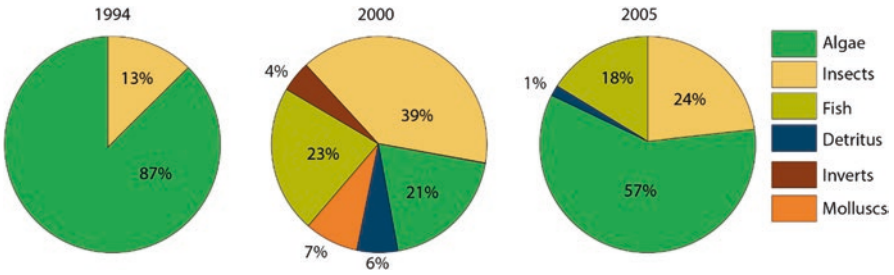


Fig. 4.8 Shifts in feeding habits of the Nile tilapia for the period of 1994–2005 (Data from Unpublished IFMP Report)

Njiru et al. (2004) found that the diet of *O. niloticus* varied with increasing size, although all size classes >5 cm TL consumed all important food items. Zooplankton (cladocerans and copepods) were the major food of *O. niloticus* under 5 cm TL, and were of little importance to fish larger than 15 cm TL. Insects were also of little importance to the diet of small *O. niloticus* (<5 cm), but were major food items of larger fish. Algae, fish and plant material were consistently important to all size groups below 55 cm TL. Fish <10 cm TL did not consume molluscs.

4.4.3 Fecundity

The fecundity of *O. niloticus* has increased from 340–3,706 eggs for fish of 17–57 cm TL (Lowe-McConnell 1958) to 864–6,316 eggs for fish of 28–56 cm TL (Lung'ayia 1994) to 1,240–6,600 eggs for fish of 27–56 cm TL (Chande and Mhitu 2005). The increase in fecundity could also be a mechanism to compensate for the intensive fishing pressure in the lake. In stable environments, fish put more effort into somatic growth as opposed to gonadal development. This tactic is more likely to increase their chance of survival and reproduction in subsequent years (Cowx 1998).

4.4.4 Length Frequency Distributions and Size at First Maturity

The percentage frequency distributions over the years are shown in Fig. 4.9. Time series data on the population characteristics of the species is very scanty on the Tanzanian side. However, trawl data for the years 1984–2002 indicates an increase in the proportions of relatively bigger fishes despite the heavy fishing pressure because of increased demand in local and foreign markets. The success of the species to sustain the fishing pressure could be due to the ability of the species to expand the food range (Njiru et al. 2004). This is further supported by the increase

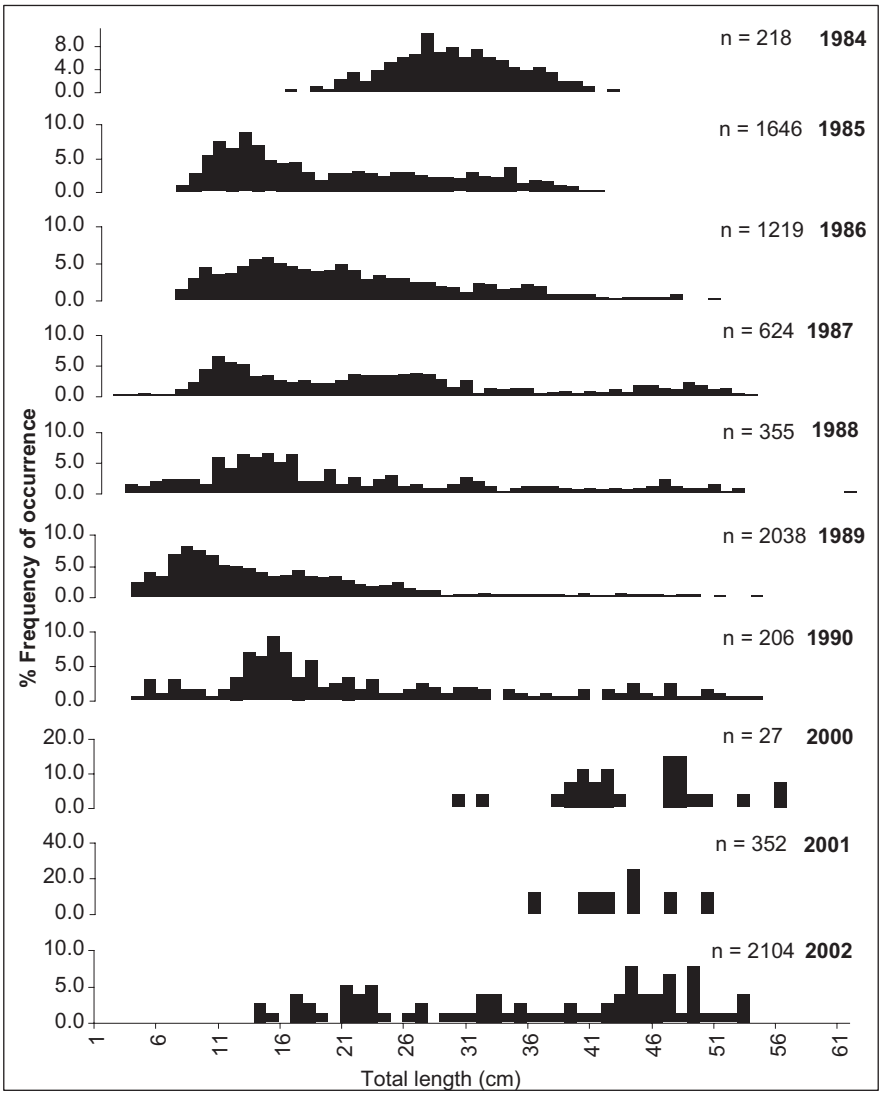


Fig. 4.9 Shifts in feeding habits of Nile tilapia for the period of 1994–2005 (Data from Unpublished IFMP Report)

in the growth curvature K for various years as follows: 0.25 for 1985–1986 (Getabu et al. 2002), 0.35 for 1980–1990 (Dache 1994), 0.56 for 1988–2000, all in Kenyan waters (Njiru 2003). It can also be said that the increase in fishing effort on the Tanzanian part of the lake might possibly explain the decrease in the size at first maturity of the *O. niloticus* in Lake Victoria (Fig. 4.10).

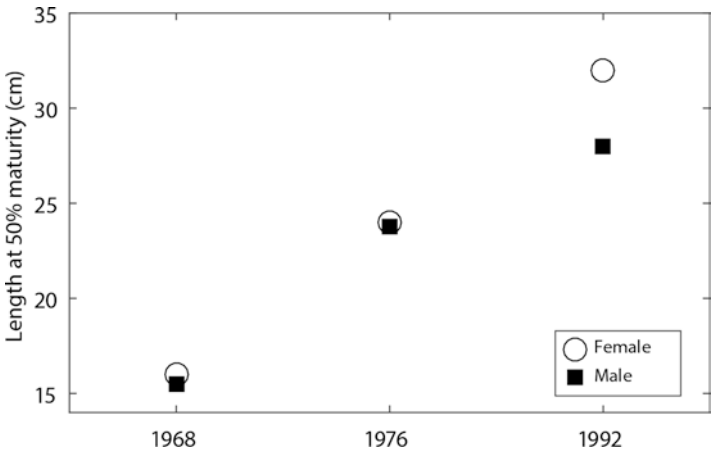


Fig. 4.10 Length at 50% maturity for *O. niloticus* (For 1968 fish length measured as SL (cm), the rest as total length) (Sources: 1968: Welcomme (1968); 1976: Wanjala and Marten (1976); 1992: Ogari and Asila (1992))

4.5 Conclusions

The data on important life history indicators (e.g., length at maturity; growth and mortality estimates; length-frequency data; trophic interactions; spatial and temporal distribution, and fecundity) for the three commercially important species is sparse and does not form a long-term series to facilitate definitive conclusions about the resources. However, the intervention by LVEMP and (to a large degree) LVFRP has provided some data and information, which form the basis for the following concluding points on the Nile perch:

- The batho-spatial distribution pattern exhibited a decline in Nile perch stock abundance with depth, an indication of a reduction in aerated habitats as a result of eutrophic conditions.
- The Nile perch disrupted the ecosystem by simplifying the food web through the elimination of haplochromines from many interactions, leading to shortening of food chain.
- Feeding habits of the Nile perch have changed concomitantly with faunal changes in the lake.
- The size at first maturity of the Nile perch exhibited a falling trend. This drop could be attributed to an increase in fishing pressure, changes in food availability and the lake environment.

4.6 Recommendations

- There is a need to make further investment in studies leading to a better understanding of the lake environment so that the factors driving diversity, abundance and community structure are identified. This is important because there is a strong link between fish productivity and the health of the ecosystem.
- The heavy exploitation of the Nile perch can be alleviated through the imposition of closed seasons and/or closed areas. These management options are difficult to implement because of scarce knowledge on the spawning behaviour, breeding and nursery areas. As such, there is a need to conduct thorough investigations on the ecology of the Nile perch in the Tanzanian part of Lake Victoria as precursor to the implementation of these management measures.
- Further studies are required to generate adequate knowledge on lower trophic levels especially the contribution of cyanobacteria, zooplankton, and macroinvertebrates to the biological productivity of the lake.
- On the basis of existing inadequacy of information on the biotic and abiotic environments within Lake Victoria, there is a need to manage the lake resources guided by the precautionary principle, and to continue analysing existing data and monitoring life history indicators.

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