Causes and effects of the Lake Victoria ecological revolution

Goudswaard, Pleun Cornelis

CHAPTER 7

Decline of the African lungfish (*Protopterus aethiopicus*) in Lake Victoria (East Africa)

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Abstract

Catch and effort data for the period 1973-1990 demonstrate a dramatic decline of lungfish in the Tanzanian waters of Lake Victoria. Bottom trawl catches in the Mwanza Gulf showed a decline in catch rates from 67.5 kg h^{-1} in 1973 to 5.5 kg h^{-1} in 1986. Trawling of commercial vessels in the Speke Gulf revealed a decline in lungfish catches from 1.3 kg h^{-1} in 1986 to 0.07 kg h^{-1} in 1990. The development of anoxia in the deeper waters of Lake Victoria, the algal blooms, and the decline of water transparency, all associated with eutrophication, are not likely to have contributed to the decreased catch rate. However, the lungfish decline may reflect the interaction of over-exploitation by the fishery and a low level of Nile perch predation that restricts lungfish to wetland refugia. We suggest that this may have been reinforced over the past few decades by large-scale conversion of wetlands to agricultural land and harvesting of nest-guarding male lungfish leading to decreased recruitment of young.

Introduction

The four species of African lungfish of the genus *Protopterus* are well-known as obligatory air breathers and for their ability to survive temporary, and sometimes extended, desiccation of their habitat (Smith, 1931; Johnels & Svensson, 1954; Curry-Lindahl, 1956; Greenwood, 1986). The African lungfish tend to inhabit shallow inshore waters, including the dense interior of swamps and marshes, although larger individuals can be found offshore in some lakes, such as Lake Victoria (Johnels & Svensson, 1954; Curry-Lindahl, 1956; Greenwood, 1966; Greenwood, 1986; Chapman et al., 1996). Their snake-like appearance and the strong taste of their flesh, places them in a particular category for fishermen and consumers. In the

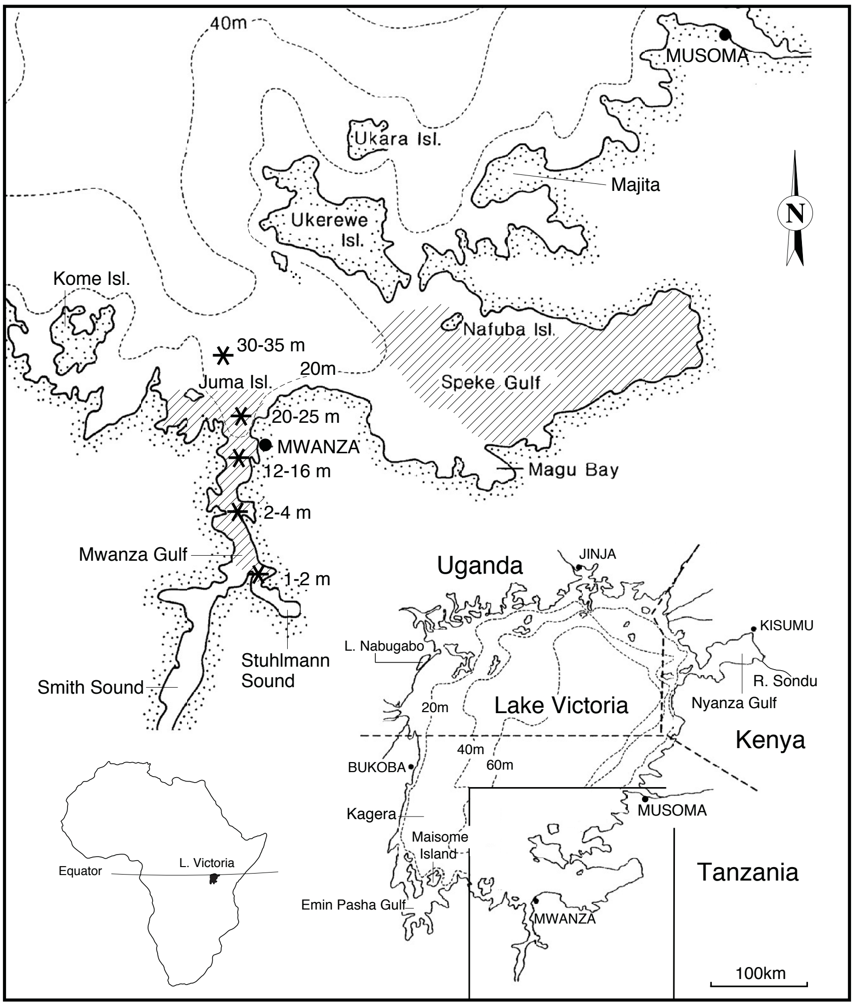

Fig. 7.1. *Study sites in Lake Victoria. Asterisks indicate the 5 sampling stations of MV Kiboko. Hatched areas in the Mwanza Gulf indicate fishing areas of MV Mdiria. Hatched areas in the Speke Gulf indicate a commercially trawled area.*

Lake Victoria basin, the African lungfish, *Protopterus aethiopicus* Heckel (1851), is locally either highly appreciated or strongly disliked. For example, for the Luo, who live south of the Nyanza Gulf (Fig. 7.1), the lungfish was particularly popular as a food fish (Graham, 1929; PCG, pers. obs.) and in Lake Nabugabo, Uganda, the lungfish contributed most to the biomass of the fish landed in the 1960s (Cambridge Nabugabo Biological Survey, unpubl. obs.). In contrast, the Sukuma, who live around the Mwanza and Speke Gulf dislike this fish.

Fishing for lungfish in Lake Victoria has been practised for a long time. However, a limited number of specialised fishermen targeted this species. Until the 1950s, the primary species exploited by most fishermen was the tilapiine cichlid *Oreochromis esculentus* (Graham, 1929). Gillnets and long lines for lungfish were placed along the lakeshore, close to the vegetation zone, mostly papyrus stands, where the best catches were made. In the long line fishery, hooks were baited with the flesh of freshwater mussels or haplochromines.

Lungfish were usually sold as sun-dried products. Both in 1928 (Graham, 1929) and in the early 1980s (PCG, pers. obs.) catches comprised only a few fish per fisherman per night. Storage of dried lungfish enabled the fishermen to collect sufficient fish to make a deal with a trader who transported the dried product to market. From the southern coast of the lake between Speke and Emin Pasha Gulf, almost all of the dried lungfish was transported to Kenya and the area north of Musoma town where the Luo people live (PCG, pers. obs.). This type of fishery, without central landing and trading places, makes the collection of catch statistics for lungfish difficult. However, a lake-wide decline in the lungfish landings between 1970 and 1990 was detected (Ogutu-Ohwayo, 1990a; Ochumba, 1995).

The upsurge in the1980s of the introduced piscivorous Nile perch, *Lates niloticus* (Linnaeus, 1758) coincided with dramatic changes in the species composition of Lake Victoria (Ogutu-Ohwayo, 1990a; Witte et al., 1992b; Goudswaard & Witte, 1997). Fisheries over-exploitation (Cadwalladr, 1965; Fryer & Iles, 1972; Witte & Goudswaard, 1985) and eutrophication (Seehausen et al., 1997a; Wanink et al., 2001) also contributed to these changes. In this study, we analyse bottom trawl catches from the period 1973-1990 in southern Lake Victoria to quantify the degree of the decline in lungfish. We discuss the possible impacts of Nile perch predation, over-exploitation and environmental changes on the lungfish stock.

Material and methods

Sources of information can be divided into four categories:

1. Data of commercial operating bottom trawlers were used: (i) MV Mdiria (120 hp, trawl headrope 25 m, codend mesh 20 mm [mesh sizes throughout the paper refer to stretched meshes]) of the Freshwater Fisheries Training Institute Nyegezi, aimed at haplochromine cichlids in the Mwanza Gulf (Fig. 7.1) at depths of 4-18 m. Data were available from 1973-1986. (ii) Three trawlers (58 hp, trawl headrope17 m, codend mesh 70 mm) aimed at Nile perch in the Speke Gulf (Fig. 7.1) at depths of 10-20 m. Data from these ships were available from 1986-1990 and were cross-checked at intervals by measuring the complete catch. In both cases, trawl shots generally lasted 2 hours. *P. aethiopicus* was bycatch.

2. Data from 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. From October 1984 until July 1990, five stations in the Mwanza Gulf (Fig. 7.1), with soft mudbottoms and depths ranging from 1-2 m in the south to 35 m in the north, were sampled on a monthly basis.

3. Data collected with long lines and gillnets (3500 and 400 mesh) by the East African Freshwater Fisheries Research Organization (EAFFRO) during the period 1973-1975 in the Tanzanian part of Lake

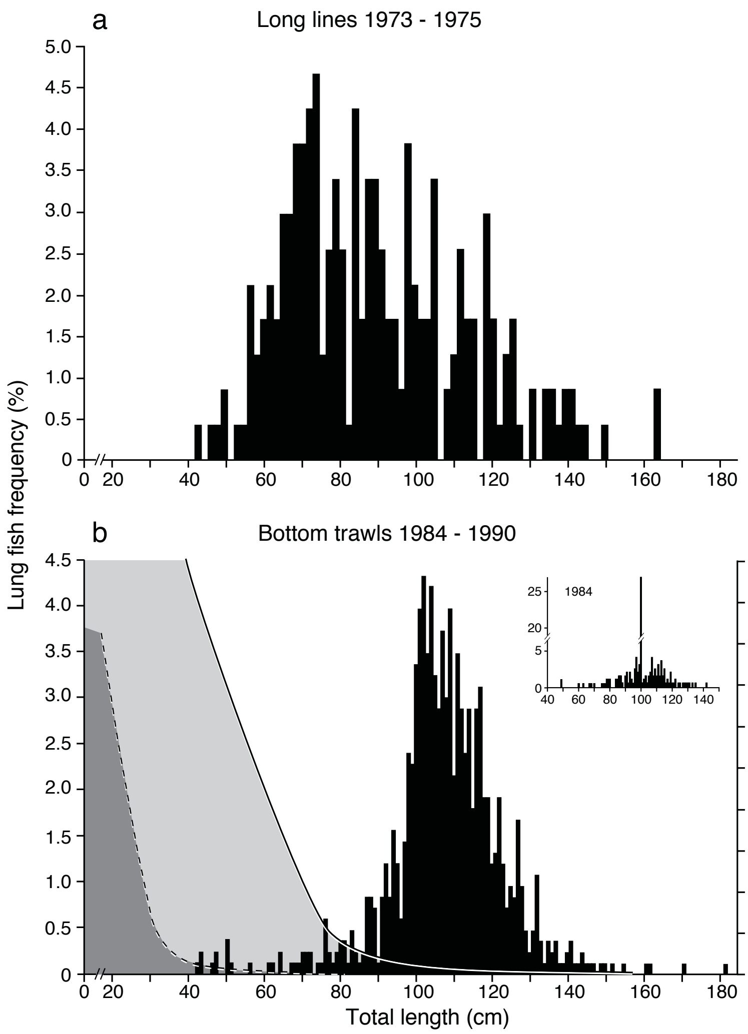

Fig. 7.2. *Length frequency distribution of lungfish: a) in long line catches in the Tanzanian waters from 1973-1975 and b) in trawl catches of MV Kiboko at 5 stations in the Mwanza Gulf during 1984-1990. The percentage of Nile perch, caught during 1984-1990, able to swallow lungfish of a particular length based on mouth gape of Nile perch is indicated by the shaded area under the solid line. The dark shaded area under dotted line indicates the percentage of Nile perch able to swallow lungfish of 50% of their own length. Inset: length frequency distribution of lungfish before the Nile perch increase in 1984.*

Victoria. The length frequency distribution from 1973-1975 (Fig. 7.2a) is based upon the long line data, because long lines are less size selective than gillnets.

4. Data collected with metal minnow traps (6.3 mm mesh) and gillnets (25.4,50.5 and 76.2 mm mesh) from 1995-1999 during surveys of twelve small swamp lagoons, deep in the interior of Lwamunda Swamp surrounding Lake Nabugabo (Fig.7.1), a satellite lake of Lake Victoria. The lagoons are separated from the main lake by 150-3000 m fringing swamp, and grade into the *Miscanthidium violaceum* dominated wetland. Seines and dip nets were used to qualitatively sample edge areas.

In the present study, the length of lungfish was measured as total length (TL) in centimetres. No correction was made for damaged tail tips, because missing parts were relatively small. Of fish collected by EAFFRO in 1973-1975, anal length (AL in centimetres; distance from the tip of the nose to the anal pore) was recorded. This was

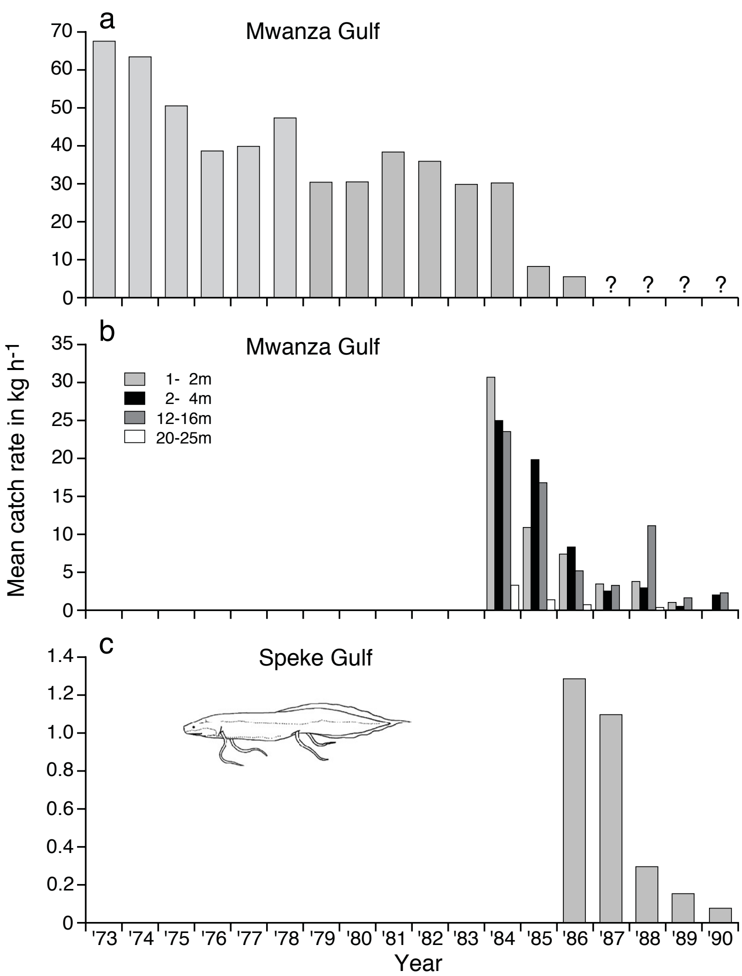

Fig. 7.3. *Lungfish catches in bottom trawls of:*
a) MV Mdiria in the Mwanza Gulf from 1973-1986 with 20 mm codend mesh,
b) MV Kiboko in the Mwanza Gulf from 1984-1990 with 20 mm codend mesh,
c) Commercial trawlers in the Speke Gulf from 1986-1990 with 70 mm codend mesh. Note the different scales on the Y-axes.

converted to TL by: TL = 1.75 AL - 0.08 (N= 27; R^2 = 0.9745).

We estimated relative vulnerability of lungfish to Nile perch predation by relating maximum body depth of lungfish to the mouth gape of Nile perch. The mouth gape (MG) of Lates niloticus is related to its total length: MG = 0.112 x TL + 0.43 (Ligtvoet & Mkumbo, 1990 -transformed to centimetres). Body depth of lungfish was calculated from maximum girth (G in centimetres) by considering the fish circular in cross-section (G= 2πR). We used girth-length relationship: G = 0.565 x AL - 1.642 (Witte & de Winter, 1995). To calculate the fraction of Nile perch able to swallow lungfish of a certain size, we used all Nile perch above 25 cm TL, caught between 1984 and 1990 at the four shallowest stations in the Mwanza Gulf (Fig. 7.1). For Nile perch greater than 25 cm, fish often constitutes a major part of the diet (Hamblyn, 1966; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b).

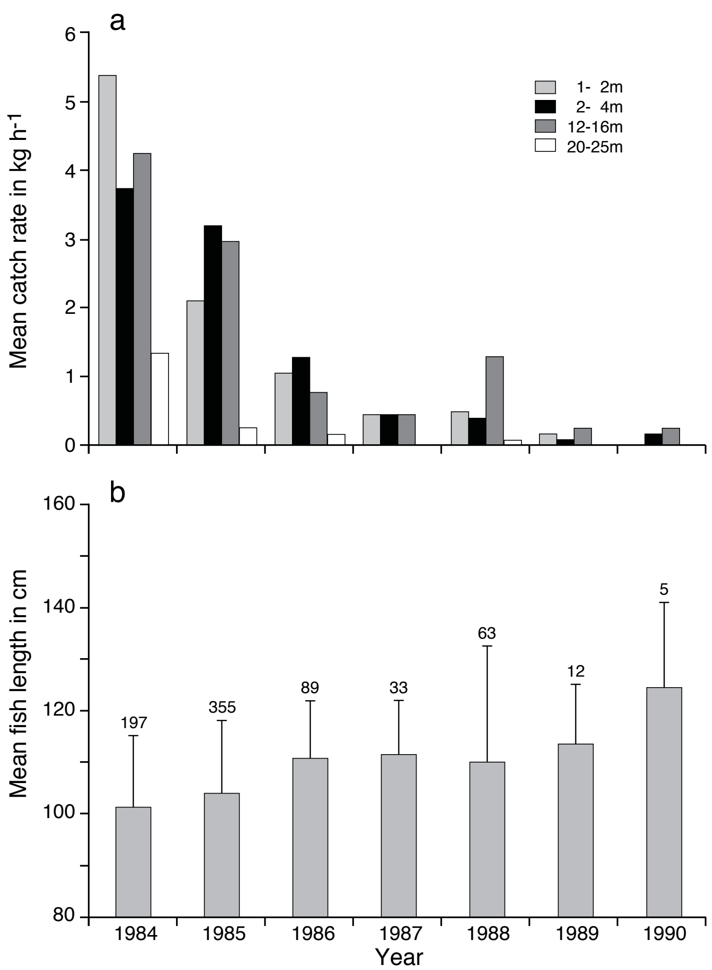

Fig. 7.4.
a) Decrease in number of lungfish at different stations and b) increase of average lungfish length at all stations combined, in trawl catches of MV Kiboko in the Mwanza Gulf from 1984-1990. Error bars indicate standard deviation.

Results

Bottom trawl catches by M.V. Mdiria in the Mwanza Gulf showed a decline in lungfish catch rates from 67.5 kg h^{-1} in 1973 to 5.5 kg h^{-1} in 1986 (Fig. 7.3a). Catches of MV Kiboko from 1984 to 1990 in the same area revealed that lungfish continued to decline (Fig. 7.3b). Trawling of commercial vessels in the Speke Gulf revealed a decline in lungfish catches from 1.3 kg h^{-1} in 1986 to 0.07 kg h^{-1} in 1990 (Fig. 7.3c).

Bottom trawling at the two deepest stations in front of the Mwanza Gulf, 30-35 and 57 m deep, did not produce any lungfish. Most fish were captured in the gulf, at the three stations shallower than 16 m, while at the 20-25 m deep station, considerably less lungfish were caught (Fig. 7.4a). Large Nile perch showed a complimentary distribution. Between 1984 and 1990, large Nile perch were most abundant in deeper waters

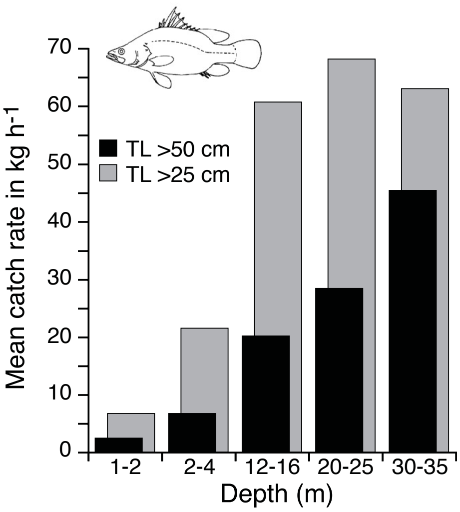

Fig. 7.5. *Mean catch rate of Nile perch >25 and >50 cm TL in bottom trawls of MV Kiboko (1984-1990) at different stations in the Mwanza Gulf.*

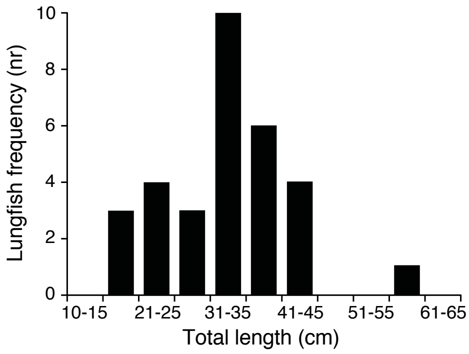

Fig. 7.6. *Length frequency distribution of lungfish caught in Lwamunda Swamp from 1995-1999 with minnow traps and gillnets.*

(Fig. 7.5). A strong decline of lungfish catches with increasing depth was also observed during a trawl survey in1969-1970 (Kudhongania & Cordone, 1974a,b). While the number of lungfish decreased during the years1984-1990 (Fig. 7.4a), the average size increased gradually at all sampling stations in the Mwanza Gulf (Fig. 7.4b; ANOVA $P < 0.000$; Pearson correlation for means $R= 0.9115$, $P= 0.0043$).

The length frequency distribution of all lungfish caught by MV Kiboko in the Mwanza Gulf during 1984-1990 ranged from 42-186 cm, 90% of the lungfish were between 90 and 130 cm (Fig. 7.2b). The length frequency distribution of lungfish from the long line fishery in 1973-1975 ranged from 42 to 164 cm with 90% of the fish between 56 and 126 cm (Fig. 7.2a). In 1974, gillnet fishermen caught fish from 45-72 cm (N= 63) with 88.9 mm (3500) mesh nets and from 44-93 cm (N= 45) with 101.6 mm (400) mesh nets.

Lungfish smaller than 40 cm, are very rare in open waters of Lake Victoria (Fig. 7.2). This is supported by data from a satellite of Lake Victoria, Lake Nabugabo. Data from the Lwamunda Swamp surrounding the satellite Lake Nabugabo (Fig. 7.1) suggest that smaller lungfish are most abundant within the fringing swamp. The length of lungfish from traps and gillnets in swamp lagoons of the Lwamunda Swamp during 1995-1999 ranged from 18 to 60 cm with 90% of the fish being between 20 and 45 cm TL (Fig. 7.6). Small lungfish (<10 cm) were dip netted and seined from within the dense *Miscanthidium* vegetation, whereas lungfish greater than 20 cm were more common in the edge areas of the lagoons. Similar observations were made by Graham (1929) and Greenwood (1966), for other parts of Lake Victoria.

Plotting cumulative frequency distributions of Nile perch with a mouth gape that could swallow a lungfish of a certain length (based on its maximum girth), revealed that a relatively small fraction of the lungfish were vulnerable to Nile perch predation in the area fished by trawlers during 1984-1990 (Fig. 7.2b). It seems like a much larger percentage would have been available to Nile perch in the 1973-1975 period (Fig. 7.2a), prior to the upsurge of the predator. However, long lines that are normally used in shallower areas caught these fish.

Discussion

Bottom trawl catches in the Mwanza and Speke Gulfs confirm the decline of lungfish indicated by commercial landing records of the three riparian countries of Lake Victoria (Ogutu-Ohwayo, 1990a; Ochumba, 1995). In the Mwanza Gulf, which was monitored most intensively during the longest period, catches dropped an order of magnitude between 1973 and 1990. This decline may reflect the impact of the fisheries, the impact of Nile perch, decline in food abundance, and/or habitat deterioration.

Impact of the fisheries

Lungfish smaller than 40 cm TL, were rarely encountered in trawl catches and in any of the catches with other gear in open waters (Okedi, 1971a; Mosille & Mainoya, 1988). Graham (1929) recorded a size range of lungfish from 61 to 126 cm in the lake and noted that small fish were rarely caught outside vegetated zones. Juvenile lungfish (5-30 cm), were found in matted roots of papyrus, and may be limited to these habitats (Graham, 1929; Greenwood, 1966). Our results indicate that the smallest individuals (<10 cm) live primarily within the dense mats of wetland vegetation, fish of 20-40 cm are also most abundant within the swamps, particularly swamp lagoons; whereas fish larger than 40 cm predominantly occur in the main lake.

The size at first maturity during the 1980s in the Mwanza Gulf was 65-75 cm for males and 75-85 cm for females (Mosille & Mainoya, 1988). Greenwood (1958) found first sexual maturity of females between 65 and 70 cm during the 1950s. The percentage of immature lungfish (<70 cm) in the catches was 22% in the 1973-1975 period, and therefore may have contributed to a modest reduction in stock recruitment. However, between 1984 and 1990, immature fish represented only 2% of the catch, and therefore stock recruitment over-fishing was negligible during this time period. Except in the Nyanza Gulf (CIFA, 1982), the specialised fishery on adult lungfish was probably not intensive enough to explain the lake-wide decline of the lungfish stocks, although it may have contributed locally to the decline. Bottom trawling for haplochromines in the Mwanza Gulf included considerable quantities of lungfish until the first half of the 1980s (Kudhongania & Cordone, 1974a; Goudswaard, 1988), and certainly could have impacted lungfish stocks. However, the decline in the Mwanza Gulf continued after 1987, when commercial trawling in this area was abandoned. Thus, trawling cannot be responsible for the decline during this period. This conclusion is supported by low catch rates (c.1.3 kg h^{-1}) in the Speke Gulf in 1986 compared to the catch rates of 24.4 kg h^{-1} in 1971 in the same area (Kudhongania & Cordone, 1974a), whereas here the commercial trawl fishery only started in 1986.

Impact of the Nile perch

Habitat overlap of haplochromine cichlids, catfish, and the cyprinid *Rastrineobola argentea* (Pellegrin, 1904) with Nile perch, was one of the major factors determining if, and at what speed, population densities declined after the Nile perch boom (Wanink, 1991; Witte et al., 1992b; Goudswaard & Witte, 1997). There is little habitat overlap between juvenile lungfish and Nile perch. Juvenile lungfish, up to 40 cm, occur primarily in swamps and swamp lagoons, which are less frequently used by Nile perch because of reduced oxygen availability and structural complexity (Schofeld & Chapman, 1999, 2000). Therefore, Nile perch predation on juvenile lungfish seems negligible. This is supported by stomach content data on Nile perch of a size most likely to consume small lungfish from lakes Victoria, Kyoga and Albert (Ogutu-Ohwayo, 1994) and Lake Nabugabo (Ogutu-Ohwayo, 1993, 1994; Schofeld & Chapman, 1999).

Nile perch greater than 25 cm TL feed to a large extent on fish (Hamblyn, 1966; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b). Piscivorous fish are generally gape-limited predators (Hambright, 1991; Brönmark & Miner, 1992). Based on mouth gape data, a Nile perch of 25 cm could theoretically swallow a lungfish of 40 cm, and the largest Nile perch encountered in the Mwanza Gulf (161cm TL) should be able to swallow a lungfish of 185 cm. However, this is a very conservative estimate because: (i) the cross-section of lungfish is not circular (see Material and methods); its body is deeper than wide, implying that our calculations, based on mouth gape, overestimate the size of the lungfish that can be swallowed. Moreover, piscivores tend to feed on prey that are smaller than the maximum size possible (Gillen, Stein & Carline, 1981; Hambright, 1991; Brönmark & Miner, 1992). (ii) Nile perch of >25 cm are predominantly caught at depths of more than 12 m and the highest numbers of Nile perch of >50 cm are caught at depths of more than 20 m, where lungfish are less abundant. (iii) The estimate, based on mouth gape, would enable Nile perch to swallow lungfish above its own length. This is unlikely, even though their eel-like body may curl up more easily than that of most other fish. The maximum fish prey size ever recorded for Nile perch approaches 50% of its own length (Ogari & Dadzie, 1988). However, most studies indicate a prey body-length to predator body-length ratio of 20-35% (Hamblyn, 1966; Gee, 1969; Okedi, 1971b). Using the upper limit of 50% of prey to predator body-length implies that the largest Nile perch in the Mwanza Gulf could swallow a lungfish of 80 cm. Consequently, most Nile perch are probably too small to feed on the available size of lungfish in the main lake (Fig. 7.2b).

Diet data on Nile perch support the idea that they do not feed intensively on large lungfish. Stomach investigations of hundreds of Nile perch in southern Lake Victoria revealed only two adult lungfishes (PCG, pers. obs.), each eaten by a Nile perch of more than 100 cm. In Lake Kyoga, lungfish is eaten in small quantities by large (>120 cm) Nile perch (Ogutu-Ohwayo, 1990b). In the Nyanza and Mwanza Gulf, lungfish was reported as rare in Nile perch stomachs (Ogari & Dadzie, 1988; Mkumbo & Ligtvoet, 1992).

Comparing the length frequency distribution of 1984 with the data from 1984 to 1990 collected with the same gear in the same areas of the Mwanza Gulf, shows that 40-80 cm lungfish were already rare in 1984 before the Nile perch increased (Fig. 7.2b). This indicates that the length frequency distribution as observed in the Mwanza Gulf has not been strongly affected by Nile perch predation.

Summarizing, an effect of Nile perch predation on the lungfish stocks cannot be excluded, but evidence suggests that it cannot alone account for the decline in lungfish catches. However, it is possible that Nile perch predation pressure on the few small individuals that venture out of the wetlands and on the occasional large lungfish may reinforce use of wetland refugia. In addition, Nile perch predation in the early1980s when the upsurge began may have contributed to the shift in size distribution observed by 1984 (compare Fig. 7.2a with inset in Fig. 7.2b). Although, as explained above, habitat differences could also account for this.

Impact of food abundance

The diet of adult and sub-adult lungfish consists primarily of molluscs, mainly the gastropods of the genus *Bellamya* and *Melanoides* (Corbet, 1961). These snails were abundant in the shallow waters of Lake Victoria (Okedi, 1990). In the second half of the 1980s, an increase in *Bellamya* was noticed during bottom trawling in shallow waters of Mwanza Gulf, and these snails then often formed the bulk of the catch (PCG, pers. obs). This increase may reflect a decline in the amount of molluscivorous flesh in the lake (Witte et al., 1992a). In the same period, mass snail mortalities were observed in the deeper parts of Speke and Mwanza Gulf, which may have been caused by deoxygenation of deeper water layers (Kaufman, 1992; Hecky, 1993; Wanink et al., 2001). Despite these mass kills, *Bellamya* remained very abundant in the habitat of large lungfish, and it is unlikely that food shortage has played a role in the lungfish decline.

Impact of habitat deterioration

Over the past three decades many dramatic environmental changes have occurred in Lake Victoria. Most striking have been an increase in algal blooms, a decrease in water transparency, and a decrease in dissolved oxygen concentration in deeper waters (Ochumba & Kibaara, 1989; Kaufman, 1992; Witte et al., 1992a; Hecky, 1993; Mugidde, 1993; Wanink et al., 2001). However, due to the dependence of lungfish on atmospheric oxygen, their ability to live in swamps, and their reliance on non-visual cues for feeding (Greenwood, 1986) the lungfish is one of the few fish species not likely to be affected by these environmental changes.

Deterioration of the lungfish breeding-habitat may be a key environmental factor affecting the lungfish population. The lungfish performs parental care in which the male prepares a nest in a pit or a hole, where he guards the eggs and young for nearly 8 weeks (Greenwood, 1958, 1966; 1986). More than one female may spawn in a nest. The nature of the nest is variable, including nests excavated in matted roots of papyrus, among plants in shallow grass-swamps, and in the sand beneath a fallen tree (Greenwood, 1958, 1966; 1986). However, in general most nests seem to occur in wetlands.

The human population bordering Lake Victoria is among the densest in East Africa and shows an annual growth of 3.8% (Bootsma & Hecky, 1993). To feed this population, large strips of swamp near the lakeshore and along inflowing rivers have been converted to agriculture (Balirwa, 1998). These cultivated areas usually reach the water where all vegetation is cleared; making these places unsuitable for lungfish to breed. However, this may not be the only explanation for the decline of lungfish because the species declined dramatically in Lake Nabugabo (Ogutu-Ohwayo, 1993; Chapman et al., 1996), without coincident loss of wetland (LJC, pers. obs.).

Between 1982 and 1990, we found two nest guarding lungfish in the Mwanza Gulf area. Both nests were in disorder within a few days after discovery, apparently after being raided. Local farmers and fishermen told on several occasions that, when they discover a lungfish nest, the guarding fish is killed by club or spear and taken for food. Similar observations were made by Wasawo (1959), with respect to the dry season burrows. We tentatively suggest that exploitation of nest guarding fish, together with breeding habitat destruction, may have contributed to the population decline through decreased recruitment of young fish. This may also explain the increase in mean weight (ageing of the stock) of lungfish during the 1980s.

To summarise, catch and effort data (bottom trawl) for the period 1973-1990, demonstrate a dramatic decline of lungfish in the Tanzanian waters of Lake Victoria. In contrast to the decline of many other fish species in Lake Victoria, Nile perch predation may not have been a key factor contributing to the dramatic decline of the lungfish. In addition, the development of anoxia in the deeper waters of Lake Victoria, the algal blooms, and the decline of water transparency, are not likely to have affected the lungfish population in a negative way. However, the decline may reflect the interaction of local over-exploitation and a low level of Nile perch predation that restricts lungfish to wetland refugia. We suggest that this may have been reinforced over the past few decades by large-scale conversion of wetlands to agricultural land and harvesting of nest-guarding males leading to decreased recruitment of young lungfish.

Preliminary observations indicate some recovery of lungfish since 1997 (Bugenyi & v.d. Knaap, 1997). The authors attribute this modest resurgence to the extraordinary spread of water hyacinth (*Eichhornia crassipes*), which invaded the lake in 1989 (Njuguna, 1991). The extensive mats of this weed along the lake's shore extend ecotonal refugia, thus potentially increasing availability of lungfish habitat. However, if lungfish really benefit from the water hyacinth infestation of the lake, it is potentially short-lived, because a dramatic decline of water hyacinth has occurred through Lake Victoria since 1999.

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