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ORIGINAL PAPER

The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes

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Abstract Nile perch, a large predatory fish, was introduced into Lake Victoria in 1954. The upsurge of Nile perch in Lake Victoria was first observed in the Nyanza Gulf, Kenya, in 1979. In Ugandan waters this occurred 2–3 years later and in the Tanzanian Mwanza Gulf 4–5 years later. At the beginning of the upsurge in the Mwanza Gulf in 1983/1984 only sub-adult and adult fishes were found. The first juveniles appeared in 1985, suggesting that the initial increase of Nile perch was mainly caused by migration of sub-adults and adults. Shortly after the onset of trawl fishery in the area in 1973, haplochromines in the Mwanza Gulf started to decline. The final disappearance of the haplochromines, in 1987, only occurred after the Nile perch boom, and despite the abandoning of the haplochromine fishery in 1986. We hypothesize that the decline of haplochromines decreased predation on and competition with juvenile Nile perch and then facilitated survival of these juveniles. Consequently the immigration of sub-adult and adult Nile perch in an area may have paved the way for successful recruitment. Over-exploitation of haplochromine cichlids in the 1970s in the Nyanza Gulf, where the Nile perch upsurge was first observed, may have played a similar role.

Keywords Species-introduction · Colonization · Extinction · Predation · *Caridina nilotica* · Haplochromine cichlids

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Introduction

Deliberate introductions of animals to areas outside their natural distribution, has taken place for centuries (Williamson 1996). However, within Africa, the transfer of fish species from one water system into another is a relatively recent phenomenon. Most species were transferred between the 1920s and 1970s with a peak (67 species) in the 1950s (Welcomme 1988). Worldwide, at least 237 fish species were transferred, of which the fate of 72 has been documented. Of these, 25 were harmful for the indigenous fauna and/or the local environment (Beverton 1992). The introduction of Nile perch, *Lates niloticus* L, into Lake Victoria is considered to belong to this last group

(Barel et al. 1985; Ogutu-Ohwayo 1990a; Kaufman 1992; Witte et al. 1992a, b).

Nile perch were unofficially introduced into Lake Victoria in August 1954, when individuals from Lake Albert were released at Jinja, Uganda (Amaras 1986). In May 1960, local fishermen reported the first Nile perch from gillnet catches near Jinja. Seven others were reported in the same year. The captured fishes were sub-adults with a size range of 28–43 cm (Hamblyn 1961).

After heavy debates (Fryer 1960; Anderson 1961; Pringle 2005), the first official introductions of Nile perch took place in May 1962 and September 1963 at Entebbe, Uganda. They originated from Lake Albert and comprised, respectively, 35 fishes between 16 and 43 cm, and 339 fingerlings (Gee 1964). In the Nyanza Gulf, Kenya, eight Nile perch from Lake Turkana were released in 1963 (Arunga 1981; Pringle 2005). During a bottom trawl survey in 1969/1970 Nile perch was caught lake wide in low densities (Kudhongania and Cordone 1974b). In the 1980s the species suddenly increased strongly, but not simultaneously, throughout the lake.

The effects of the Nile perch boom on the indigenous fauna of Lake Victoria, has been discussed in several publications (Barel et al. 1985; Hughes 1986; Acere 1988; Harrisson et al. 1989; Ogutu-Ohwayo 1990a; Kudhongania et al. 1992; Witte et al. 1992a, b; Goldschmidt et al. 1993; Bundy and Pitcher 1995; Kudhongania and Chitamwebwa 1995; Goudswaard and Witte 1997; Goudswaard et al. 2002a, b). Remarkably, the process by which Nile perch established itself successfully in Lake Victoria is an underexposed aspect in the whole discussion. In this paper we present data on Nile perch densities, length frequency distributions, the appearance of recruits, and the decline of the haplochromines during successive periods at different localities in Lake Victoria. Although the data sets from several areas are incomplete, to our knowledge they are the best available. With the aid of these data, we make an attempt to elucidate the process of colonization of Lake Victoria by Nile perch.

Material and techniques

In the Tanzanian waters of Lake Victoria fishing was done with MV Kiboko (105 hp, bottom trawl head rope 18 m, codend mesh 20 mm), which made trawl shots of half an hour. The sampling period ran from October 1984 until July 1990. Most frequently fished was the Mwanza Gulf, where 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 monthly (Fig. 1). The sixth station at a depth of 57 m (Fig. 1) was fished until the end of 1986. Quarterly samples were taken at: (i) Kagera—an open water area in the western part of the lake with a mud/clay bottom. Samples were collected at depths ranging from 4 m in the west to 48 m in the east. The shallow areas (<10 m) were restricted to Chigoga and Kemondo Bay as well as the area near Bukoba harbour. (ii) Speke Gulf—a large bay in the south-east corner of the lake with a soft muddy bottom and a depth ranging from 2 m in the east to 34 m in the west. (iii) The Emin-Pasha Gulf in the southwest corner of the lake was surveyed in 1985 and 1986. The area is up to 18 m deep and has a mud and sandy bottom. Directly north of this gulf the lake floor deepens to 48 m.

Information was also gathered from other vessels like: MV Mdiria (170 hp, trawl head rope 25 m, codend mesh 20 mm and 90 mm) fishing in the Mwanza Gulf and incidentally elsewhere; four boats of the Nyanza Fishing and Processing Company (NFPC) (170 hp, trawl head rope 21 m, codend mesh 90 mm) fishing in the Emin Pasha Gulf from November 1975 to August 1976; three trawlers (75 hp, head rope 17 m, codend mesh 70 mm) from a commercial company operating in the Speke Gulf. These boats started fishing in 1986 and records were available up to June 1990. For commercial reasons Nile perch was separated by the crew in small (<35 cm TL) and big (>35 cm) fishes. Data in this paper from other ships than MV Kiboko are based on catch records of the crews.

Catch records of Nile perch and haplochromines were standardized to kg h^{-1} for all vessels. Trawl data from Ugandan and Kenyan waters were obtained from literature (Table 1). The total length (TL) of Nile perch was measured and rounded to the nearest cm below.

Catch data were tested for normal distribution with a Kolmogorov-Smirnov Test. Most Nile perch catches were not normally distributed. Therefore, we used Mann–Whitney *U*-tests to test for differences in catch sizes between years

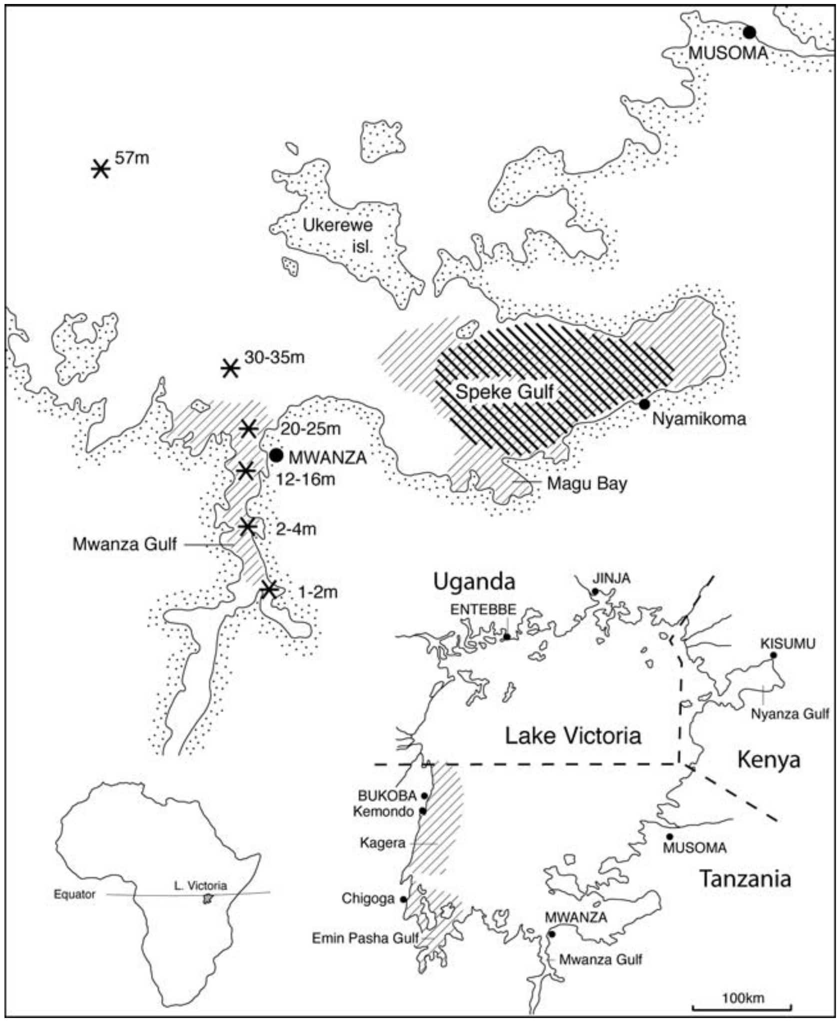

Fig. 1 Map of Lake Victoria with main fishing areas discussed in the present study. Hatched areas in the Mwanza Gulf were fished by MV Mdiria. Asterisks in the Mwanza Gulf were sampling stations of MV Kiboko. The hatched area in the Speke Gulf was fished by MV Mdiria and MV Kiboko. The double hatched area in the Speke Gulf was also fished by commercial trawlers. The hatched areas in the Emin Pasha Gulf and Kagera area were fished by MV Kiboko and before 1984 occasionally by MV Mdiria and trawlers of the NFPC (for details see ''Material and techniques'' section)

and for differences in catch sizes of different size groups. Sequential Bonferroni corrections were applied in case of repeated use of data. A correlation between mean monthly catch rates of Nile perch by commercial trawlers in the Speke Gulf and months was calculated. As mean monthly catch rates were normally distributed, the Pearson correlation test was used. All tests were done in SPSS10.0 for Windows.

Results

Nile perch appearance in the Tanzanian waters

In the early 1970s, Nile perch catches in the Mwanza Gulf were low (Fig. 2a, b). A slow increase was observed in the second half of the 1970s and the beginning of the 1980s. In 1983 a strong increase was noticed (Fig. 2a, b).

Most Nile perch caught in the Mwanza Gulf between 1977 and 1983 were adults or sub-adults (personal observation). The same was observed in bottom trawl catches from 1982/1983 (Fig. 3a) and from the last quarter of 1984 (Fig. 3b). In 1987 small fishes (1–20 cm) were abundant in the catches (Fig. 3c). Detailed observations on the increase of small Nile perch were collected at the station of 12–16 m deep in the Mwanza Gulf. In 1984 there were less small (1–10 cm TL) than medium and large sized Nile perch (21–50 cm and >50 cm; Mann–Whitney *U*-test, $P \leq 0.002$ in each case). The number of small sized Nile perch started to increase in 1985. In

Table 1 Mean catch rates (kg h^{-1}) of Nile perch and haplochromines in bottom trawl catches made in the Ugandan waters, the Nyanza Gulf (Kenya) and in four different areas in Tanzania

Year	Uganda		Kenya		Tanzania							
			Nyanza Gulf		Kagera		Speke Gulf		Mwanza Gulf		Emin Pasha Gulf	
	Hap.	Np.	Hap.	Np.	Hap.	Np.	Hap.	Np.	Hap.	Np.	Hap.	Np.
1969	327	+	440	1	610	+	–	–	548	0	–	–
1973	–	–	–	–	–	–	–	–	1235	0	–	–
1974	–	–	149	6	–	–	1294	0	1376	0	–	–
1975	–	–	–	–	308	0	1025	0	1365	1	–	–
1976	–	–	–	–	–	–		–	1915	1	–	–
1977	–	–	–	–	490	0	–	–	1165	1	540	+
1978	–	–	–	–	–	–	–	–	1095	1	–	–
1979	–	–	59	***46**	–	–	1005	0	1182	1	–	–
1980	–	–	–	–	–	–	–	–	709	4	–	–
1981	392	4	0	169	–	–	–	–	789	4	–	–
1982	298	**45**	0	169	–	–	–	–	682	4	–	–
1983	265	54	–	–	–	–	288	**101**	629	19	–	–
1984	114	140	–	–	–	–	–	–	290	**82**	–	–
1985	18	235	–	–	38	***146**	–	–	326	*103	108	***71**
1986	0	80	9	273	0	259	–	–	93	174	0	76
1987	–	–	–	–	0	244	–	–	4	203	–	–
1988	–	–	0	145	0	199	0	*224	0	115	–	–
1989	–	–	0	–	0	118	0	119	0	107	–	–
1990	–	–	–	–	–	–	0	163	1	133	–	–

Nile perch catches for the first time reaching values ≥45 kg h^{-1} (an arbitrarily chosen density) are given in bold. *indicates the first year that juvenile Nile perch ≤10 cm were observed; +indicates presence of low densities of Nile perch, without precise data for the records used. All 1969 data are from Kudhongania and Cordone (1974a, b). The Nyanza Gulf data are from Benda (1981), Okemwa (1981), Fisheries Department Nairobi Kenya (1988) and Ogari and Asila (1990). Data from Ugandan waters are from Acere (1988). Tanzanian data from 1973 till 1983 are from MV Mdiria and from 1984–1990 from MV Kiboko. Hauls made in 1969 and in Ugandan waters were made with trawlers ranging from 105–180 hp, utilizing conventional bottom trawls with head ropes of 18–25 m and 19 and 38 mm codend mesh. In the Nyanza Gulf, part of the catches was made with a 85 hp trawler, towing a net with a 13.7 m head rope. In this area mainly a 38 mm codend mesh size was used. Hap., Haplochromines, Np., *Lates niloticus*

1986 and 1987 densities of 1–10 cm Nile perches were significantly higher than in each of the previous years (Fig. 4a; Mann–Whitney *U*-test, $P = 0.000$ in each case). In the following years the densities fluctuated around the same level. From 1987 onwards the densities of 1–10 cm class Nile perch were significantly higher than the densities of all other classes (Mann–Whitney *U*-test, *P* values ranging from 0.000 to 0.027), with the exception of 1990, when the densities of the 21–50 and the 1–10 cm class did not differ significantly ($P = 0.055$).

In the Emin Pasha Gulf Nile perch catches showed a similar pattern as in the Mwanza Gulf (Fig. 4b). In 1973 and 1974 MV Mdiria, with a 60 mm codend mesh, for 74 h caught no Nile perch. Between November 1975 and August 1976, bottom trawlers of NFPC caught 6 large Nile perch with a total weight of 172 kg in 850 h. In 1977 MV Mdiria caught 28 kg Nile perch (possibly one individual) in 12 h trawling (2.3 kg h^{-1}), using either a 20 or a 90 mm codend mesh. In June 1985 MV Kiboko caught 71 kg Nile perch h^{-1} in the Emin Pasha Gulf (Table 1), with relatively few juveniles (1–10 cm TL, Fig. 4b). The densities of these juveniles did not differ significantly from those of other length classes. In August 1986 the numbers of juveniles had increased (Mann–Whitney *U*-test, $P = 0.000$) and were higher than those of large sized Nile perch (Mann–Whitney *U*-test, $P = 0.000$).

The Kagera area in 1985 and 1986 revealed similar densities of juvenile Nile perch as found in the Mwanza Gulf in the same years (Fig. 4a, c). The same held for the densities in the Emin Pasha Gulf in October 1985 and August 1986 (Fig. 4b).

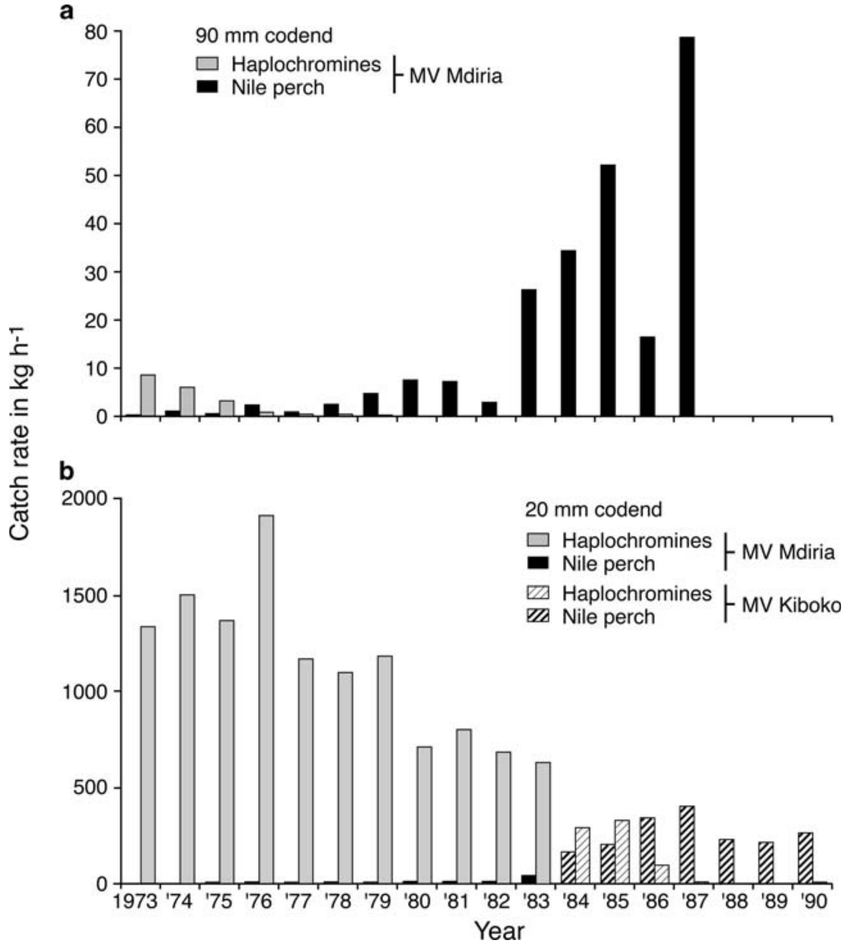

Fig. 2 Catch rates of Nile perch and haplochromines by bottom trawlers in the Mwanza Gulf. (**a**) 90 mm codend mesh during the period 1973 till 1987 (3875 h trawling); (**b**) 20 mm codend mesh during the period 1973–1990. The data from 1984 till 1990 (543 h trawling) for the 20 mm net are from MV Kiboko, all other data from MV Mdiria (2176 h trawling)

The average monthly catches of large Nile perch in commercial trawlers in the Speke Gulf, decreased over time (Fig. 5a, Pearson correlation test, $R = -0.513$, $P = 0.000$, $N = 58$), while the catches of small Nile perch increased (Fig. 5b, Pearson correlation test, $R = 0.812$, $P = 0.000$, $N = 58$).

Nile perch upsurge in Kenyan and Ugandan waters of Lake Victoria

In the Kenyan and Ugandan waters, a strong increase of Nile perch occurred earlier than in the Mwanza Gulf (Table 1). A Nile perch catch rate of 46 kg h^{-1} was observed in the Nyanza Gulf in 1979. Values ≥45 kg h^{-1} were first observed in the Ugandan waters in 1982 and in the Mwanza Gulf in 1984. Catches above 100 kg h^{-1} were reached 1 or 2 years later at each of these stations. Juveniles (<10 cm) were present in the Nyanza Gulf in 1979, while they appeared in 1985 for the first time in the Mwanza Gulf.

Nile perch and haplochromines

The catches of haplochromine cichlids in the Mwanza Gulf declined from the onset of their exploitation with bottom trawlers in 1973 (Fig. 2a, b). Large haplochromines (mainly piscivores > 17 cm SL) declined much faster than the smaller ones and by 1980 they had disappeared from the catches (Fig. 2a). The small species also declined, but at a much slower rate (Fig. 2b). Commercial exploitation of haplochromines ended in 1986. The trawl survey by MV Kiboko at five different depth zones in the Mwanza Gulf

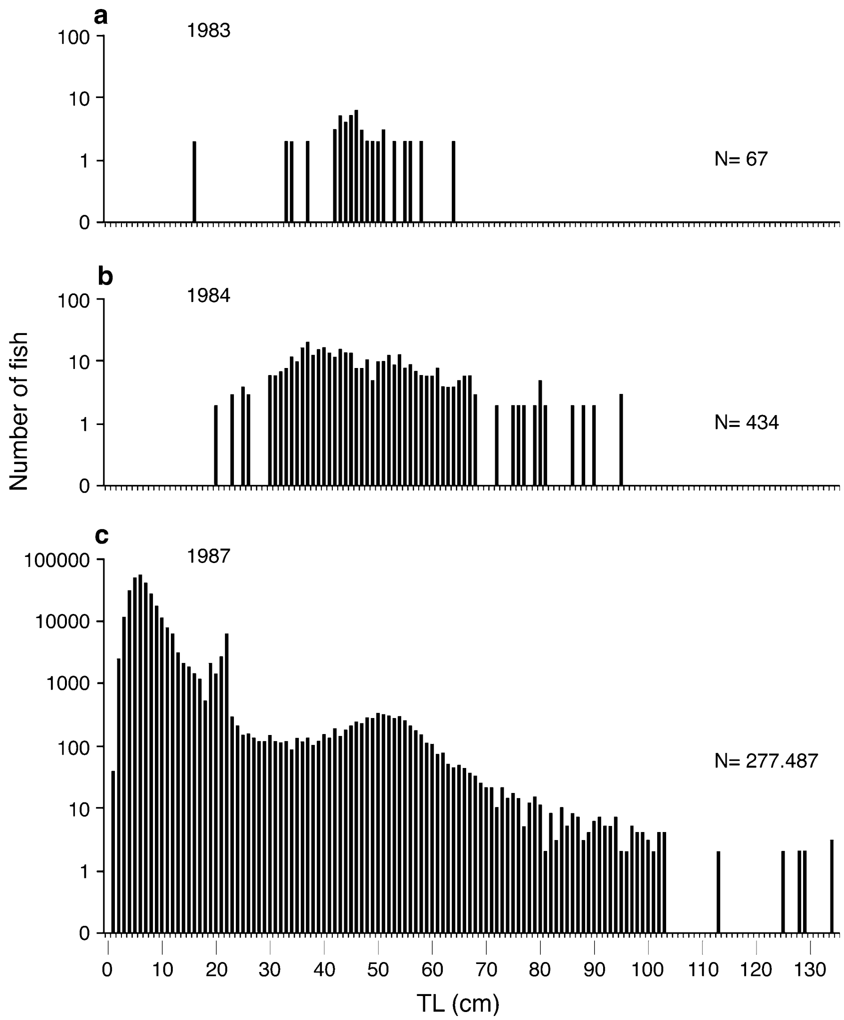

Fig. 3 Length frequency distribution of Nile perch in the Mwanza Gulf. (**a**) October 1982–April 1983, (*N* = 67); (**b**) October–December 1984, (*N* = 434); (**c**) January–December 1987 (*N* = 277 487). Catches from 1982–1983 were made with NFPC trawlers, those from 1984 and 1987 with MV Kiboko. Note log scale of the *Y*-axes

showed an increase in Nile perch catches and a concomitant decline of the haplochromines (Table 1, Fig. 6). This observation was also noted at other places in the lake (Table 1, Fig. 6). Between November 1975 and August 1976 NFPC trawlers with 90 mm codend mesh fished in the Emin Pasha Gulf for 850 h and caught on average 21.9 ± 7.9 kg h^{-1} large-sized haplochromines. In 1977 MV Mdiria made two hauls with 20 mm codend mesh, which contained an average catch of haplochromines of 540 kg h^{-1} (Table 1). Nile perch were also caught in this period (see above). In June 1985, both haplochromines and Nile perch were present in bottom trawl catches with MV Kiboko (Table 1, Fig. 6). Large haplochromines were rare. In October 1985 the stock of haplochromines in the 11–20 m deep zone had vanished (Fig. 6), while in the shallow water (1–10 m deep) only a fraction of the original stock was still present. In August 1986 catches of haplochromines had been reduced to a few individuals in both depth zones, resulting in weights that are not visible in Fig. 6.

In the Kagera area, we found haplochromines in all depth zones in the second quarter of 1985. After 1985 at Chigoga- and Kemondo Bay as well as near Bukoba harbour (all <10 m deep), we collected very small quantities (<<1 kg) of haplochromines in 3.5 h trawling. In the 11–20 m and 21–48 m zones that were fished 16.5 and 299 h, respectively, hardly any haplochromines were caught.

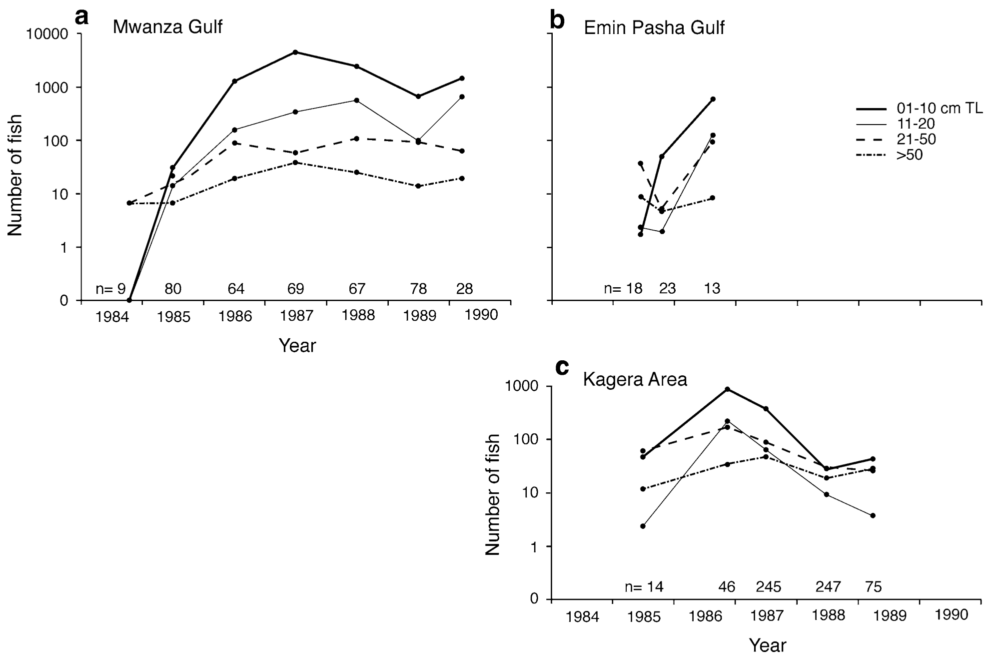

Fig. 4 Development of the number of Nile perches over time, in different size classes. (**a**) Mwanza Gulf (12–16 m deep) 1984–1990; (**b**) Emin Pasha Gulf (4–18 m deep) June1985–August 1986; (**c**) Kagera area (6–48 m deep) 1985–1989. *Note* log scale of the *Y*-axes. Numbers above *X*-axes indicate the number of trawl shots

Discussion

The colonization process

Around 400 Nile perch from Lake Albert (339 fingerlings and 35 fishes of 16–43 cm) were introduced into Lake Victoria (Gee 1964; Amaras 1986; Pringle 2005). Additionally, eight fishes of unknown size were introduced from Lake Turkana in 1963 (Gee 1964; Arunga 1981; Pringle 2005). Apart from *Lates niloticus*, each of these lakes harbours a deep-water *Lates* species, *L. macrophthalmus* Worthington 1929 and *L. longispinis* Worthington 1932, respectively. Allozyme data indicate that Nile perch of Lake Victoria were mainly *Lates niloticus* from Lake Albert, although there were indications for some genetic contribution of *L. macrophthalmus* (Hauser et al. 1998).

Although Nile perch was introduced in 1954, it was first reported from a catch of a fisherman in Uganda in May 1960 (Gee 1964). Several others were caught later that year. The eight fishes recorded in 1960 from the northeast corner of the lake, were 28–43 cm long (Hamblyn 1961). They were probably offspring of those introduced in 1954, as in 6 years time the introduced individuals would have attained a much greater length (e.g., Hughes 1992). According to Gee (1964) a breeding population existed in the lake in 1962/1963, probably centered in Hannington Bay and down the Buvumu Channel.

According to Pringle (2005), the first Nile perch reported from Tanzanian waters was caught near Mwanza in October 1961. Other reports suggest that Nile perch was landed for the first time from Tanzanian waters of the lake in August 1963 at Musoma (Kudhongania and Cordone 1974a). During a bottom trawl survey in 1969–1970 Nile perch was rarely caught in Tanzanian waters. Catches constituted approximately 0.01 kg h^{-1}, while the catches in Uganda and Kenya were 0.48 and 1.12 kg h^{-1}, respectively (Kudhongania and Cordone 1974a, b).

In the Nyanza Gulf the average catch rate of Nile perch was 46 kg h^{-1} as early as 1979. These catches contained all stages from early juveniles to adults. In contrast, in the Mwanza Gulf Nile perch catches above 45 kg h^{-1} were not observed

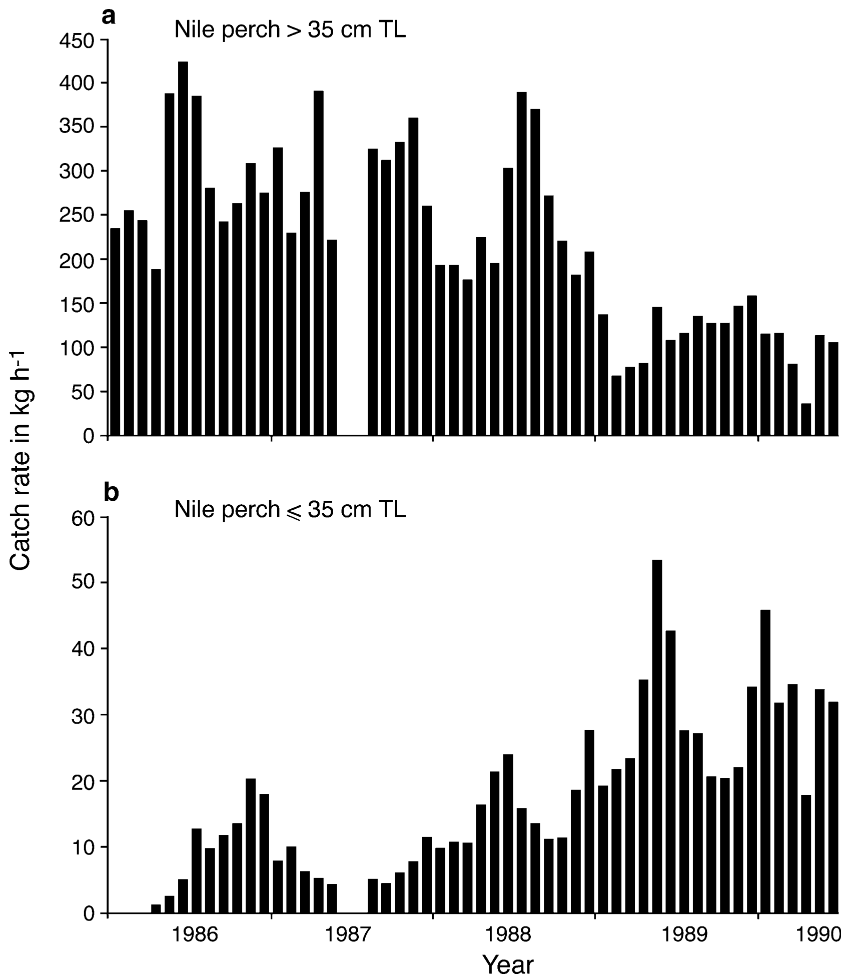

Fig. 5 Length frequency distribution of Nile perch caught by commercial trawlers in the Speke Gulf, based on 12 539 h of bottom trawling during the period 1986–1990. (**a**) large Nile perch > 35 cm TL; (**b**) small Nile perch < 35 cm TL

before 1984, and juveniles were first caught in 1985 (Table 1). Up to 1985, all Nile perch found in the Mwanza Gulf apparently had been born elsewhere. The length frequency distribution of Nile perch from trawl catches in 1983 and 1984 (Fig. 3) indicates that the strong increase in number of Nile perch in the Mwanza Gulf in 1983–1984 was caused by sub-adult fishes. It is most likely that these fishes arrived by immigration. In Ugandan waters and in the Speke Gulf, Nile perch catches around 45 kg h^{-1} were observed 1–2 years earlier than in the Mwanza Gulf, and 3 years later than in the Nyanza Gulf (Table 1). These observations suggest that Nile perch spread from the Nyanza Gulf towards the North and the South. Zaret and Paine (1973) described the spread of the introduced predator *Cichla ocellaris* in Lake Gatun in Panama. They note that 'the fish have not diffused haphazardly throughout the lake, but have moved as a wave, with a leading edge composed of sub-adults'. Though there are many gaps, our data suggest a similar process for Nile perch in Lake Victoria. A similar migration of sub-adults of an introduced predator fish, *Parachanna obscura* (Steindachner, 1879), was noticed in the upper course of the Zambian Congo River. Between 1996 and 1999 a migration from a local nucleus at the Luapula River towards Lake Mweru was observed (PCG unpublished data).

Although allozyme electrophoresis provided some indication for genetic differentiation of Nile perch within Lake Victoria (Hauser et al. 1998), preliminary results of a tagging program in the Mwanza region revealed that Nile perch was able to cover 50 km per week (Ligtvoet and Mkumbo

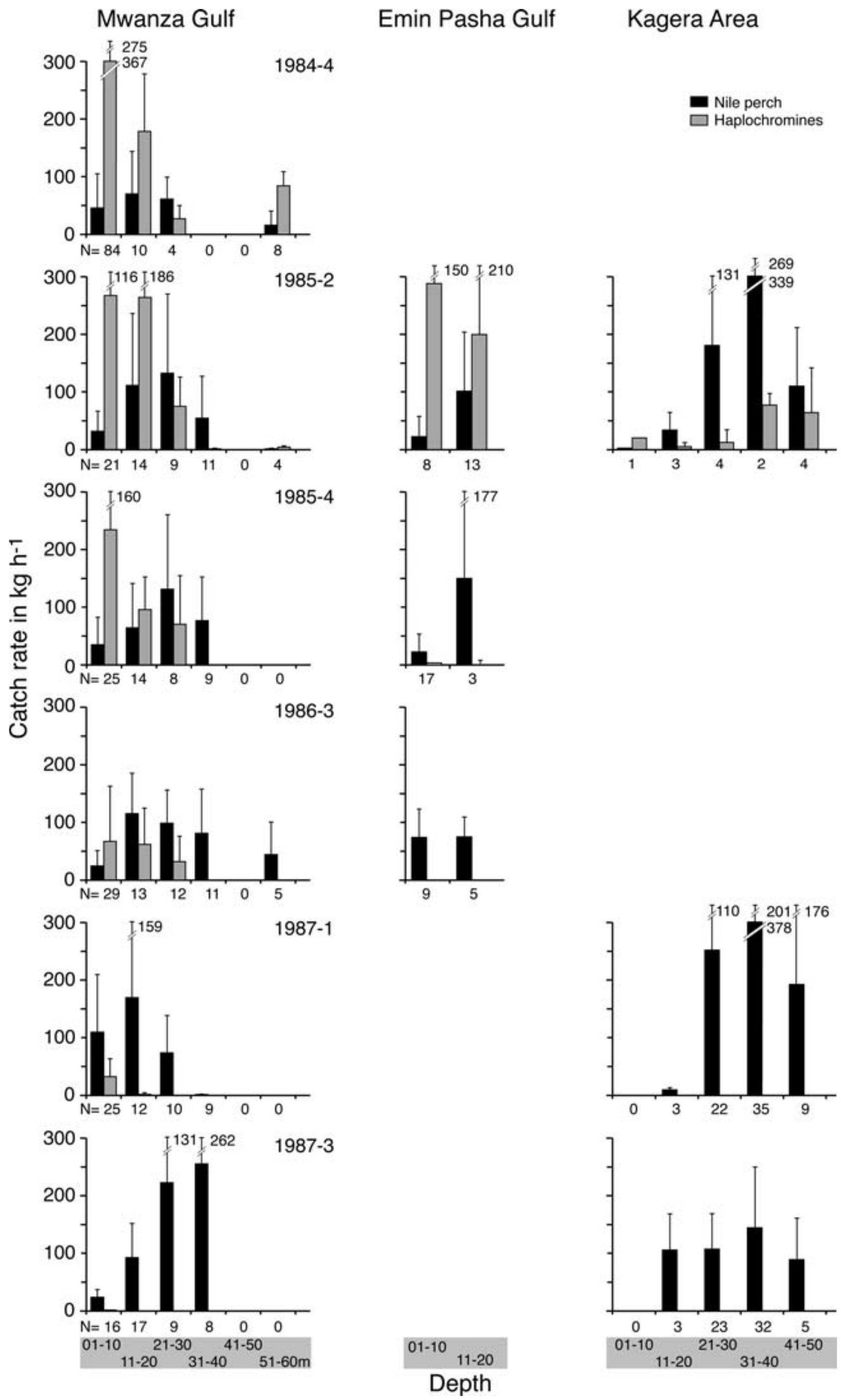

Fig. 6 Average catch rates (kg h^{-1}) of Nile perch and haplochromines in bottom trawls according to depth zone in different years. (**a**) Mwanza Gulf; (**b**) Emin Pasha Gulf; (**c**) Kagera area. Numbers under *X*-axes indicate the number of trawl shots. Numbers after years indicate the quarters of the year that catches were made

1990). This is well within the range that Nile perch could cover based on a cruising speed fish of 1–2 body lengths s^{-1} (Videler 1993), and implies that Nile perch was able to cover the distance from Kenyan waters to the Mwanza Gulf in a few months. However, after the Nile perch became abundant in the Nyanza Gulf in Kenya in 1979, it took 4 years before the sub-adult Nile perch "wave" reached the Mwanza Gulf. This might indicate that there was no need for these fishes to migrate in large numbers at that time. Nile perch boomed in the Ugandan and the Tanzanian waters after haplochromines had been depleted in the Nyanza Gulf (Table 1). Consequently, it is possible that local resource depletion caused more fish to disperse away from their natal site.

Decline of haplochromines

Evidence has been given by Ogutu-Ohwayo (1990b) and by Witte et al. (1992a, b) that the decline and extinction of several hundreds of haplochromine species was due to predation by Nile perch. Other causes for the decline of the haplochromines were local over-exploitation (Witte and Goudswaard 1985; Acere 1988; Harrisson et al 1989; Bundy and Pitcher 1995; Kudhongania and Chitamwebwa 1995) and eutrophication, leading to oxygen deficiencies (Hecky 1993; Hecky et al. 1994; Verschuren et al. 2002; but see Witte et al. 2005) and to increased turbidity (Seehausen et al. 1997).

Exploitation of a virgin stock generally leads to a stock reduction and changes in species composition. Larger species, which mature above the 50% retention size of the net, are generally more sensitive to over-exploitation than small sized species. In Lake Malawi commercial trawl fishery on haplochromine cichlids resulted in a change in dominance from medium and large sized species to small sized species (Turner et al. 1995). The same was observed in the Mwanza Gulf, where the large species had vanished in the catches with the 90 mm codend by 1979 (Fig. 2b). The catch per unit of effort (in kg h^{-1} trawling) also declined for the small sized haplochromines. However, for the following reasons, the steep decline in the Mwanza Gulf, after 1984 cannot be attributed to fishing only: (1) After the trawl fishery in the Mwanza Gulf was stopped in 1986, the decline of the haplochromines continued (Table 1); (2) In areas where fishing pressure for haplochromines was low, e.g., Emin Pasha Gulf and Kagera area, they vanished as well (Table 1); (3) In all areas the disappearance of the haplochromines was concomitant with a strong increase of the Nile perch, thus suggesting a major impact of this predator (Table 1).

With respect to eutrophication, especially increased turbidity may have had a strong impact, as cichlids are highly dependent on vision for feeding and reproduction (Seehausen et al. 1997, 2003; Seehausen and Van Alphen 1998; Witte et al. 2005). Because the Nile perch upsurge in Lake Victoria and the increase of eutrophication both occurred in about the same period (Verschuren et al. 2002), it is difficult to establish the relative impact of these phenomena separately. Nevertheless, as indicated above, predation by Nile perch was a major factor.

Large Nile perch as a pioneer for juvenile Nile perch?

It is remarkable that after the first release of Nile perch in Lake Victoria it took more than 25 years before a sudden increase of its population took place, resulting in its dominance in the demersal fish stock. The initial abundance of haplochromine cichlids suggests that food cannot have been a limiting factor for the piscivorous Nile perch between its introduction and the early 1980s. Therefore, we assume that other factors have played a role. An important factor could have been the survival of very young Nile perch and the food abundance for these fishes. Although we have no evidence from stomach contents, it is likely that the abundant haplochromines fed upon eggs and larvae of Nile perch, whenever available. Moreover, the haplochromines were probably competing with juvenile Nile perch for zooplankton and insect larvae. During the colonization process the adult and sub-adult Nile perch fed heavily upon haplochromine cichlids (Hughes 1986; Ogutu-Ohwayo 1990a, b; Ligtvoet et al. 1990) and reduced their numbers to extremely low levels, thus enhancing the chance of survival of eggs and larvae of Nile perch. Further, it has been suggested that the reduction of haplochromine cichlids also reduced the predation on juvenile shrimps, *Caridina nilotica* (Roux, 1833) (Goudswaard et al. 2006). Apart from zooplankton and insect larvae, juvenile shrimps also appeared to be an important food item for small (<10 cm) Nile perch (Goudswaard et al. 2006; Katunzi et al. 2006). Both shrimps and insect larvae increased after the disappearance of the haplochromines (Kaufman 1992; Mbahinzireki 1992; Goldschmidt et al. 1993; Goudswaard et al. 2006), which were their predators. In this situation adult Nile perch facilitated the food availability for juvenile Nile perch by eradicating the former competitors of their juveniles.

If the foregoing is correct, then Nile perch initially could have been successful in reproduction only at places where the haplochromine stock was reduced. Before the Nile perch upsurge this must have been an area where the reduction of haplochromines was caused by other factors than predation by Nile perch. The heavily exploited Nyanza Gulf in Kenya might have acted as such a place, as already in the early 1970s over-exploitation of haplochromines was reported for this area (Marten 1979).

Nile perch after the boom

After the disappearance of the haplochromines and the establishment of a large stock of shrimps, the Nile perch became a resident species of which successive year classes were present. Juvenile Nile perches became one of the main food sources of adult Nile perch >50 cm (Hughes 1986, 1992, Ogari and Dadzie 1988; Ogutu-Ohwayo 1990b; Mkumbo and Ligtvoet 1992; Katunzi et al. 2006). In the Speke Gulf the amount of large Nile perch in trawl catches declined (Fig. 5a). As Nile perch fishery mainly aimed at large fishes, fishing may have caused this reduction. It has been observed in Kenyan waters that size at 50% maturity has declined from 102 cm for females and 74 cm for males before 1986 (Asila and Ogari 1988) to 55 cm for males and 70 cm for females around 1990 (Ogari and Asila 1992).

The explanation of the simultaneous increase of small (<35 cm) individuals is more complex. It might be the combined result of: (1) Growth of the recruits that were born in the area after the initial invasion of the sub-adults; (2) A relatively high predation pressure on juvenile Nile perch by adult Nile perch in the early years when the densities of large Nile perch were still high.

Conclusions

Several hypotheses for the Nile perch boom have been published. For instance, Hecky (1993) suggested that the increasing turbidity and deoxygenation, caused by the eutrophication, broke down the complexly balanced food web in Lake Victoria, resulting in increased abundances of insect larvae and the shrimp, *Caridina nilotica*, that favored survival of juvenile Nile perch. Verschuren et al. (2002) suggested that deepwater oxygen loss caused the deepwater haplochromines to migrate to shallower depth ranges where they augmented the food base for Nile perch. However, he correctly adds that there is no evidence that characteristic deepwater haplochromines migrated to shallow areas, and that densities of haplochromines at depths of more than 30 m used to be significantly lower than in shallow habitats.

We hypothesize the following steps in the colonization process of Nile perch in Lake Victoria. (1) Initially, over-fishing of haplochromines in the Nyanza Gulf facilitated a local recruitment of juvenile Nile perch due to a decrease of predation by and competition with haplochromines. (2) Colonization of other areas in the lake took place at different moments. In each of these areas the first step in the process comprised the invasion of sub-adults from neighbouring areas, where haplochromines had been depleted. (3) Subsequently, the local haplochromine stock vanished, and both juvenile Nile perch and juvenile shrimps had a higher survival rate than before. (4) As a consequence a strong recruitment of Nile perch occurred in the area.

Thus, the pioneering sub-adult Nile perch created, by eradication of the haplochromines, a changed species composition in favour of juvenile Nile perch.

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