

Guilty as charged: Nile perch was the cause of the haplochromine decline in Lake Victoria

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Abstract: Debate on the contribution of Nile perch (*Lates niloticus*) to the demise of Lake Victoria's 500+ endemic haplochromine cichlids centers around the "top-down" and "bottom-up" hypotheses. The former suggests Nile perch destroyed the haplochromines, causing the disruption of food chains and nutrient cycling and so initiating the accelerated eutrophication of the lake. The latter proposes that haplochromines suppressed Nile perch by preying on its eggs and fry or competing with juveniles for food. A recent paper argued that accelerated eutrophication caused by a climatic event led to their collapse, allowing Nile perch to explode. However, the Nile perch population grew before haplochromines decreased, and they only collapsed once Nile perch biomass exceeded theirs. The chronology indicates that accelerated eutrophication of the lake followed rather than preceded the haplochromine collapse, suggesting that eutrophication was not its cause. A size-selective predation model developed to support the bottom-up hypothesis is discussed in light of existing data, but does not support the bottom-up hypothesis. It was concluded that the top-down model better fits the data and conforms to the law of parsimony.

Résumé : Le débat sur le rôle de la perche du Nil (*Lates niloticus*) dans l'effondrement des plus de 500 cichlidés haplochrominés endémiques du lac Victoria s'articule autour des hypothèses de l'effet descendant et de l'effet ascendant. La première hypothèse postule que les perches du Nil ont détruit les haplochrominés, entraînant la perturbation des chaînes trophiques et des cycles de nutriments, initiant ainsi l'eutrophisation accélérée du lac. La seconde hypothèse postule plutôt que les haplochrominés ont réduit l'abondance des perches du Nil en consommant leurs œufs et leur fretin, ou du fait de leur concurrence pour la nourriture avec les perches juvéniles. Un article récent arguait que l'eutrophisation accélérée causée par un événement climatique avait mené à l'effondrement des haplochrominés, ce qui a permis l'explosion de la perche du Nil. L'accroissement de la population de perches du Nil précède toutefois le déclin des haplochrominés, et ces derniers ne se sont effondrés qu'après que la biomasse des perches du Nil ait dépassé la leur. La chronologie indique que l'eutrophisation accélérée du lac a suivi plutôt que précédé l'effondrement des haplochrominés, donnant à penser que l'eutrophisation n'était pas la cause de cet effondrement. Un modèle de prédation sélective selon la taille développé pour soutenir l'hypothèse de l'effet ascendant est abordé à la lumière des données existantes, mais il n'appuie pas cette hypothèse. Nous concluons que le modèle d'effet descendant concorde mieux avec les données et respecte la loi de la parcimonie. [Traduit par la Rédaction]

Introduction

Nile perch (*Lates niloticus*) in Lake Victoria (Fig. 1) is the quintessential invasive species, having been introduced 60 years ago by colonial officials in Uganda who overrode scientific advice and the concerns of their colleagues in Kenya and Tanzania (Jackson 2000; Pringle 2005). The consequences only became apparent after its population exploded around 1980 and two dramatic changes occurred in the lake. The first was the apparent extirpation of its native fishes, notably the 500+ endemic haplochromine cichlid species (Barel et al. 1985; Ogotu-Ohwayo 1990a; Witte et al. 1992), an event described as the greatest vertebrate extinction of recent times (Kaufman 1992). The second was the lake's relatively abrupt change from an oligotrophic-mesotrophic system to a eutrophic one, marked by the development of blue-green algal blooms, anoxia, and fish kills (Ochumba 1988, 1990; Ochumba and Kibaara 1989; Hecky 1993; Hecky et al. 1994).

Early workers attributed these changes to a "top-down" series of cascading effects that followed the loss of both biomass and diversity within and between trophic levels as a result of the haplochromine extirpation. This was assumed to have broken down the complex food chains and nutrient recycling pathways that previ-

ously existed in the lake, making nutrients available for algal blooms (Barel et al. 1985; Ligetvoet and Witte 1991; Kaufman 1992).

Over the years there has been considerable debate over this question, beginning with Bundy and Pitcher (1995), who suggested that Nile perch may not have been solely responsible for this situation. A review of the impacts of eutrophication on Lake Victoria fishes concluded that the haplochromine decline was caused by Nile perch (Witte et al. 2005), but it was later suggested that it was not possible to separate the effects of Nile perch and eutrophication since both occurred in the same time period (Witte et al. 2007a, 2013). Other authors have argued that "bottom-up" influences are a more valid explanation for the changes in Lake Victoria, with Nile perch being just one of a multiplicity of stressors (Kolding et al. 2008; Hecky et al. 2010).

Hecky et al. (2010) suggested that the transition to a new ecosystem state, with a highly productive algal community and dramatically altered food webs, may have been triggered by a period of low wind stress, along with climate warming during the 1970s. This approach culminated in a recent paper in this journal that questioned whether Nile perch was the cause or a consequence of the haplochromine decline (van Zwieten et al. 2016). These au-

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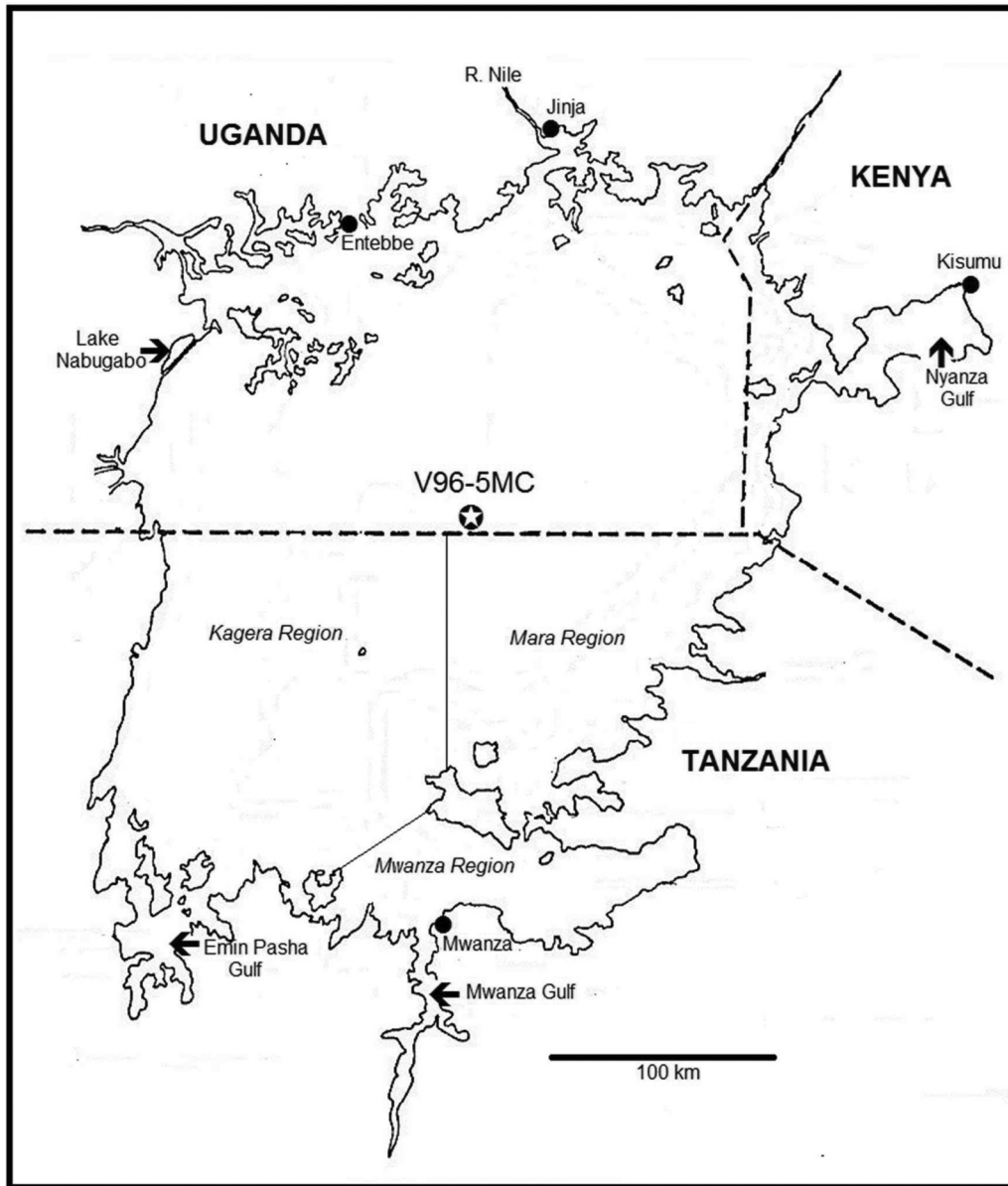
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Fig. 1. Lake Victoria, showing places mentioned in the text, including the location of the deep-water sediment core V96-5MC.



thors argued that haplochromines suppressed the growth of the Nile perch population, and an external event was needed to reduce their numbers and allow the Nile perch population to grow. This event was a period of low wind stress from 1976 to 1983 that was said to have triggered eutrophication and increased anoxia, leading to the demise of the haplochromines and allowing the Nile perch population to explode.

If this is correct, it would mean that Lake Victoria could be one of the first examples of a whole-ecosystem change brought about by recent climatic events. This would certainly be of importance in the present era of rapid climate change and merits further discussion.

The fish and fisheries of Lake Victoria

The most important characteristic of Lake Victoria’s fish community was its astonishingly diverse community of haplochromine cichlids. The exact number of species is unknown, but estimates have risen from around 150 species in 1970 to 500+ in 2000 (Witte et al. 2007b). They are small fish, mostly around 6–10 cm in length, with a few species reaching 15–17 cm (Witte

and van Oijen 1990, 1995), and they display an extraordinary range of trophic specializations. At least 16 major trophic categories have been identified with further specializations within each of them. Very little is known about the ecology of these fish, the interactions among species, their role in the Lake Victoria ecosystem, or even their distribution in the lake. Because of their small size, the difficulties in identification, and the large numbers involved, most fishery surveys (historically and presently) simply lump them together as “haplochromines” without separating the species. The exception to this is the work of the Haplochromine Ecology Survey Team in the Mwanza Gulf, Tanzania (Witte and van Densen 1995), who described the community structure and the rapid changes associated with a trawl fishery and Nile perch. Thus, while there is a considerable amount of information after the Nile perch introduction, at least in the Mwanza Gulf, almost nothing is known about the haplochromine community structure anywhere in the lake before the Nile perch introduction. Assumptions before the Nile perch introduction should therefore be treated with caution.

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About 40 non-haplochromine species also occurred in the lake. Two cichlids, the tilapias *Oreochromis esculentus* and *Oreochromis variabilis*, were the target of the commercial gill-net fishery that began in 1908, and their stocks were rapidly depleted in intensively fished areas. In the Nyanza Gulf, Kenya, for instance, the catch of *O. esculentus* fell from 25 fish per net in 1908 to 8 in 1920, 2 in 1940, and 0.5 in 1970 (Kudhongania and Chitamwebwa 1995), while in Pilkington Bay, Uganda, the catch in 4-inch nets (1 inch = 2.5 cm) fell from a mean of 15 fish per net in 1955 to one fish per net in 1957 (Anonymous 1958). Several non-native tilapias were introduced into the lake in the 1950s in an effort to restore this fishery (Welcomme 1964), but only one of them, the Nile tilapia (*Oreochromis niloticus*), became important in the fishery and then only after the Nile perch explosion (Goudswaard et al. 2002).

Haplochromines had always been utilized by local communities (Graham 1929), but colonial officials considered them to have little value. Proposals were made to utilize them for fish meal, and a commercial trawl fishery was eventually established in the Mwanza Gulf for this purpose in 1973. Maintaining the tilapia fishery seems to have been the main management priority during the 1970s. Discussions about the state of the Lake Victoria fisheries centered around the need to maintain this fishery, with Nile perch only being mentioned as a potential threat to tilapias rather than haplochromines (e.g., Fryer 1972, 1973a, 1973b; Worthington 1972; Jackson 1973; Stoneman et al. 1973). A proposal to target predators such as *Clarias*, *Bagrus*, and *Protopterus* to improve tilapia catches made no mention of Nile perch (Marten 1979a) even though they were increasingly being taken in commercial fisheries at the time (Okedi 1970; Achieng 1990). It is regrettable that Nile perch was not investigated more thoroughly at that time, as this might have prevented subsequent controversies over the sequence of events.

Nile perch growth and haplochromine decline

It is unclear when Nile perch were introduced into Lake Victoria, but some were caught in 1960, before the official introductions in 1962 and 1963 (Gee 1964). These may have been introduced surreptitiously by the Uganda Wildlife Service (Pringle 2005). Its subsequent population growth conformed to the population growth depicted in any elementary ecology textbook, an S-shaped logistic curve with three phases: establishment, expansion, and stability (Shigesada et al. 1995). This can be most easily seen in the northern part of the lake (Uganda and Kenya), where it was introduced and first became numerous (Kudhongania and Cordone 1974).

Establishment phase (Kenya and Uganda)

This phase lasted for about 20 years, and its length is most probably explained by introduction effort, a critically important factor in the establishment of introduced species (Jeschke and Strayer 2005; Lockwood et al. 2005; Simberloff 2009). The official introductions consisted of 35 fish ranging from 16.0 to 43.5 cm in length in May 1962, followed by 339 fingerlings in September 1963 (all from Lake Albert) and eight fish from Lake Turkana in 1963, giving a total of 382 fish (Gee 1964). The extent of postintroduction mortality is unknown, and the number of survivors may have been lower than this. The number introduced before this time is unknown (Pringle 2005), but doubling the official number gives a total of 764 fish, a very small number of fish for such a large lake. It is not surprising that it took some time for the population to build up.

Nevertheless, the East African Freshwater Fisheries Organisation knew by 1963 that Nile perch were breeding in the lake, and surveys revealed that they were dispersing along its northern shores (Anonymous 1964, 1966). The number brought to the Massee Fish Market in Jinja (Uganda) increased exponentially, from a monthly mean of 32 in 1963 to 62 in 1964 and 195 in 1965. The

Table 1. Age structure (%) of Nile perch at the Massee Fish Market, Jinja, Uganda, 1964–1977.

	Age (years)				
	1	2–3	4–5	6–10	>10
1964–1965	99.6	0.4	—	—	—
1965–1966	99.6	0.3	0.1	—	—
1966–1967	97.2	2.2	0.3	0.3	—
1967–1968	73.1	25.7	0.6	0.6	—
1968–1969	77.3	20.8	1.1	0.8	—
1969–1970	3.6	57.2	7.1	32.1	—
1970–1971	0	7.9	25.4	63.5	3.2
1974–1975	0	1.0	9.4	82.3	7.3
1975–1976	0.7	2.8	17.6	70.4	8.5
1976–1977	28.7	2.3	5.8	54.0	9.2

Note: Values >20% are highlighted in bold for clarity. Data are from Acere (1984).

Nile perch population in the area serving the market was said to have increased by between 500% and 700% in 1964 (Gee 1965).

From 1964 to 1967 almost all the Nile perch brought into the market were about 1 year old, further confirming the establishment of a breeding population (Table 1). Older fish then began to appear in the market, and from 1970 to 1977 the catch was dominated by fish aged 6–10 years old. At this time, fishermen began targeting the more profitable large fish by switching to large-meshed gill nets (Acere 1988), and this may not reflect a failure of recruitment. This was confirmed by Okedi (1970), who sampled commercial catches and found the smallest Nile perch were 21.0 cm (males) and 18.5 cm (females) in length; these fish would have been about 5–6 months old (Hughes 1992). The shift back to 1-year-old fish, which began in 1976 (Table 1), may reflect either an increase in their numbers or a decrease in large individuals just before the expansion phase began.

Nile perch made up 0.04% of the catch from an early bottom trawl survey carried out in Uganda in 1966 (Gee and Gilbert 1967), and this proportion increased threefold to 0.12% in Ugandan waters during the lake-wide 1969–1971 survey (Kudhongania and Cordone 1974). This survey estimated that the standing stock of Nile perch in the lake as a whole was 402 t, of which 385 t (97%) was in Kenya and Uganda. The total mass of the fish that was introduced is not known, but if the 339 fingerlings weighed 10 g each then their total mass would have been less than 4 kg, while the 43.5 cm fish, the largest one introduced, would have weighed about 1.0 kg (Hughes 1992). Consequently, no more than 20–30 kg of fish might have been introduced, and thus the biomass of Nile perch in 1969–1971 had increased by at least four orders of magnitude since their introduction.

Expansion phase (Kenya and Uganda)

This explosive phase began in the northern waters of the lake around 1980–1981. In Uganda, the Nile perch catch rate rose from 0.5 kg·h⁻¹ in the 1969–1971 trawls to 3.5 kg·h⁻¹ in 1981, an increase of 700% (Table 2). This was followed by an increase from 3.5 to 234.7 kg·h⁻¹ between 1981 and 1985, representing a mean increase of 1600% per annum. The haplochromine biomass rose slightly between 1969–1971 and 1981 but it did not double, as stated by van Zwieten et al. (2016; p. 627). It fell from 391.7 kg·h⁻¹ in 1981 to 264.6 kg·h⁻¹ in 1983, a 48% decrease, followed by a collapse to zero in 1986. The biomass of other species declined from 1982 onwards, with the most rapid collapse beginning in 1984 when the biomass of Nile perch exceeded that of all other species.

The situation was similar in Kenya, where the biomass of Nile perch came to exceed that of all other species between 1977 and 1982, leading to a collapse in the haplochromines (Table 3). These findings are supported by data from commercial fisheries, where landings increased exponentially, from 17 t in 1969 to 68 000 t in 1988 (Fig. 2). Fish catches may of course be influenced by fishing

Table 2. The relative abundance ($\text{kg}\cdot\text{h}^{-1}$) of demersal fish species caught in bottom trawls in the Ugandan waters of Lake Victoria.

	1969–1971	1981	1982	1983	1984	1985	1986
<i>Haplochromis</i> spp.	327.4	391.7	295.7	264.6	113.9	17.8	—
<i>Lates niloticus</i> *	0.5	3.5	45.3	54.3	140.2	234.7	80.1
<i>Oreochromis niloticus</i> *	0.9	12.2	7.3	5.2	1.8	5.0	7.1
<i>Oreochromis esculentus</i>	2.6	0.5	0.1	—	—	—	—
<i>Oreochromis variabilis</i>	0.6	5.6	2.5	0.9	—	—	—
<i>Bagrus docmak</i>	23.5	9.0	9.3	11.3	4.3	1.5	0.3
<i>Clarias gariepinus</i>	17.3	14.4	8.0	4.4	1.8	0.1	—
<i>Protopterus aethiopicus</i>	5.8	4.9	0.1	0.8	0.6	0.1	—
<i>Synodontis</i> spp.	15.4	2.9	0.5	0.4	0.2	0.1	—
Other species	0.9	0.2	1.6	4.7	0.3	0.3	—
Total	394.9	444.9	370.4	346.6	264.3	259.6	87.5

Note: Data are from Kudhongania and Cordone (1974) and Acere (1988). An asterisk (*) indicates an introduced species, and dashes indicate zero values; the original data do not include confidence limits.

Table 3. The biomass ($\text{kg}\cdot\text{ha}^{-1}$) of dominant fish species in bottom trawls in the Kenyan waters of Lake Victoria (from Ochumba 1995).

	1969–1971	1975	1977	1982–1983	1989–1990
Haplochromines	35.8	32.7	28.7	—	0.5
Nile perch	—	0.8	2.8	29.0	32.7
Other species	17.2	26.6	4.4	3.3	1.3
Total	53.0	60.1	35.9	32.3	34.5

Note: Dashes indicate zero values; the original data do not include confidence limits.

effort, but the catch per unit effort increased steadily from 1980 to 1990, indicating that this was a real population increase. In contrast, the haplochromine catches increased slightly from 6400 t in 1969 to 6600 t in 1979, after which they fell to zero in 1984. This collapse began in 1980 once the catch, and by implication the biomass, of both haplochromines and Nile perch were about equal.

In both countries the tipping point seems to have been reached when the Nile perch biomass equalled that of its prey, which were then unable to sustain their own populations. Thus, the fish communities in the lake changed catastrophically from a seemingly stable haplochromine-dominated state to one dominated by Nile perch. As Scheffer et al. (2001) point out, such catastrophic changes can occur unannounced with “early-warning signals” being difficult to obtain. They also noted that sudden change could occur once an ecosystem lost resilience, which they define as the maximum perturbation a system can withstand without shifting to an alternative stable state. The early warning signal in Lake Victoria, the steady increase in the Nile perch population, seems to have been overlooked.

Stabilization phase (Kenya and Uganda)

The haplochromine collapse appears to have marked the end of the Nile perch expansion phase, but whether this resulted in a “stable” condition is debatable. The Nile perch population might have been expected to collapse once its principal food source was exhausted, but it survived because alternative food sources became available. The most important of these were the atyid shrimp *Caridina nilotica* and the endemic sardine-like cyprinid *Rastrineobola argentea* (dagaa), while cannibalism was frequent. The total catch of Nile perch peaked at around 300 000 t in 1990–1991 and subsequently levelled off around 250 000 t per annum, obtained from a biomass fluctuating around one million tonnes (Taabu-Munyaho et al. 2016). It has been suggested that Lake Victoria could have supported a larger Nile perch biomass (van Zwieten et al. 2016), but this is questionable given the high incidence of cannibalism (Hughes 1986; Ogari and Dadzie 1988; Ogutu-Ohwayo 1990b) and the deterioration of their length–mass

relationships and condition that followed the haplochromine collapse (Ogutu-Ohwayo 1999).

Nile perch in Tanzania

The situation in Tanzania differed in that Nile perch were initially scarce, with an estimated biomass of only 7 t in 1969–1971 (Kudhongania and Cordone 1974). The expansion phase began later, evidently driven by subadult fish moving southwards from Kenya (Goudswaard et al. 2008). This movement is not well documented, but Nile perch accounted for >50% of the catch in the Mara region (on the east coast south of the Kenya border) in 1984 and in the Mwanza region (south of Mara) in 1986 (Bwathondi 1990).

The growth of the fishery in Tanzania was similar to that in Uganda and Kenya, with explosive growth (four orders of magnitude in 5 years) increasing the catches from about 270 t in 1981 to 184 000 t in 1985 (Fig. 3a). Haplochromine catches fluctuated but declined rapidly from about 24 000 t in 1983 to 17 000 t in 1986, to 1500 t in 1987, and zero in 1988. As in Kenya and Uganda, the decline of the haplochromines in the commercial fishery began once the Nile perch catch exceeded that of all other species, a point reached in 1986 with the Nile perch catch being 124 000 t compared with 79 000 t for all other species (Bwathondi 1990).

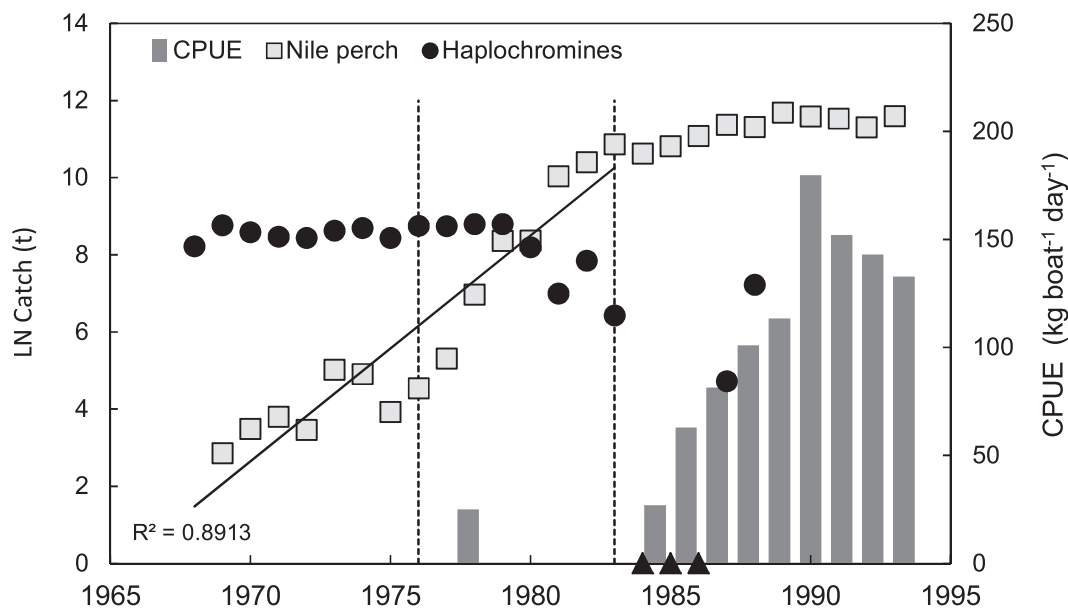
A unique situation developed in the Mwanza Gulf where a commercial trawl fishery had been established in 1973 to catch haplochromines for fish meal, with 10 trawlers operating in the gulf by 1985 (Witte and Goudswaard 1985). The mean catch rate in research trawls from 1975 to 1979 (excluding the very high 1976 value) was $1236 \text{ kg}\cdot\text{h}^{-1}$, but the stock collapsed thereafter, falling to zero in 1988 (Fig. 3b). All commercial trawling was suspended in 1987 (Goudswaard and Ligtoet 1987) and it has never resumed.

Nile perch first appeared in these catches in 1975, with catch rates of $1 \text{ kg}\cdot\text{h}^{-1}$ until 1979 and $4 \text{ kg}\cdot\text{h}^{-1}$ up to 1982, after which they rose to a maximum of $203 \text{ kg}\cdot\text{h}^{-1}$ in 1987 (Fig. 3b). Although the biomass of Nile perch exceeded that of the haplochromines by 1986, the growth of the Nile perch population in the Mwanza Gulf was less explosive (only two orders of magnitude in 5 years) than elsewhere in Tanzania. Perhaps the growth of this population may have been limited by a lack of food, since the haplochromines had almost collapsed before the expansion phase began. Shrimps only appeared in the bottom trawls in 1987, after the haplochromine collapse, when the maximum catch was 436 in a 10 min haul, although it exploded to 200 000 in 1988 (Goudswaard et al. 2006).

The diet of Nile perch

The sequence of events in the lake can be tracked by a consideration of the diet of Nile perch. Small ones (1–5 cm) fed mostly on zooplankton and midge larvae in shallow water (<5 m) but shifted to shrimps in deeper water (Katunzi et al. 2006). After the Nile perch explosion, the diet of fish <20 cm in length consisted pri-

Fig. 2. The catch of haplochromines and Nile perch in the Kenyan sector of Lake Victoria, 1968–1988, plotted as natural logarithms to indicate the exponential growth of Nile perch between 1969 and 1983. The catch per unit effort (CPUE) is indicated by the shaded columns; the broken vertical lines denote the 1976–1983 climatic event; solid triangles denote haplochromine values of zero, which cannot be shown on a logarithmic plot. Data are from *Achieng (1990)* and *Asila (1997)*.



marily of shrimps and other invertebrates, and shrimps remained important after the haplochromine recovery although piscivory increased (Table 4). Haplochromines had been a minor component of this size class diet in Tanzania in 1988–1989 (Katunzi et al. 2006), and the shift reflected their continuing recovery.

The earliest record of Nile perch diet in Lake Victoria came from fish in the 20–40 cm size range caught in Uganda in 1964 (Fig. 4). Their diet was varied, with the major food items being haplochromines (37%), tilapias and unidentified cichlids (33%), mormyrids (20%), and other fish species (10%). Nile perch were established and expanding in the period 1968–1977, and in Uganda, fish in both the 20–40 and 40–60 cm size classes were feeding primarily on haplochromines with a small proportion of dagaa and other species. After the haplochromines collapsed, shrimps were the principal food item in both size classes in Kenya (1982–1983), followed by smaller Nile perch and dagaa. By 1988, these were less important in Uganda, where small Nile perch and dagaa were the major food items. There was no evidence of a haplochromine recovery in either country before 1988.

The collapse of the haplochromines was also clearly shown in the diets of fish from the Mwanza Gulf in Tanzania (Fig. 4). Nile perch catches peaked in 1987, and although the diet in both size classes was predominantly haplochromines, the appearance of cannibalism and dagaa suggests that these were beginning to decline. This was confirmed in 1988 and 1989 when the diet was dominated by shrimps, dagaa, and Nile perch (especially in the 40–60 cm fish). Very few haplochromines were taken in those years, but by 2006–2008 the haplochromine recovery made them once again an important component of Nile perch diet, notably in the larger fish.

There are few data on the diet of Nile perch >60 cm in length. They were almost entirely cannibals in Kenya and Uganda during the 1980s (Hughes 1986; Ogari and Dadzie 1988; Ogutu-Ohwayo 1990b). In Tanzania, they fed mostly on haplochromines in 1986 (about 85% of the diet), with a sudden shift to dagaa and Nile perch in 1987. By 1988 their diet consisted of juvenile Nile perch (40%), dagaa (50%), and other fish (10%) (Mkumbo and Ligtoet 1992). There are no recent data for fish in this size class, but it may be assumed that their diet is similar to that of the 40–60 cm fish, with haplochromines being the major component.

Ecological consequences: the eutrophication of Lake Victoria

The cause of eutrophication, excessive nutrient loading resulting from population growth in the lake's basin (Verschuren et al. 2002), is not disputed, but there is some debate over its timing and the sequence of events. The "eutrophication" of Lake Victoria is usually considered to be its relatively sudden transition in the mid-1980s from an oligotrophic-mesotrophic condition to a eutrophic one, with the phytoplankton changing from a diverse community of diatoms and green and blue-green algae (Talling 1966, 1987) to one apparently dominated by colonial blue-green algae such as *Microcystis* (Mugidde 1993). It is now known that eutrophication began much earlier than this, but the evidence was invisible until revealed in sediment cores in the 1990s (Hecky 1993; Verschuren et al. 2002; Stager et al. 2009; Hecky et al. 2010). There is no indication that scientists working on the lake before the 1980s were concerned about eutrophication. Fryer's (1972) review of challenges facing the African Great Lakes, for instance, only mentioned pollution as a future problem, while Jackson (1973) asserted that there was no evidence of future eutrophication or of organic oxygen-demanding pollution in any of these lakes.

This is important because the literature on the impacts of eutrophication on Lake Victoria is mostly based on events that occurred after the abrupt changes in the mid-1980s. Knowledge of what occurred before then is entirely retrospective, and the extrapolation of present conditions backwards to the past should be carefully considered.

The earliest suggestion that the lake was becoming eutrophic came from Hecky and Bugenyi (1992), who noted that the concentration of chlorophyll *a* in bays along the lakeshore had increased from 3–20 $\mu\text{g}\cdot\text{L}^{-1}$ in March 1961 to 13–71 $\mu\text{g}\cdot\text{L}^{-1}$ in May 1988. They wrote "... the evidence for increased algal biomasses in Lake Victoria is worrisome, especially if it is shown to be lakewide, as this eutrophication could lead to increased oxygen demand in the lake's deep water and decrease the hypolimnetic volume habitable by fish during seasonal stratification." Data from 1990 to 1991 confirmed that open waters, at least in the north of the lake, had

Fig. 3. Changes in the catch of haplochromines and Nile perch catch in (a) Tanzania, all areas, 1969–1987 (from Reynolds and Greboval 1988; Bwathondi 1990; and Mkumbo and Ligetvoet 1992) and (b) Mwanza Gulf, 1973–1990 (from Goudswaard et al. 2008). The vertical broken lines indicate the 1976–1983 climatic event; symbols are the same in both panels.

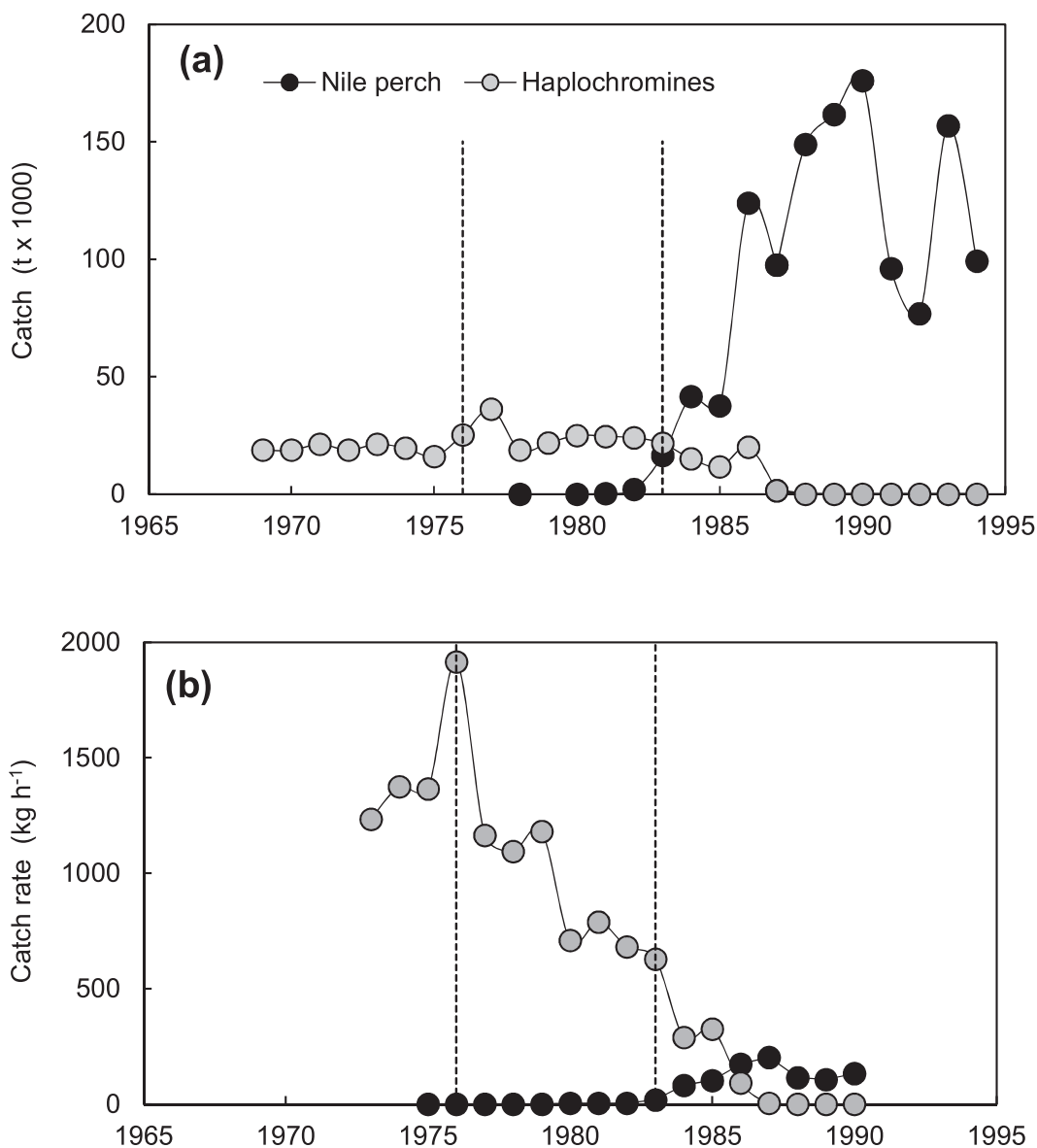


Table 4. The diet of Nile perch <20 cm total length in Lake Victoria.

	Kenya 1982 (%N)	Kenya 1983 (%N)	Tanzania 2006–2008 (%F)	Uganda 2006–2008 (%IRI)
Nile perch	1.0	—	0.5	—
Dagaa	6.0	1.0	1.5	9.0
Haplochromines	2.0	—	18.7	3.8
<i>Caridina</i> (shrimps)	79.0	88.0	77.8	33.5
Other invertebrates	12.0	3.7	5.0	30.2
Unidentified fish remains	—	7.3	9.1	22.0
Other items	—	—	—	1.5

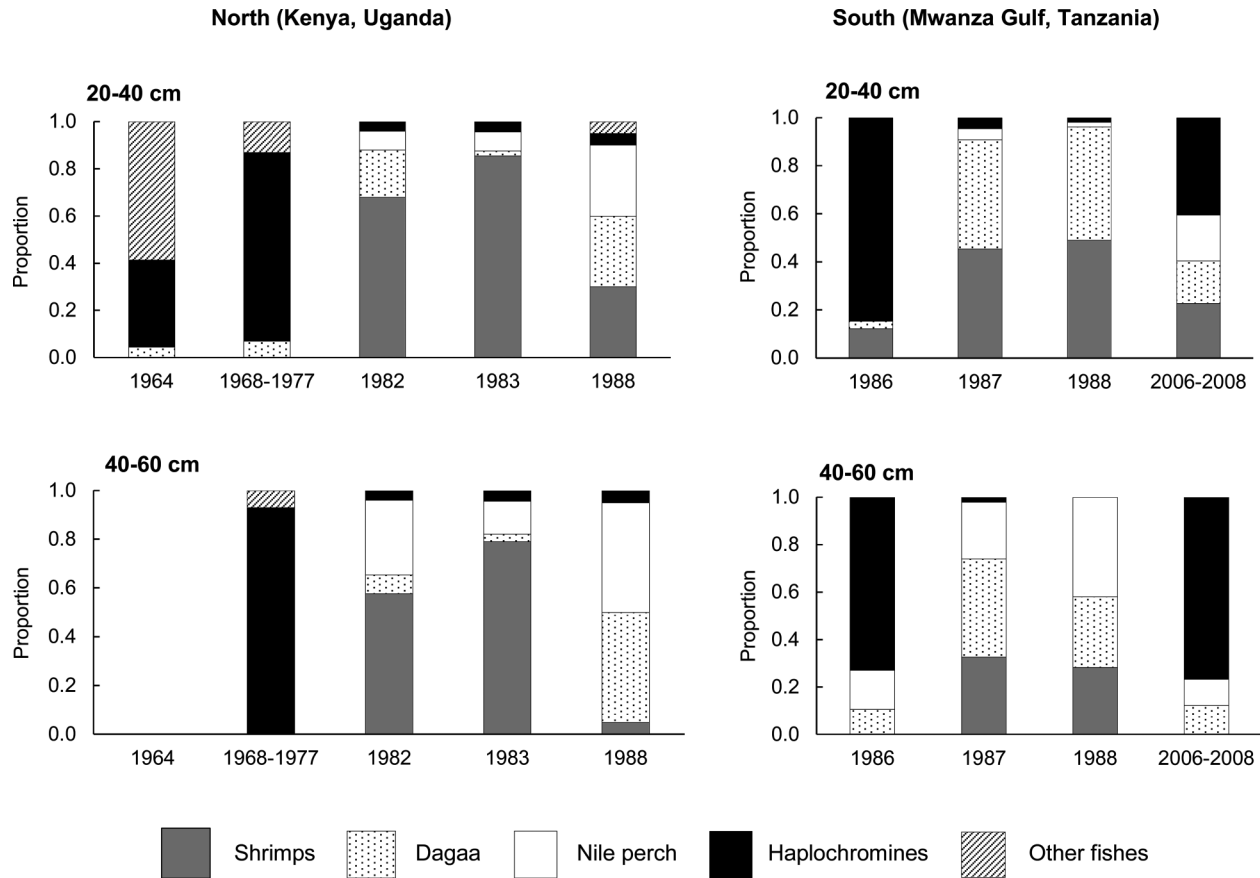
Note: Values from 1982 and 1983 were collected shortly after the haplochromine collapse, while those from 2006 to 2008 were after the haplochromines had begun to recover. Data are expressed as percentages, by numbers from Kenya (%N), by frequency of occurrence from Tanzania (%F), and by Index of Relative Importance from Uganda (%IRI) (from Ogari and Dadzie 1988; Hughes 1986; Kische-Machumu et al. 2012; Nkalubo et al. 2014).

become eutrophic and the deeper waters seasonally deoxygenated (Hecky 1993; Hecky et al. 1994).

It was known that deoxygenation occurred below the thermocline (Anonymous 1952), and the periodic deoxygenation of deeper waters in 1960–1961 was described in more detail by Talling (1966). The suggestion that this may have been an early manifestation of eutrophication (van Zwieten et al. 2016) may be incorrect because it is well known that even oligotrophic tropical waters frequently develop anoxic hypolimnia owing to the rapid breakdown of organic matter at high temperatures (Ruttner 1953; Fryer 1972; Beadle 1981). Fish kills, sometimes caused by anoxia, have been reported in many African lakes (Beadle 1981; Talling and Lemoalle 1998), and large fish mortalities were known to have occurred in Lake Victoria (Graham 1929). Details of most were not collected, but major kills were reported in 1927 and 1953 (Corbet 1961; Ochumba 1988) well before any obvious evidence of eutrophication.

Fish kills were identified as one of the consequences of eutrophication, but those reported in the mid-1980s were attributed

Fig. 4. Changes in the diet of Nile perch, 1964–2008. The bars show the proportion of five major food sources in the diet; items such as insects or molluscs are omitted because their numbers were too low to be shown in the figure. Uganda data are from [Gee \(1964\)](#) and [Ogutuhwayo \(1990b\)](#), Kenya data are from [Hughes \(1986\)](#) and [Ogari and Dadzie \(1988\)](#), Tanzania data are from [Mkumbo and Ligtvoet \(1992\)](#) and [Kishe-Machumu et al. \(2012\)](#).



to stormy weather in the Kagera region of Tanzania in April–May 1984, algal blooms (undated), and an influx of acidic and deoxygenated swamp waters in Kenya after the 1984 drought ([Ochumba 1988](#)), which killed about 2400 t of fish ([Ochumba 1990](#)). Mortality was caused by high levels of suspended detritus and algae following a storm, which clogged the gills of the fish, and to low dissolved oxygen, low pH, and high concentrations of algae. Eutrophication was not specifically cited as a cause, although high concentrations of blue-green algae were reported from the Kenyan sector of the lake in 1984–1986 ([Ochumba and Kibaara 1989](#)).

One of the most striking features of eutrophication in Lake Victoria is its association with Nile perch and the haplochromine collapse. Prior to this event, phosphorus concentrations in two shallow-water cores increased progressively from about 1960 ([Hecky et al. 2010](#)), but the most dramatic change occurred at the deep-water station V95-5MC ([Fig. 5a](#)). Here the concentration increased from about 0.5 mg·g⁻¹ in 1940 to about 0.8 mg·g⁻¹ in the mid-1960s, where it remained until 1984. It then rose rapidly to 2.8 mg·g⁻¹ in 1995. This was attributed to prolonged anoxia liberating phosphorus deposited as organic matter, mostly from the algal blooms ([Hecky et al. 2010](#)). Importantly, this occurred in the mid-1980s after the haplochromines had collapsed in Kenya and Uganda and were beginning to collapse in Tanzania.

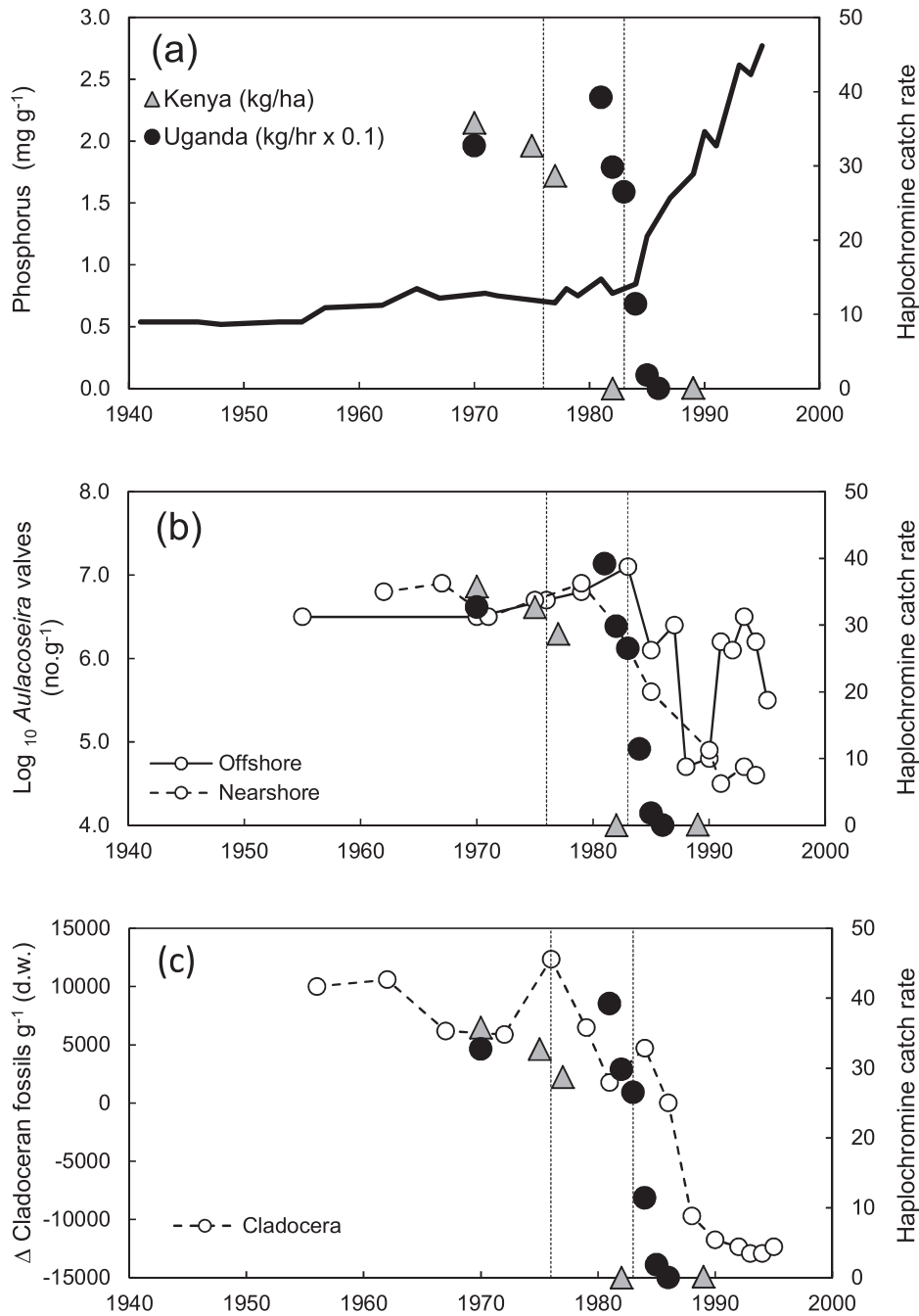
Other major indicators of a change in the lake's status included the transition of its dominant diatom flora from *Aulacoseira* to a long form of *Nitzschia*. This occurred rather suddenly when the number of *Aulacoseira* valves in the sediment core decreased sharply from about 1980 onwards ([Fig. 5b](#)). A third indicator of

change was a sharp decrease in the number of subfossil cladocerans in the sediments, which began around 1980 ([Fig. 5c](#)). In both cases, these decreases occurred mostly after the haplochromines began to collapse, which suggests a link between the two events. These data strongly suggest that the Lake Victoria ecosystem lost its resilience with the collapse of the haplochromines and shifted to a new state following the disruption of food chains and nutrient cycling that previously existed.

Another interesting linkage appears to be the relationship between cladocerans and Nile perch, which strongly suggests that the collapse of one is linked to the expansion of the other ([Fig. 6](#)). There are three possible explanations for this, but the first, that it is simply a coincidence, is improbable. The second is that eutrophication caused the collapse of the cladocerans but how does it explain the rise of Nile perch? Finally, it is reasonable to suppose that great numbers of Nile perch fry must have been produced from about 1979 onwards to drive the population explosion that took place. Small Nile perch (<5 cm) feed on zooplankton ([Katunzi et al. 2006](#)), and if they select cladocerans, as do other non-native zooplanktivores such as *Limnothrissa miodon* ([Dumont 1986](#); [Marshall 1991](#); [Isumbisho et al. 2006](#)), then this could explain their collapse. The loss of these relatively large grazing zooplankters could, in turn, have promoted the blooms of blue-green algae and aggravated the symptoms of eutrophication.

The result was a simplified fish community, dominated by three species, Nile perch, Nile tilapia, and dagaa. Nile tilapia co-exists with Nile perch in its native habitat and presumably has innate defence mechanisms that allow it to do so, and it evidently benefited from the loss of the haplochromines by exploiting food

Fig. 5. The relative abundance of haplochromines (same symbols in all panels) in the northern waters of Lake Victoria in relation to some variables in sediment cores. Ugandan catch rates have been divided by 10 to align them with those from Kenya. The broken vertical lines indicate the 1976–1983 climatic event. (a) Phosphorus concentrations in sediments at site V96-5MC (solid line), from Hecky et al. 2010). (b) The number of *Aulacoseira* valves, from van Zwieten et al. (2016); (c) Anomalies in the number of cladoceran fossils, from van Zwieten et al. (2016). Haplochromine data are from Kudhonganja and Cordone (1974), Acere (1988), and Ochumba (1995).

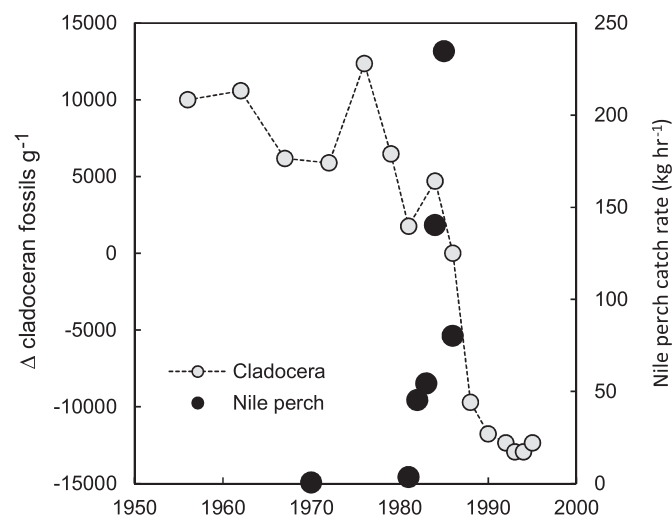


resources previously unavailable to it (Njiru et al. 2004). Daga is a small, shoaling species with high relative fecundity (Table 5) and presumably a high production/biomass ratio, as well as being a less favoured food item for Nile perch (Fig. 4). Another consequence of the haplochromine collapse was an upsurge in the shrimp population, presumably because they were released from predation or competition for food resources (Goudswaard et al. 2006).

It is difficult to imagine that the virtually instantaneous destruction of most of the native fish biomass, estimated to be

around 700 000 t in 1969–1971 (Kudhonganja and Cordone 1974), in Lake Victoria between 1981 and 1986 had little ecological impact. The complete disruption of the complex food chains that previously existed in the lake must have changed the nutrient recycling patterns in the lake and resulted in the algal blooms that developed in the mid-1980s. Nevertheless, the idea that the destruction of the haplochromines could have caused these ecological changes still meets with resistance. For example, Witte et al. (2012) concluded that algal blooms were unlikely to have been caused by a top-down effect caused by the absence of grazing by

Fig. 6. The relationship between cladoceran abundance in Grant Bay, Uganda, and Nile perch densities in trawl samples from Uganda. Data are from van Zwieten et al. (2016), Kudhongania and Cordone (1974), and Acere (1988).



phytoplankton-eating haplochromines. However, this work was based on the plankton consumption rates of two species from Lake George, Uganda (*Haplochromis nigrippinis* (endemic) and Nile tilapia), both of which were feeding almost exclusively on the blue-green algae *Microcystis* (Moriarty and Moriarty 1973). Applying their food consumption rates to the diverse pre-Nile perch haplochromine community feeding on the more diverse phytoplankton flora in Lake Victoria is questionable.

Ultimately, of course, it is not the loss of one trophic group that might have been responsible for algal blooms but the almost complete breakdown of all food chains in the lake. The notion that a single species could have such a profound effect on a very large and diverse ecosystem like Lake Victoria might be difficult to accept, since diverse ecosystems are conventionally thought to be more stable and resistant. Natural food-web structures enhance ecosystem stability provided that consumer–resource interactions are relatively weak (McCann 2000; Ives and Carpenter 2007), and Lake Victoria must have had an extremely wide variety of such consumer–resource interactions, both within the haplochromine community and between them and other components of the ecosystem. In contrast, Nile perch “...eats anything that moves...” (Hamblyn 1962), and its powerful consumer–resource interactions broke down those previously existing in the lake. This in turn would have disrupted nutrient cycling across the entire ecosystem. The extinction of fish can alter nutrient recycling in tropical fresh waters (McIntyre et al. 2007), while biodiversity, especially trophic complexity, plays an important role in the functioning of ecosystems (Duffy et al. 2007). Nowhere was this demonstrated more clearly than in Lake Victoria, where the loss of both biodiversity and trophic complexity resulted in major ecological disruption.

The haplochromine recovery

One of the remarkable features of Lake Victoria is the recovery of at least some haplochromine species to the point where the haplochromine fishery in the lake now yields around 120 000 t per annum or about 16% of the total catch (Mkumbo and Marshall 2015). Details of this recovery are only available from the Mwanza Gulf, where the lowest catch of 0.7 fish per 10 min trawl was recorded in 1987–1988 (Witte et al. 2007a). This rose to 877 and 749 per haul in 2006 and 2008, respectively, which is comparable with the value of 772 per haul in 1979 (Kishe-Machumu et al.

Table 5. Mean and relative fecundity in some Lake Victoria fishes.

	Habitat	Mass (g)	Fecundity (no.)	Relative fecundity (no.·kg ⁻¹)
Haplochromines	Pelagic (6 spp.)	6.3	25.2	4 408
	Benthic (10 spp.)	12.6	60.3	6 526
	Rocks (3 spp.)	14.3	28.3	2 862
Dagaa	—	—	—	583 000
Nile perch	—	2 000	805 000	402 500
	—	5 000	1 195 000	239 000
	—	10 000	1 845 000	184 500

Note: Haplochromine and dagaa data are from Duponchelle et al. (2008); Nile perch data are from Ogutu-Ohwayo (1988).

2015a). Their original diversity has not recovered, however, with 72 species being recorded in 1979–1980 but only 27 in 2006–2008.

The factors responsible for this recovery have been extensively discussed (Witte et al. 2000, 2007a, 2013; Kishe-Machumu et al. 2015a, 2015b), and there is general agreement that the demographic changes in Nile perch, brought about by intensive fishing, was a major factor. These are well illustrated by data from the Speke Gulf, Tanzania, where the catch rate of Nile perch >35 cm in length remained relatively constant at around 300 kg·h⁻¹ in 1986–1987, fell to about 250 kg·h⁻¹ in 1988, but then collapsed to <100 kg·h⁻¹ in 1990 (Fig. 7a). In contrast, the catch rate of fish <35 cm rose steadily throughout the period, and by 1990 the catch rates of the two groups were more or less equal.

Consequently, the Nile perch population is now dominated by fish <25 cm in length (Fig. 7b) that feed primarily on shrimps (60%–98% frequency of occurrence). The larger fish (25–45 cm) preyed on haplochromines, while fish >45 cm increasingly fed on other Nile perch (Kishe-Machumu et al. 2008). This demographic change reduced predation pressure on the haplochromines and enabled some to recover, which was predicted by a bioenergetics model that concluded that they would recover once Nile perch stocks were depleted by increased exploitation (Kitchell et al. 1997).

Many of the recovering species have exhibited novel adaptations to the new conditions in the lake, which, predictably, took some time to become apparent. These include changes to their diet, habitat extensions such as inhabiting deeper or shallower waters than before, and morphological adaptations that enabled them to survive in the new conditions in the lake (Katunzi et al. 2003; Kishe-Machumu et al. 2008, 2015a, 2015b; Witte et al. 2008; van Rijssel et al. 2017). Witte et al. (2007a) concluded that this differential recovery may have been caused by interspecific differences in ecology and adaptability that already existed within species before the lake changed or simply by chance. It has also been suggested that the recovery may also have been facilitated by a more benign environment in the lake (Kishe-Machumu et al. 2015b; van Zwieten et al. 2016), indicated by the reduced stratification and anoxia noted in 2007–2009 (Sitoki et al. 2010; Marshall et al. 2013).

The situation is fluid, however, and may be partly driven by changes in the biomass of Nile perch and shrimps. In acoustic surveys carried out from 1999 to 2001, Nile perch made up 54% of the biomass but that proportion was approximately halved in 2005–2010 (Table 6). The biomass of dagaa increased in 2005–2010 and again in 2014–2016, but haplochromine biomass fluctuated in relation to Nile perch. Thus, Nile perch fell by 52% between 1999–2001 and 2005–2010 while haplochromines increased by 88%, but in 2014–2016 Nile perch increased by 234% and haplochromines fell by 19%. This suggests that Nile perch regulates haplochromines to some extent, but its influence is lessened by the fact that most Nile perch in 2014–2016 were 20–30 cm in length with haplochromines being a relatively small proportion of their diet (Fig. 4).

Fig. 7. (a) The catch rates ($\text{kg}\cdot\text{h}^{-1}$) of Nile perch caught by commercial trawlers in the Speke Gulf, Tanzania, 1986–1990. Open circles indicate fish > 35 cm total length (TL), solid circles indicate fish < 35 cm TL. The horizontal lines indicate the mean catch for fish > 35 cm in each year. Data are from Goudswaard et al. (2008). (b) The length–frequency distribution of Nile perch caught in bottom trawls, 2006 ($N = 3843$) and the proportion of haplochromines (points) in their diet in relation to length. The triangles indicate the length at 50% maturity of male (M) and female (F) Nile perch. Length–frequency and maturity data are from Lake Victoria Fisheries Organization (unpublished), haplochromine data are from Kische-Machumu et al. (2012).

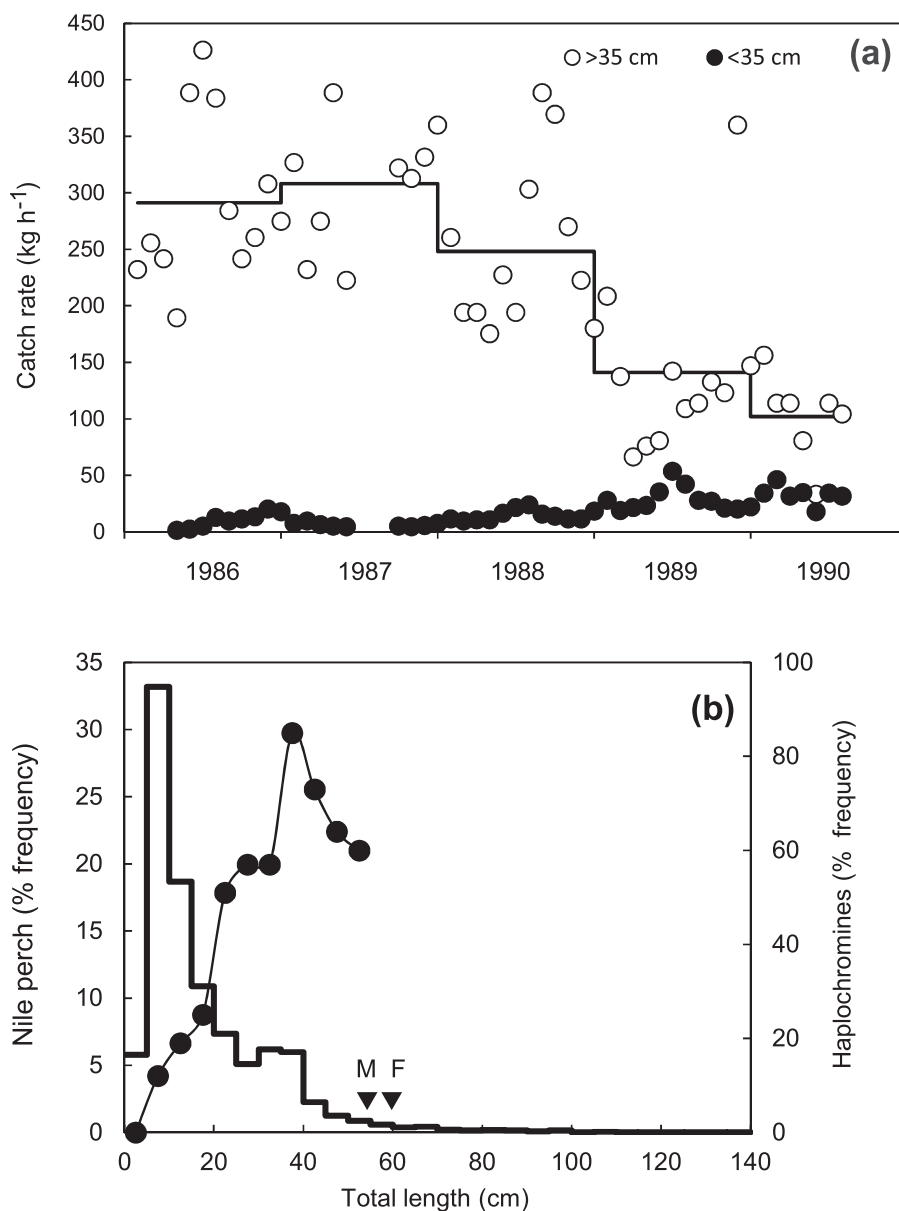


Table 6. The estimated biomass ($\text{t} \times 1000$) of Nile perch, dagaa, haplochromines, and shrimps in Lake Victoria (mean values).

	Nile perch	Dagaa	Haplochromines	Shrimps
1999–2001	932.2	518.1	277.5	—
2005–2010	455.7	980.7	524.3	—
2014–2016	1142.6	1135.2	426.6	251.9

Note: Data are from Everson et al. (2013), Taabu-Munyaho et al. (2016), and reports of the Acoustic Working Group, Lake Victoria Fisheries Organization.

Finally, rapid evolutionary processes are the key to haplochromine diversity in the African Great Lakes (Kaufman et al. 1997). If this is the case, could some of Lake Victoria’s surviving species have evolved the predator recognition and avoidance mechanisms that were lacking when they first encountered Nile perch?

The bottom-up hypothesis

Recruitment depensation

The key to the bottom-up hypothesis is that the long delay between the introduction of Nile perch and its population explosion resulted from a failure of recruitment caused by haplochromine predation on Nile perch eggs or fry or competition for food between them. This notion was first proposed by Jackson (1971), although he provided no evidence to support it. The idea gained traction from the Mwanza Gulf, where haplochromine populations declined rapidly from about 1979 onwards while the Nile perch population only began to explode in 1984 (Fig. 3b). It was noted that haplochromines were initially abundant, and therefore Nile perch would not have been limited by a lack of food (Goudswaard et al. 2008). It was suggested that haplochromines

may have inhibited recruitment of Nile perch, which only ended when larger individuals migrated from the north and were able to prey on haplochromines, thus ending recruitment depensation. From this it was concluded that Nile perch could only become established after some external factor depleted the haplochromines. After that, Nile perch would have reduced the numbers of piscivores and zooplanktivores in the haplochromine population, further enhancing the survival of their own eggs and fry.

These conclusions led to the development of a “recruitment depensation” model (van de Wolfshaar et al. 2014), which suggested that once haplochromine mortality increased, Nile perch were released from depensation, and so their numbers increased. The result was a transition to a state where Nile perch dominated Lake Victoria and haplochromines no longer controlled its recruitment. While this model seems to explain the apparent delay between the introduction and expansion of the Nile perch population in Lake Victoria, it is not supported by data.

Depensation is said to occur in a population when its per-capita growth rate increases once its population density is reduced to low levels. In fisheries, it is usually associated with stocks that have been reduced by overfishing (Liermann and Hilborn 2001; Hutchings 2014). The situation of Nile perch in Lake Victoria was, of course, quite different because it was not a component of the lake’s fish community. Its initial low population density was the result of low introduction effort and not necessarily increased mortality. Its per-capita growth rate is unknown, but its population grew continuously from the time of its introduction (Tables 2, 3; Figs. 2, 3) and cannot be described as depensatory.

Could haplochromines control the recruitment or population growth of Nile perch? Before addressing that question, it is useful to consider some biological attributes of Nile perch. Its natural habitat, the rivers extending from Senegal to the Nile, vary both seasonally and from year to year and are relatively harsh environments where most fish species experience high mortality rates (Jackson 1961; Welcomme 1985; Lowe-McConnell 1987; Lévêque 1997). The characteristics that enable it to survive in these situations, such as rapid growth, high fecundity, and a catholic diet, are commonly found in other successful invasive species. It is also an effective predator capable of feeding on prey up to 38% of its length (Lévêque 1997) as well as small prey such as shrimps (maximum length ~15 mm; Goudswaard et al. 2006) or dagaa (maximum mass ~2.0 g; Douthwaite 1976). An indication of its effectiveness as a predator — and a portent of things to come — was the discovery of 35 haplochromines in the stomach of a 55 cm Nile perch (Gee 1969).

In their native habitats, such as Lake Albert, Nile perch spawn in shallow water, and their fry shelter among vegetation where their disruptive colouration would help them to avoid predators (Gee 1964). In Lake Victoria, they are known to spawn in similar situations, and ripe and ripe-running females were recorded throughout the year, suggesting the possibility of continuous spawning although with a seasonal peak in November–December (Ligtvoet and Mkumbo 1990). Their ability to spawn throughout the year and to breed in a variety of conditions was suggested as a reason for their success as an introduced species (Ogutu-Ohwayo 1988).

While there is no direct evidence that haplochromines preyed on Nile perch eggs or fry, some must have done so, but they may not have had any substantial impact on Nile perch recruitment. The specialized egg-eating haplochromines, adapted to seizing relatively large and conspicuous eggs from mouth-brooding females (Witte and van Oijen 1995), were probably unable to adapt to eggs of Nile perch, which float but are small and transparent (Okedi 1970; Moreau 1982). These eggs are said to be planktonic (van Zwieten et al. 2016), in which case they might have been eaten by planktivores, but being laid among vegetation close to the shore they are probably not an important component of the zooplankton. Nile perch eggs are about 0.4 mm in diameter

(Moreau 1982) and therefore larger than most rotifers, but zooplankton samples that included rotifers have not reported any Nile perch eggs or larvae (Mavuti and Litterick 1991; Waya and Mwambungu 2004; Ngupula et al. 2010; Kiggundu et al. 2012). This is supported, furthermore, by evidence that small Nile perch are most abundant in shallow water and move into deeper waters as they grow larger (Katunzi et al. 2006).

Finally, the reproductive strategy of Nile perch may have minimized any impact of haplochromine predation. At the time of the Nile perch explosion, females reached maturity at about 70 cm (Ogutu-Ohwayo 1988) and their modal length was around 100 cm (Hughes 1992), which means they could produce from 1.1 to 3.1 million eggs per fish. Nile perch are total spawners, where all ova ripen at the same time and are shed in one batch (Lévêque 1997). This is the well-known reproductive strategy of predator swamping (Ims 1990), which ensures that a considerable number of eggs or larvae will survive even when mortality is high (Furey et al. 2016). Thus, even if only 0.0001% of these eggs survived, each Nile perch female would leave 100–300 descendants in a single spawning (many more than a single haplochromine could produce).

The proportion of piscivores in the haplochromine community before the Nile perch introduction is unknown, but scattered data suggest they may not have been numerous. In 1964, nine *Haplochromis* species were collected in the Bugungu Lagoon, Uganda, of which five were piscivores and made up 6.6% of the total catch (Welcomme 1965). This semi-enclosed lagoon may not, however, represent the lake as a whole, and a possibly more representative sample of 47 975 haplochromines, collected in Uganda in 1965, mostly by poisoning, included only 291 “predators” or 0.61% of the total (Hamblyn 1966). An estimate from the Mwanza Gulf in 1978 found that they made up 1.1% of the samples in 1978 (Witte et al. 2007a) but only 0.26% of samples in 1979–1980 (Witte et al. 1995).

This is much less than the predation pressure Nile perch are exposed to in their native range. In Lake Albert, for instance, the top piscivores Nile perch and *Hydrocynus* spp. made up around 25%–35% of the catch in seine and gill nets, while omnivores capable of preying on juvenile Nile perch such as *Bagrus bajad* made up to 15% of the 51 mm seine catch (Ogutu-Ohwayo 1995). Elsewhere in the Nile system, they co-exist alongside a diverse array of piscivores and omnivores (Abdel-Latif 1984; Hickley and Bailey 1987), and their fry must possess innate predator recognition and avoidance mechanisms that enable them to survive in these situations. These would have helped them to avoid haplochromine predation in Lake Victoria.

In any case, the window of opportunity for haplochromines to prey on Nile perch would have been very small, since they grow rapidly, reaching 5 cm in about 2 months (Hughes 1992). Piscivorous haplochromines, mostly 10–16 cm in length (Witte and van Oijen 1995), would have been unable to feed on Nile perch at this size. There is therefore little evidence to support the notion that haplochromines substantially influenced Nile perch recruitment and population growth. The recruitment depensation hypothesis is further undermined by the fact that the Nile perch population grew continuously throughout the expansion phase.

Impact of fishing

Even without recruitment depensation, the “bottom-up” hypothesis still requires an external influence to bring about a haplochromine decline prior to the Nile perch explosion. The intensive industrial trawl fishery in the Mwanza Gulf clearly depleted haplochromine stocks (Fig. 3b), but the situation here was not representative of the lake as a whole. It has also been argued that fishing selectively depleted the population of haplochromine piscivores, thus improving the survival of Nile perch fry. There is no evidence to support this view, and notions of a differential decline need to be considered more closely.

Table 7. The mean number of haplochromines in the major trophic groups caught in the Nyanza Gulf, 1979–1992.

Main trophic group	1979–1980	1981–1982	1983–1984	1985–1986	1987–1988	1990–1992
Detritus–phytoplankton	1101.2	791.2	216.3	18.8	0	1.0
Zooplankton	153.1	187.9	45.7	62.8	0.3	18.3
Insects	25.6	15.5	1.1	0	0	0
Molluscs	5.4	0.5	0.1	0	0	0
Fish	3.5	2.0	0.1	0	0	0
Other items	32.8	7.3	0.1	0	0	0
Total	1321.5	1004.4	263.5	81.5	0.3	19.3

Note: Data are from station G and are expressed as the mean number in a 10 min bottom trawl (from Witte et al. 1995).

Table 8. The biomass (kg·ha⁻¹) of haplochromines and Nile perch in the Nyanza Gulf, Kenya, 1969–1977.

	1969–1970	1975	1977
Haplochromines	35.8	32.7	28.6 (–6.5)
Nile perch	0	0.8	2.8 (169.0)

Note: The values in parentheses represent the annual rate of change (%) between 1975 and 1977 (from Muller and Benda 1981).

In the Mwanza Gulf, the total number of haplochromines caught in 10 min bottom trawls decreased by 94% between 1979–1980 and 1985–1986, with the least numerous groups apparently declining most rapidly (Table 7). If the values are standardized, with the highest value equal to 1.0 and plotted against time, then both the most numerous group, the detritivore–phytoplanktivores, and the piscivores declined at the same rate (slope $b = -0.35$ in both). This suggests that piscivores were not selectively removed by fishing, and their catch rate would have fallen to 0.06 per haul or effectively zero by 1985–1986. Moreover, the 1979–1980 data are derived from a total of 32 hauls, while there were only eight hauls in 1985–1986, and the likelihood of catching scarce individuals will diminish when sampling effort is low.

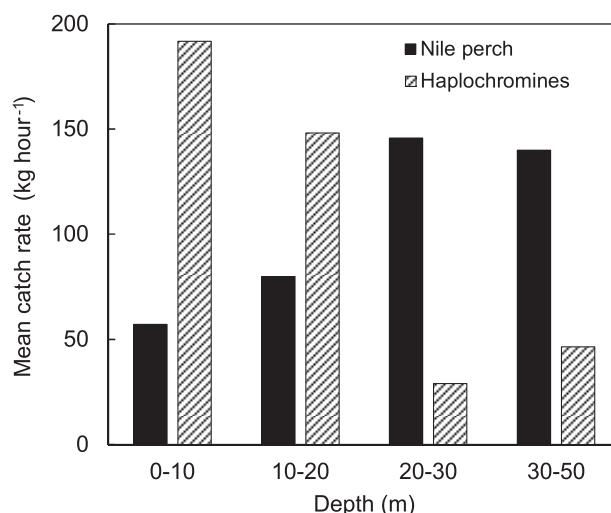
There is no evidence from anywhere else in the lake that haplochromines decreased substantially before the Nile perch explosion (Tables 2 and 3). Small-meshed gill nets and beach seines were being used around the lake to catch haplochromines and the juveniles of larger species (Marten 1979b). Mosquito nets, used mainly to catch dagaa but also small haplochromines and juvenile Nile perch, were becoming increasingly common and were believed to have damaging effects on fish stocks (Asila 1997). It is not obvious, however, that these gears depleted either haplochromines or Nile perch. Trawl surveys in the heavily fished Nyanza Gulf indicated a small (6%) decline in haplochromine biomass but a very large increase (169%) in Nile perch between 1969–1970 and 1977 (Table 8).

Eutrophication

Widespread hypoxia caused by eutrophication was said to be primarily responsible for the loss in haplochromine abundance and diversity (Kolding et al. 2008; Hecky et al. 2010; van Zwieten et al. 2016). The question that needs to be asked in connection with eutrophication is if conditions in the lake deteriorated to the point where almost all native species, including air-breathing species, such as the catfish *Clarias gariepinus* and lungfish *Protopterus aethiopicus*, succumbed to hypoxia, then how did Nile perch, Nile tilapia, and dagaa survive and flourish? This question is especially pertinent in view of the fact that haplochromines are substantially more tolerant of hypoxia than Nile perch, while dagaa is the least tolerant species (Witte et al. 2005).

It was suggested that hypoxic deep waters (>40 m), where Nile perch could not survive, provided a refuge for haplochromines, but as anoxia increased they were forced into shallow water, where they were exposed to the predator (Kaufman and Ochumba 1993; Hecky et al. 1994; Bundy and Pitcher 1995; Ochumba 1995). This idea is countered by evidence that Nile perch penetrated

Fig. 8. Catch rates of haplochromines and Nile perch in bottom trawls, in relation to depth, Emin Pasha Gulf, Tanzania, June 1985. Data are from Goudswaard and Ligetvoet (1987).



deep water from the beginning of its population explosion. For example, trawl samples from the Emin Pasha Gulf, Tanzania, in June 1985 (just before the haplochromine collapse) revealed that Nile perch was most numerous at depths of 20–50 m while haplochromines were mostly found from 0 to 20 m (Fig. 8). Similar findings were reported from the Mwanza Gulf (Goudswaard and Ligetvoet 1987). Furthermore, Nile perch is known to enter the hypoxic layer regularly and can probably forage there for short periods (Wanink et al. 2001).

Another consequence of eutrophication was the fish kills that occurred in the mid-1980s, but these had little impact on the haplochromines, since they had already collapsed. The 1984–1985 kills in Kenya involved only Nile perch and Nile tilapia (Ochumba 1990). There were no kills attributable to hypoxia in the Mwanza Gulf between 1977 and 1987, but after the haplochromine collapse, several mass mortalities of Nile perch occurred, with a particularly large one in April 1988 (Wanink et al. 2001; Witte et al. 2005).

Increased turbidity resulting from dense algal blooms interferes with mate choice in haplochromines, since females select males on the basis of colouration. There is evidence that poor visibility caused by these algal blooms may have affected their reproduction resulting in hybridization (Seehausen et al. 1997a, 1997b; Witte et al. 2007a) and even breeding failure in some species (Witte et al. 2000). It was further suggested that decreased prey selectivity resulting from low visibility would lead to increased interspecific competition as a result of loss of feeding specialization. This would have a negative impact on species co-existence, especially in those species that are visual predators of highly evasive prey (Seehausen et al. 2003).

Table 9. Changes in the mean (\pm standard deviation) Secchi disc visibility (m) measured in inshore (<20 m) and offshore (>20 m) waters of Lake Victoria during lake-wide surveys.

Date	Inshore	Offshore
1927	2.2 \pm 0.84	7.5 \pm 1.9
2000–2001	2.0 \pm 0.62	3.2 \pm 1.1
2006–2009	1.4 \pm 0.62	3.3 \pm 1.2

Note: Data are from Graham (1929) and Sitoki et al. (2010).

The difficulty here is that these findings postdate the haplochromine collapse, and it remains unclear how much turbidity contributed to this event, especially as average inshore transparency did not change considerably between 1927 and 2000–2001 and much less than in offshore waters (Table 9). The decrease in inshore transparency between 2000–2001 and 2006–2009 could reflect increasing silt loads from degraded land in the basin, estimated to be about 6.5×10^6 t \cdot year $^{-1}$ (Mnyanga et al. 2005). Transparency is, of course, highly variable and can be affected by differences in sediment and phytoplankton concentrations, which can also affect spectral attenuation as well. Thus, transparency decreased substantially in the Mwanza Gulf (Witte et al. 2005), possibly because of an increase in sediment loading, since the gulf is at the mouth of a river and the surrounding catchment is heavily degraded (Mnyanga et al. 2005). If turbidity was affecting haplochromine reproduction, it would surely have been localized and any impacts on the population would most likely have been progressive and cumulative. It is difficult to see how this could have contributed to the catastrophic collapse of the haplochromines.

Finally, van Zwieten et al. (2016) suggest that long-term eutrophication could have contributed to the haplochromine decline by reducing resources specifically available to them but not to Nile perch. Their argument centered around changes to the zooplankton, specifically the reduction of cladocerans, which was said to have changed the availability and quality of food at the base of the haplochromine food web. This was thought to have depleted the food resources available to juvenile and zooplanktivorous haplochromines. It is unclear why changes in the plankton should have deprived the haplochromines of a major food source while at the same time allowing planktivorous Nile perch fry and dagaa to flourish.

A fourfold increase lake fly abundance, including the zooplanktivorous dipteran *Chaoborus*, is mentioned in van Zwieten et al. (2016), although they did not specifically identify them as a food source for Nile perch, haplochromines, or dagaa or directly implicate them as a cause of the plankton decline. There are few quantitative estimates of dipteran abundance in Lake Victoria, but those that are available do not indicate a major increase at the time of the Nile perch explosion (Table 10). Benthic invertebrate populations can vary extensively, depending on the nature of the substrate, aquatic vegetation, and so on, and they remain as a major gap in the ecological data from Lake Victoria.

The climatic event

The second external factor that might support the bottom-up hypothesis is the climatic event that lasted from 1976 to 1983 (van Zwieten et al. 2016). The data in this paper come from a single locality on the western shore of the lake and may not reflect the full complexity of the lake's climate, which varies from north to south, while it also generates its own climate (Song et al. 2004; Anyah et al. 2006).

During this period, air temperature and wind speeds were well below average while relative humidity was above average. It was inferred that this prolonged period of low wind stress led to strengthened stratification in the lake (Kolding et al. 2008; MacIntyre 2013; MacIntyre et al. 2014). This was thought to have

limited vertical mixing, resulting in a larger anoxic volume in the deeper waters and substantially increasing the availability of phosphorus liberated from internal sedimentary sources. The resultant algal blooms together with anoxia were then thought to have contributed to the demise of the haplochromines. This event was said to have been exacerbated by an El Niño event in 1982–1983, which led to increased stratification.

There is no direct evidence to support this contention owing to the lack of limnological data from Lake Victoria between the 1960s (Talling 1966) and the 1990s (Hecky 1993; Mugidde 1993; Hecky et al. 1994). Conclusions based on data from the 1990s, after the major changes in the lake had already occurred, entail the risk of projecting existing conditions back into the past. It was suggested that there had been a steady decline in offshore oxygen concentrations from about 1960 onwards and that in the 1970s and 1980s waters deeper than 70 m experienced severe anoxia (Hecky et al. 1994; Verschuren et al. 2002). This was inferred from a shift in the dominant chironomid genera found in the deep-water sediment core V95-5MC (Verschuren et al. 2002). While this reflects the conditions in the sediments and at the sediment-water interface, the explanation may be less simple, since *Chironomus* can be abundant in oxygenated water. For instance, it was common in Ekunu Bay, Uganda, in water 10 m deep where oxygen saturation ranged from 60% to 80%, and although samples were not fully quantitative, the mean and maximum densities were approximately 800 and 1000 m $^{-2}$, respectively (MacDonald 1956). *Chironomus* was also abundant and the only genus in newly inundated drawdown zones, rich in organic matter but well-oxygenated, of two Zimbabwean reservoirs, one oligotrophic and the other eutrophic (McLachlan 1970; Marshall 1978).

The size-based model

The size-spectrum model proposed by van Zwieten et al. (2016) addressed four specific questions related to the depensation hypothesis, namely (1) was stable co-existence between haplochromines and Nile perch possible and if so, then was it likely that (2) fishing, (3) predation, or (4) limnological conditions weakened depensation sufficiently to initiate the Nile perch explosion. Questions 2, 3, and 4 seem to be redundant since there is no evidence that haplochromines exerted any depensatory effects on Nile perch. Indeed, the fact that Nile perch numbers grew throughout the establishment phase confirms this, while the biological characteristics of Nile perch suggest that they would be able to resist haplochromine predation.

It is unclear what “stable co-existence” might mean, but van Zwieten et al. (2016) concluded that this had been the situation during the two decades prior to the Nile perch expansion. If this means that populations remained more or less the same, varying within narrow limits, during this period, then it did not exist in Lake Victoria. In fact, the Nile perch population was expanding quite rapidly in the northern waters of the lake from the time of its introduction. As mentioned, the early warning signal of increased Nile perch recruitment was evidently overlooked even though this fish was becoming increasingly important in the fisheries (Achieng 1990; Acere 1988; Asila 1997). The extent of this oversight is revealed by a statement in van Zwieten et al. (2016), who wrote “... large numbers of Nile perch recruits only appeared in Tanzania in the second half of 1985 and in Uganda perhaps as late as 1989.” While this may be true for Tanzania, it is highly improbable for Uganda where the cumulative Nile perch catch between 1980 and 1988 exceeded 600 000 t (Ogutu-Ohwayo 1995) and could not have been achieved without massive recruitment.

The hypothesis proposed by van Zwieten et al. (2016) is that a switch from haplochromine dominance to Nile perch depended on size-related differences in mortality caused by predation on eggs and juveniles. They attributed the relatively stable co-existence between adult Nile perch and haplochromines over two decades to intraguild, size-dependent predation. This presumably

Table 10. Estimates of the density of dipteran larvae in the sediments of Lake Victoria, 1951–1952 to 2001–2002.

Locality	Density (no.·m ⁻²)	% <i>Chaoborus</i>	Source
Ekunu Bay, Uganda, 1951–1952	3000	75	MacDonald 1953
“Lake Victoria”, 1970–1972	1700	—	Marx 1978
Northern waters, 1995–1997	1266	66	Mwebaza-Ndawula et al. 2004
Kenyan waters, 1996–1997	330	—	Muli 2005
Fielding Bay, Uganda, 2001–2002	1104	+	Sekiranda et al. 2004
Hannington Bay, 2001–2002	276	22	Sekiranda et al. 2004
Murchison Bay, 2001–2002	459	+	Sekiranda et al. 2004

Note: The symbol “+” indicates that *Chaoborus* were present but in insignificant ($\alpha > 0.05$) numbers. The estimate from Marx (1978) is an approximation; she presented the data in an unusual form and this value is based on her station V9, which recorded the highest density of invertebrates. She did not report any *Chaoborus*.

refers to predation of Nile perch eggs and fry by haplochromines, suggested by the size difference between haplochromine fry at the time they leave the female’s mouth and Nile perch hatchlings. This is illustrated in their Fig. 2, which shows a relatively advanced haplochromine juvenile about 13 mm in length and a Nile perch larva one-tenth its size (about 1.5 mm). This figure implies that the seemingly helpless Nile perch would be easy prey for the haplochromine, but this is misleading. It takes no account of the fecundity and breeding behaviour of Nile perch or predator avoidance mechanisms of the fry, which include disruptive colouration that varies according to habitat (Nyboer et al. 2014).

The maternal mouth-brooding strategy of haplochromines can protect their juveniles from predation, allowing them to be released at a relatively advanced stage of development. But this will be a successful strategy only if they are able to defend their broods and minimize losses from predators. Once they were exposed to Nile perch, this advantage was lost because a mouth-brooding female haplochromine swallowed whole by a Nile perch leaves no descendants and will never spawn again.

The final question was whether or not limnological changes weakened depensation and contributed to the Nile perch upsurge. This too has already been discussed, and it is sufficient to comment that if there was no depensation then limnological changes could not have weakened it. More pertinently, would the haplochromines have collapsed so catastrophically if Nile perch had not been present? It seems improbable, because although the lake might have changed progressively, it is likely that haplochromines would have adapted, as some have already done (Katunzi et al. 2003; Kishe-Machumu et al. 2008, 2015a, 2015b; Witte et al. 2008; van Rijssel et al. 2017).

Finally, some of the conclusions drawn from this model do not reflect reality. One of these is that the continued expansion of Nile perch into deep offshore waters, as well as its continued increase in relative biomass, indicates that the colonization of Lake Victoria by Nile perch is not yet complete (van Zwieten et al. 2016). This is a puzzling conclusion, since Nile perch have been in the lake for 60 years and its population exploded 35 years ago. What parts of the lake remain to be colonized? In fact, Nile perch occur throughout, although they tend to be more numerous in inshore waters (Getabu et al. 2003; Everson et al. 2013; Taabu-Munyaho et al. 2014) and at most depths, with numbers declining at depths >50 m (Okaronon and Ntiba 2000; Mkumbo et al. 2005; Taabu-Munyaho et al. 2013; Table 11). The biomass of Nile perch varies (Table 6), but there is no reason to suppose that it is continuously increasing.

Two recent papers discussed theoretical models of the Nile perch population growth in Lake Victoria. The first (van de Wolfshaar 2014) proposed recruitment depensation as a mechanism that delayed the explosive growth of this species. The second (Downing et al. 2014) modelled various options, including depensation and predation, and concluded that the timing of the Nile perch explosion could be explained by simple logistic growth. However, they argued that data on the introduction and invasion of Nile perch in

Table 11. Catch rates (kg·h⁻¹) of haplochromines (Haplos) and Nile perch in relation to depth in Lake Victoria, 1969–1971 and 1997–1999.

Depth (m)	1969–1971		1997–1999	
	Haplos	Nile perch	Haplos	Nile perch
0–9	493.8	2.0	3.7	173.5
10–19	800.2	0.6	2.9	136.3
20–29	639.5	0.4	1.5	168.3
30–39	507.5	—	1.5	137.9
40–49	448.0	—	1.1	30.9
50–59	486.3	—	0.2	9.9
60–69	196.3	—	—	—
70–79	29.6	—	—	—

Note: Data for 1969–1971 are for the lake as a whole, since Kudhongania and Cordone (1974) did not give catch rates by species for each country; 1997–1999 values are from Uganda (Okaronon et al. 1999), since there were no comparable data from the other countries.

Lake Victoria were too few and scattered to produce any insight into the mechanisms or biology behind the invasion process. While there is some truth in this conclusion, there are sufficient data to explain the growth of Nile perch in Lake Victoria and confirm the view that logistic growth alone can explain the Nile perch explosion.

The top-down hypothesis is straightforward, requires few assumptions, and is essentially a simple predator–prey relationship that conforms to the law of parsimony. It also gains credibility from the fact that similar impacts of introduced predators are well known in both terrestrial and aquatic ecosystems (Pitt and Wilmer 2007). Whole-lake ecosystem disruption following the introduction of a non-native predator was first documented over 40 years ago (Zaret and Paine 1973), and many cases have since been reported (e.g., Eby et al. 2006; Pelicice and Agostinho 2009; Cucherousset and Olden 2011; Atkinson and Domske 2015). Lake Victoria is yet another example, albeit on a larger scale than many others.

The chronology of events also supports the view that the collapse of the haplochromines preceded and may have caused the cascading sequence that led to accelerated eutrophication. It confirms the chronology published in Verschuren et al. (2002), which indicated that the Nile perch explosion, which led to the haplochromine collapse, began in about 1980 and massive algal blooms followed in about 1985.

Events that followed the introduction of Nile perch into other lakes also support this hypothesis. It devastated haplochromine populations in Lakes Nabugabo and Kyoga (Uganda), although there has been some recovery in both after intensive fishing of Nile perch (Chapman et al. 2003; Paterson and Chapman 2009; Mbabazi et al. 2004; Ogutu-Ohwayo et al. 2013). Some satellite lakes of Lake Kyoga, inaccessible to Nile perch, still retain their haplochromine fauna, further confirming the impact of this predator. Aquatic vegetation played an important role in both of these

lakes by sheltering haplochromines, and the importance of cover was emphasized in Lake Victoria by the fact that rock-dwelling species were less severely reduced by Nile perch than those living in open waters (Witte et al. 2007a).

The bottom-up hypothesis founders on the lack of direct evidence and relies heavily on assumptions that are not supported by data. An examination of the biological aspects of Nile perch and haplochromines suggests that its cornerstone, recruit depensation, has been overstated and predation by haplochromines may have had little impact on Nile perch. The possibility that cannibalism may have been the major cause of mortality in Nile perch cannot be discounted; it became important towards the end of the expansion phase but could have occurred during the establishment phase as well.

So far, the most important drivers of change in the fish stocks of Lake Victoria are Nile perch and fishing, the former causing native species to decrease and the latter by enabling some recovery through the removal of Nile perch. No one would disagree that eutrophication is an important ecological driver in the lake, but the view that it is an unrelenting and continuous process and the major long-term threat to the fisheries in Lake Victoria (Kolding et al. 2008) has yet to be substantiated. Its most important impact so far is a dramatic increase in fisheries productivity, with the annual catch now around one million tonnes, a tenfold increase on catches before 1980 (Mkumbo and Marshall 2015).

The model developed by van Zwieten et al. (2016) attempted to determine whether or not there could be a “stable co-existence” between haplochromines and Nile perch. Given the changes that have occurred in the lake, it seems unlikely. Such a co-existence seemed to prevail from the time Nile perch were introduced until the time its population exploded some 20 years later, but this was illusory. Instead, Nile perch was steadily increasing until reaching a point where the haplochromine population lost its resilience and collapsed. For the next 20 years the lake was essentially a Nile perch-dominated lake, with only dagaa and Nile tilapia surviving in any numbers. The lake now seems to be entering a new phase, with haplochromines beginning to recover and Nile perch possibly declining. How long this will last and what changes may occur in future remains to be seen.

Management plans for the lake (e.g., Anonymous 2009, 2013) call for a “recovery” of the Nile perch stocks (i.e., increasing the number of more profitable large fish). If this objective were to be achieved, the result could be another haplochromine collapse and aggravated eutrophication. Little-noticed, but potentially very important, is the growing commercialization of the shrimp stocks, which are caught both for poultry feed and export to neighbouring countries (Budeba and Cowx 2007). If shrimps were severely depleted by fishing (or through competition from the recovering haplochromines), the survival of young Nile perch could be severely compromised, thus negating any management measures designed to “recover” the Nile perch fishery.

The model presented by van Zwieten et al. (2016, p. 637) concluded with the statement that “Haplochromines and *Lates* species co-exist in other African Great Lakes as well, and so the Nile perch outburst in Lake Victoria, possibly a consequence of the haplochromine demise, was perhaps an anomaly.” This view is disingenuous and misleading. Nile perch do indeed occur naturally in Lakes Albert and Turkana, but their fish faunas are Nilotic and co-evolved with Nile perch. Importantly, both lakes lack the diverse and highly specialized haplochromine species flocks that evolved in isolation in the other Great Lakes. Lake Tanganyika is the only one that supports both a haplochromine species flock (with many fewer species than Lakes Victoria and Malawi) as well as four relatively specialized endemic *Lates* spp. (Coulter 1991). These two groups share a long evolutionary history, perhaps extending over 9–12 million years (Cohen et al. 1993).

The situation in Lake Victoria is not an anomaly but is the entirely predictable consequence of introducing a voracious top

predator into an ecosystem where no such species had ever existed. Nile perch has a high reproductive potential, can withstand heavy mortality, and faced no competition in the lake. Furthermore, its main prey species were naïve and had never been exposed to such a predator. It was introduced into the lake specifically to utilize the haplochromines (Anderson 1961), which it did with remarkable efficiency. The potential impacts of introduced species were known at the time of the introduction (Elton 1958), but the extent and severity of its consequences were evidently unforeseen. The data and sequence of events presented here clearly indicate that Nile perch was the cause, and not the consequence, of the haplochromine decline and was thus the principal agent of change in Lake Victoria.

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