Spatial and seasonal patterns in the feeding habits of juvenile *Lates niloticus* (L.), in the Mwanza Gulf of Lake Victoria

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Abstract

Flexibility in the feeding habits of juvenile Nile perch (1–30 cm total length) was studied from September 1988 to September 1989 at four sites (depth range: 1–25 m) in the Mwanza Gulf of Lake Victoria. During this period haplochromine cichlids were virtually absent in the area. We looked at the combined effects of predator size, season and habitat. Stomach content analysis showed that with increase in size, the diet of Nile perch shifted from zooplankton and midge larvae, to macro-invertebrates (shrimps and dragonfly nymphs) and fish. At a size of 3–4 cm Nile perch shifted from size-selective predation on the largest cyclopoids to predation on the largest, less abundant, calanoids. Zooplanktivory ended at a size of ca. 5 cm. Although an ontogenetic shift in the diet of juvenile Nile perch was obvious at all sampling stations, the contribution of prey types appeared to be habitat related. With increasing water depth the frequency of occurrence in the diet of most prey types decreased, but that of shrimps increased. At the entrance of the gulf (20–25 m deep) shrimps were the main food source throughout the year. Halfway the gulf (12–16 m), Nile perch showed seasonality in their feeding behaviour. Shrimps were taken there especially during the rainy season (January to May) when their densities at this station were high, whereas cannibalism prevailed during the rest of the year. In an environment with Nile perch and dagaa as alternative prey, shrimps were taken almost exclusively. They could be regarded as a key prey for Nile perch between 5 and 30 cm.

Introduction

In the 1950s and early 1960s Nile perch, *Lates niloticus* (L.), from Lake Albert (Uganda) and Lake Turkana (Kenya) were introduced into Lake Victoria (Hamblyn, 1962; Arunga, 1981; Welcomme, 1988; Pringle, 2005). The Nile perch population rapidly increased in the 1980s (Ogutu-Ohwayo, 1990a). In the Mwanza Gulf, southern part of Lake Victoria, Nile perch have been recorded from experimental trawl catches since 1972. However, until 1982 the mean catch rates were low (< 5 kg h^{-1}). In 1983 Nile perch catches suddenly increased to ca. 20 kg h^{-1}, and in 1987 mean catch rates were over 100 kg h^{-1} (Barel et al., 1991; Witte et al., 1992). Concomitant with the increase of Nile perch, the haplochromine cichlids in the sub-littoral and offshore waters vanished almost completely. In contrast, the catch rates of the cyprinid *Rastrineobola argentea* (Pellegrin), locally called dagaa, increased (Wanink, 1991, 1999). Densities of the shrimp *Caridina*

nilotica (Roux) also increased strongly during this period (Goudswaard et al., 2006). At about the same time, a strong eutrophication of the lake was noticed. This resulted in algae blooms (Ochumba & Kibaara, 1989; Hecky, 1993; Mugidde, 1993), decreased levels of dissolved oxygen (Kaufman, 1992; Hecky et al., 1994, Wanink et al., 2001) and decreased water transparency (Seehausen et al., 1997; Witte et al., 2005).

During the past decades several studies (Hamblyn, 1966; Gee, 1969; Ogari, 1985; Hughes, 1986, 1992; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b, 1993; Mkumbo & Ligtvoet, 1992; Schofield & Chapman, 1999) have been made on the diet of Nile perch in Lake Victoria, and in lakes Kyoga and Nabugabo where the species had been introduced as well. A shift in diet, from one dominated by haplochromine cichlids to one dominated by the shrimp *C. nilotica*, was noted in lakes Kyoga and Victoria in the years after the introduction (Hamblyn, 1966; Hughes, 1986; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b; Mkumbo & Ligtvoet, 1992). In Lake Nabugabo, where shrimps appeared to be absent, fish (mainly dagaa and juvenile Nile perch) were the main prey types (Ogutu-Ohwayo, 1993; Schofield & Chapman, 1999). The above-mentioned studies explored changes in diet in relation to predator size, habitat and season, but not in a single study. As these factors are likely to be interdependent, they should be combined in one study to get a proper picture of Nile perch foraging. Such knowledge is important as, for instance, ontogenetic niche shifts may affect the dynamics of predator populations (Olson, 1996; Van Densen et al., 1996; Ludsin & DeVries, 1997; Salminen et al., 2001; Post, 2003). The present study aims to establish the feeding habits of juvenile Nile perch with a size range of 1–30 cm total length (TL) during a 1 year period along a trajectory in the Mwanza Gulf, from the very shallow inner parts to the deep entrance of the gulf. The major question was to what extent habitat and season influence size related diet shifts in Nile perch. The data were collected at a time when haplochromine densities in the area were extremely low (Witte et al., 1992) and provide an important reference point for current studies, as some haplochromine cichlids have shown resurgence in recent years (Witte et al., 2000).

Material and methods

Study area and fish sampling

The Mwanza Gulf is one of the larger gulfs at the southern end of Lake Victoria (Fig. 1). It has a length of about 60 km. The average width of the gulf is about 5 km. Four sampling stations were chosen along the north–south axis of the gulf (Fig. 1). Depths of the stations one to four were 1–2, 2–4, 12–16 and 20–25 m, respectively. The main body of the Mwanza Gulf has a soft muddy bottom and, apart from depth, the major difference among the habitats at these stations was the oxygen concentration. At the two deeper stations oxygen concentrations at 1 m above the bottom were low (<2 mg l^{-1}) during the months December to May in 1985–1987 (Wanink et al., 2001). Nile perch were sampled with MV Kiboko, a 105 HP trawler, using a bottom trawl with a head rope of 18 m and a 20 mm stretched codend mesh. Between September 1988 and September 1989 once a month four 30 min hauls were made at each sampling station. No sample was collected at station 1 in December 1988. All Nile perch up to 30 cm (or a sub-sample) were measured for total length to the nearest cm (digits ending at 0.5 were rounded to the nearest cm above) and analysed for stomach contents. These fish were mainly juveniles of less than a year old. At the time of the study, first maturity of male and female Nile perch in the Mwanza Gulf was at 35–40 and 50–60 cm, respectively (Witte & de Winter, 1995).

Zooplankton sampling

Zooplankton samples were taken with a 20 cm diameter zooplankton net (150 μm mesh) from a canoe during daytime (at the same time as trawling) at the two central stations (2 and 3) in the Mwanza Gulf. These stations were selected because they were closest to the research institute at Nyegezi, and juvenile Nile perch (<5 cm) were common at these localities. Both stations were sampled monthly from October 1988 till October 1989. In February 1989 no sample was taken at station 2. Three hauls were made per station in the lower three meters of the water column. This is the depth range where juvenile Nile perch concentrate during daytime
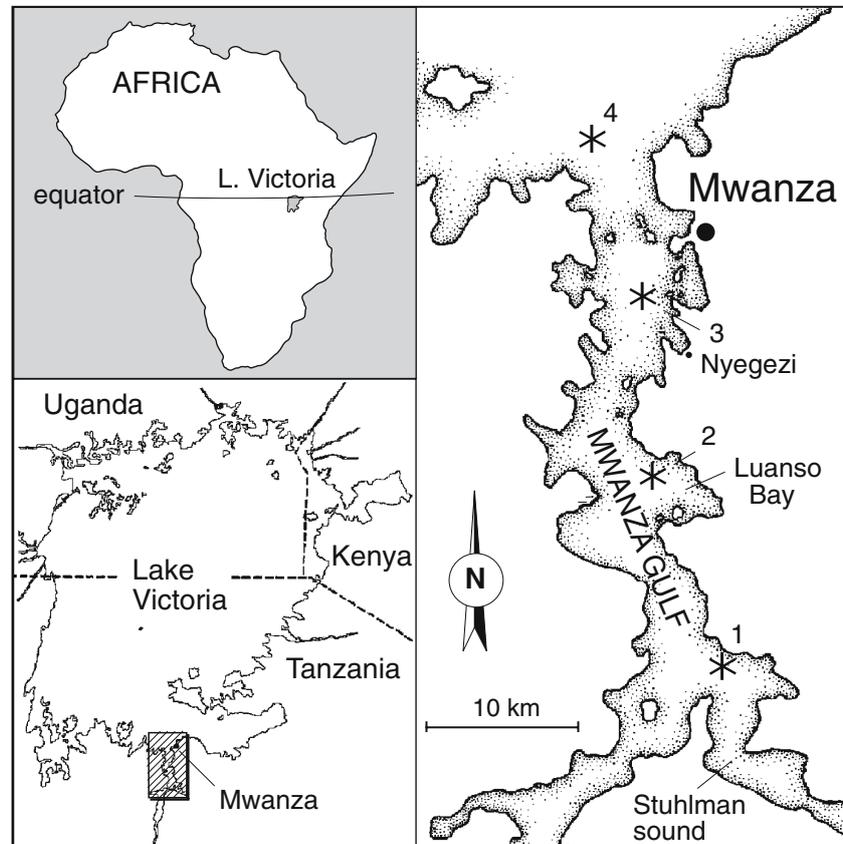
Figure 1. Mwanza Gulf with sampling stations: 1, 1–2 m; 2, 2–4 m; 3, 12–16 m; 4, 20–25 m deep.

(Goudswaard et al., 2004). The contents of the three hauls were mixed in a bottle containing a 5% formaldehyde solution. Each sample of zooplankton was divided into 10 equal parts with a whirling apparatus of Kott, and one tenth was counted under a microscope (Mous et al., 1995). Zooplankton was identified as cladocerans, or cyclopoid or calanoid copepods. In October 1988, when both densities of zooplankton and juvenile Nile perch were relatively high, the body length of copepods collected at station 2 was measured (up to 0.01 mm) as the distance from the head tip to the point where the abdomen joins the body. Due to time limitations, this was the only occasion on which sizes of zooplankters were measured.

Stomach examination

A total number of 6000 stomachs (station 1, 1612; station 2, 1208; station 3, 1574; station 4, 1606) were checked, with a minimum of 10 and a maximum of 135 per length class, per month, per station. The food categories distinguished were zooplankton (mainly cyclopoid and calanoid copepods), larvae of midges (chironomids and chaoborids), nymphs of dragonflies (Odonata, mainly Anisoptera), the atyid shrimp *C. nilotica*, and two fish species (dagaa and small Nile perch). The frequency of occurrence of a particular food item was calculated by expressing the stomachs containing this item as percentage of all stomachs containing food. The advantage of this method is that it is quick so that large numbers of stomachs can be studied. The disadvantage is that it gives little indication of the relative amount of each food category present (Hyslop, 1980).

In October 1988, fishes up to 4 cm from stations 2 and 3 were stored in 5% formaldehyde to investigate the occurrence of ontogenetic shifts in the selection for type and size of zooplankton. For that purpose stomach contents of about 30 fishes of the same cm-group were mixed. At least 200

zooplankters were counted. They were differentiated into calanoid and cyclopoid copepods. From stomachs of each cm group of Nile perch up to 4 cm, collected at station 2 in October 1988, the body lengths of 50 copepods were measured. It should be noted that size selection was investigated during a peak level in zooplankton density (see above). According to optimal foraging theory the chance of finding size selection is higher at high than at low prey densities (Krebs, 1978).

Statistics

Differences in monthly catch rates of size classes of Nile perch at each station were tested for normal distribution using the Kolmogorov–Smirnov test, with each month considered as an independent data point. As they were not normally distributed at all stations, the Kruskal–Wallis test was used to test for differences in catch rates (numbers per hour bottom trawling) at different stations. This test requires independence of the samples. We considered the monthly Nile perch catches at each station as independent data points because of the abundance of Nile perch, their high mobility (Ligtvoet & Mkumbo, 1990) and the large surface of the Mwanza Gulf. A Pearson correlation coefficient was calculated between the percentages of empty stomachs (combined for all stations) and fish size (per cm class). Correlation coefficients (1 tailed) were computed for the abundance of 1–5 cm Nile perch in trawl catches and their frequency of occurrence in stomach contents of larger individuals. When data were normally distributed we computed the Pearson correlation coefficient. When data were not normally distributed we computed the non-parametric Spearman's rank correlation coefficient. In case of multiple comparisons, the improved Bonferroni procedure was used to adjust the critical p-values (Haccou & Meelis, 1992). Statistical tests were performed with SPSS 11.5 for Windows.

Results

Spatial distribution of juvenile Nile perch

The mean abundance of 1–5 cm Nile perch was relatively low at station 4 (Fig. 2). The differences
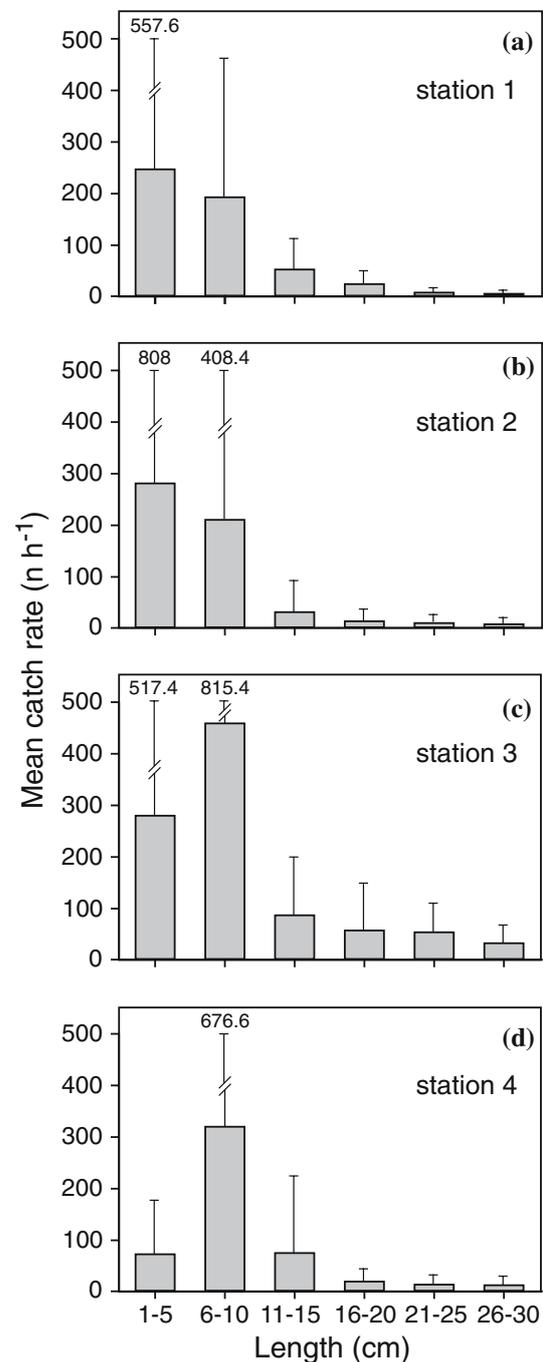

Figure 2. Mean catch rate (n h^{-1} + standard deviation) per 5-cm length class for juvenile Nile perch at stations 1–4 in the Mwanza Gulf.

in abundance between the four stations, however, were not significant (Kruskal–Wallis $p = 0.550$), because the high means at the other three stations

Table 1. Monthly catch rates (n h^{-1}) of 1–5 cm Nile perch, in trawl catches between September 1988 and September 1989, at stations 1–4 in the Mwanza Gulf

Month	Station 1	Station 2	Station 3	Station 4
Sept	1722	2218	570	47
Oct	635	796	24	78
Nov	28	141	25	72
Dec	0	35	27	0
Jan	92	124	22	0
Feb	11	2	70	94
Mar	20	231	15	148
Apr	18	37	528	157
May	356	4	594	0
Jun	11	1	1130	2
Jul	3	4	536	68
Aug	5	0	60	40
Sept	4	0	40	155

were the result of a few extremely large catches (Table 1). Months with high abundances of 1–5 cm Nile perch were September and October 1988 at stations 1 and 2, and September 1988, as well as April through July 1989 at station 3 (Table 1). The mean abundance of all other size classes did not differ among the four stations (Fig. 2; Kruskal–Wallis $p > 0.05$).

Ontogenetic and spatial foraging patterns

On average $21.2 \pm 5.6\%$ of all studied stomachs were empty. The average percentage of empty stomachs per cm class was positively correlated with fish length (Pearson correlation coefficient: $r = 0.459$, $p = 0.011$, $n = 30$) and ranged from 8.5% in the 3 cm class to 32.4% in the 23 cm class.

With the exception of station 4, where dagaa and dragonfly nymphs were not encountered in the stomachs, almost all prey types were eaten at each station (Fig. 3). However, there were clear differences in the frequency of occurrence of the prey types in the Nile perch stomachs in relation to both predator size and station. Over the whole study area, zooplankton formed an important food source for Nile perch <4 cm. Fishes of 4 to 5 cm switched to midge larvae at stations 1 and 2, to shrimps and midge larvae at station 3 and to shrimps only at station 4. At stations 1 and 2, the midge larvae were replaced by small Nile perch

(<5 cm) and by dagaa in fishes between 5 and 20 cm length, whereas dragonfly nymphs were mainly included in the diet of fishes >20 cm. The length range of dragon fly nymphs (Anisoptera) that were mainly eaten by Nile perch of that size was 4-18 mm (J.H.W., unpublished data).

At station 3 midge larvae and dragonfly nymphs were less important than at stations 1 and 2, and at station 4 they were absent from the diet. At stations 3 and 4, Nile perch of 3–4 cm and larger fed primarily on shrimps and to a lesser degree on juvenile Nile perch. At station 3 some dagaa were included in the diet of Nile perch >5 cm.

At stations 2 and 3, where planktivory was studied in detail, mean densities ($\pm$ standard deviation) of zooplankton in the lake during the period October 1988–October 1989 were 14.1 ± 11.9 and 46.5 ± 71.3 individuals per litre, respectively. The samples contained almost only copepods. Cladocerans and ostracods were encountered in 4 of the 23 samples, and in each of these only in low densities (cladocerans <1% and ostracods <4% of the total number of individuals). In October 1988 the zooplankton densities at stations 2 and 3 were relatively high (26.2 and 121.2 individuals per litre, respectively). In this month cladocerans were absent at station 2 and made up 0.3% of the zooplankton numbers at station 3 (Table 2). Zooplanktivorous Nile perch (<5 cm) at both stations consumed only copepods (Table 2). The proportion of the relatively large calanoids increased with fish size, and made up between 35 and 80% of the diet in fishes of 3–4 cm. It is likely that Nile perch of this size range were selectively preying on calanoids, since less than 10% of the copepod community in the lake consisted of calanoids. In a sample of Nile perch (1–4 cm) collected at station 3 in September 1988, cladocerans accounted for 2.4–7.6% of the diet, with no trend related to fish size. In this month the ratio of cyclopoids and calanoids eaten by 1–4 cm Nile perch showed a similar trend in relation to fish size as in October. However, the zooplankton composition in the lake was not determined in September.

At station 2, size-selective predation by Nile perch of both calanoid and cyclopoid copepods was observed. Fishes from 1 to 3 cm selected the largest cyclopoids from the size range available in the lake (Fig. 4a–c). The same was found for the calanoids in 4 cm Nile perch (Fig. 4d).
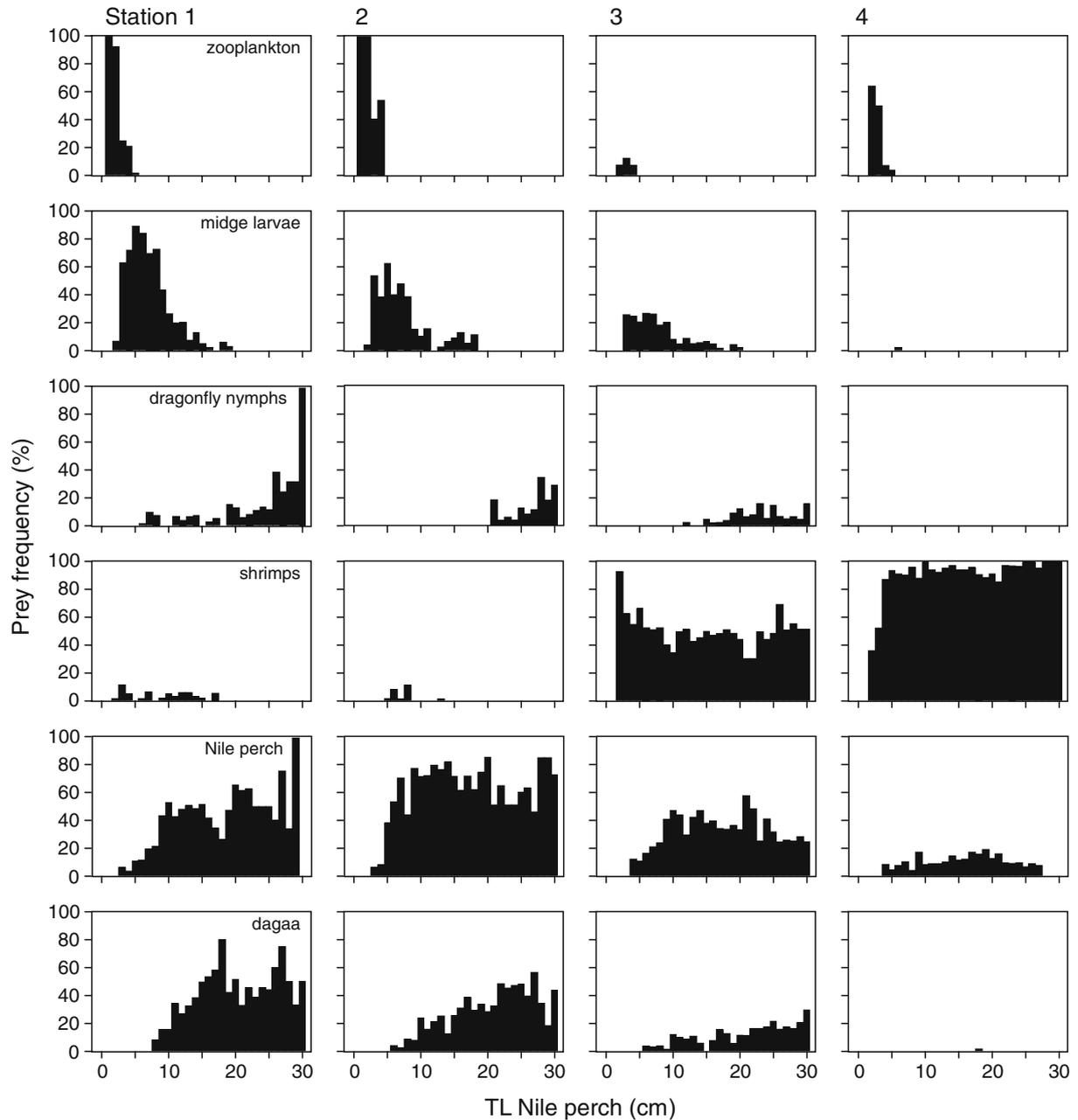
Figure 3. Frequency of occurrence of prey types in juvenile Nile perch per cm length class at stations 1–4. Dragonfly nymphs mainly comprise Anisoptera.

Seasonal patterns

As examples of seasonal patterns, the dominant prey types in stomach contents of the size classes 11–15 and 21–25 cm (Fig. 3) are depicted in Figure 5. At stations 1 and 2 (1–4 m deep) the main prey of Nile perch > 10 cm were juvenile Nile perch and dagaa, whereas at stations 3 and 4 (12–25 m deep) shrimps and Nile perch dominated their diet (Fig. 3). The only clear seasonal pattern was revealed by the high frequency of occurrence of shrimps in the diet at station 3 during the months January through May, whereas cannibalism was more important in the other months

Table 2. Zooplankton composition in the lake and in the diet of small Nile perch at station 2 and 3 in October 1988

Sample origin	Station 2			Station 3		
	% cycl.	% cal.	% clad.	% cycl.	% cal.	% clad.
Lake	93.1	6.9	0	92.9	6.8	0.3
Nile perch (1 cm)	91.9	8.1	0	84.0	15.9	0
Nile perch (2 cm)	91.8	8.1	0	59.7	40.3	0
Nile perch (3 cm)	64.0	35.9	0	39.4.	60.6	0
Nile perch (4 cm)	19.8	80.2	0	–	–	–

cycl. = cyclopoid copepods; cal. = calanoid copepods; clad. = cladocerans.

(Fig. 5e and f). Similar seasonal patterns were found for the size classes 16–20 and 26–30 cm. At station 4 no clear seasonal pattern was present and the frequency of occurrence of shrimps was high throughout the year (Fig. 5g and h). It should be noted, however, that during several months no Nile perch ranging from 11–15 to 21–25 cm were caught at station 4 (Fig. 5g and h).
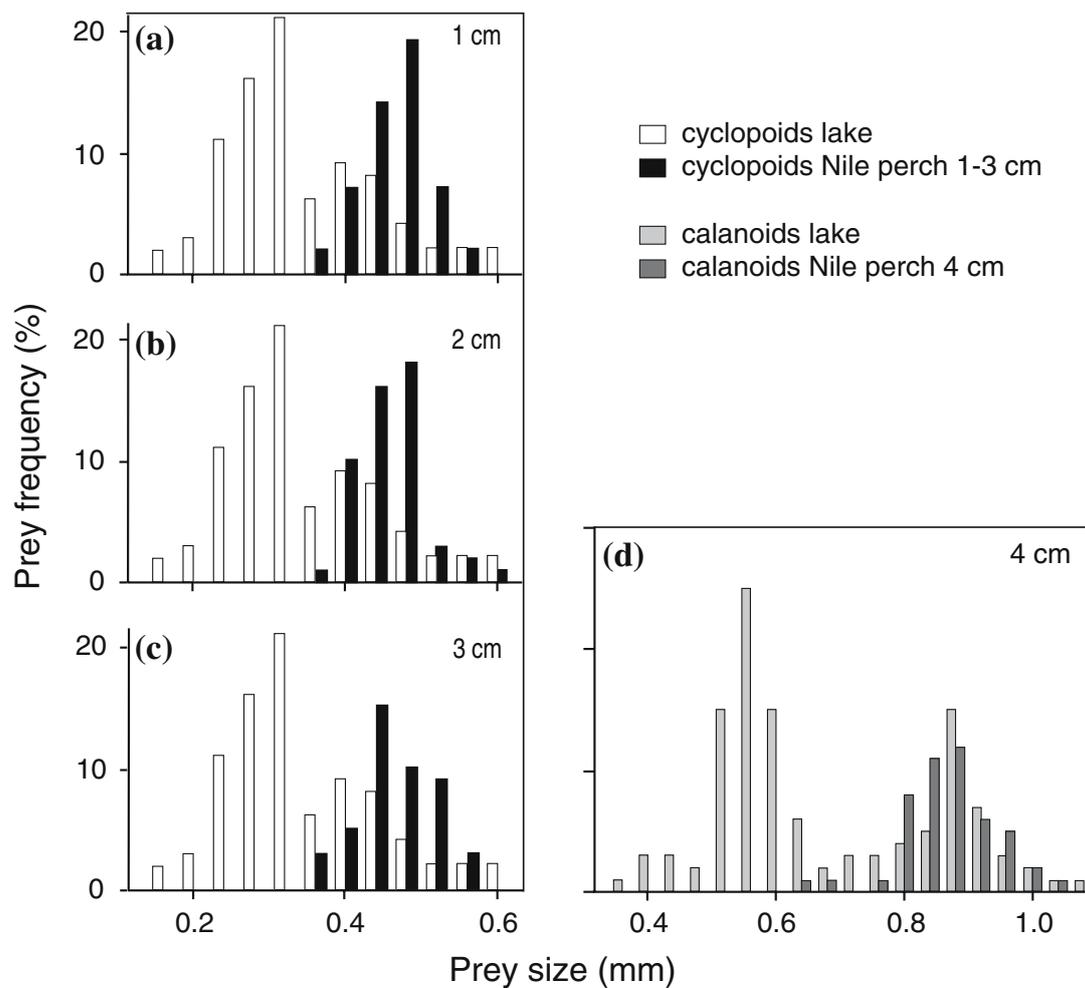

Figure 4. Size frequency distributions of cyclopoid and calanoid copepods in the lake and in the diet of Nile perch of: (a) 1 cm, (b) 2 cm, (c) 3 cm, (d) 4 cm length. Samples were taken at station 2 in October 1988.
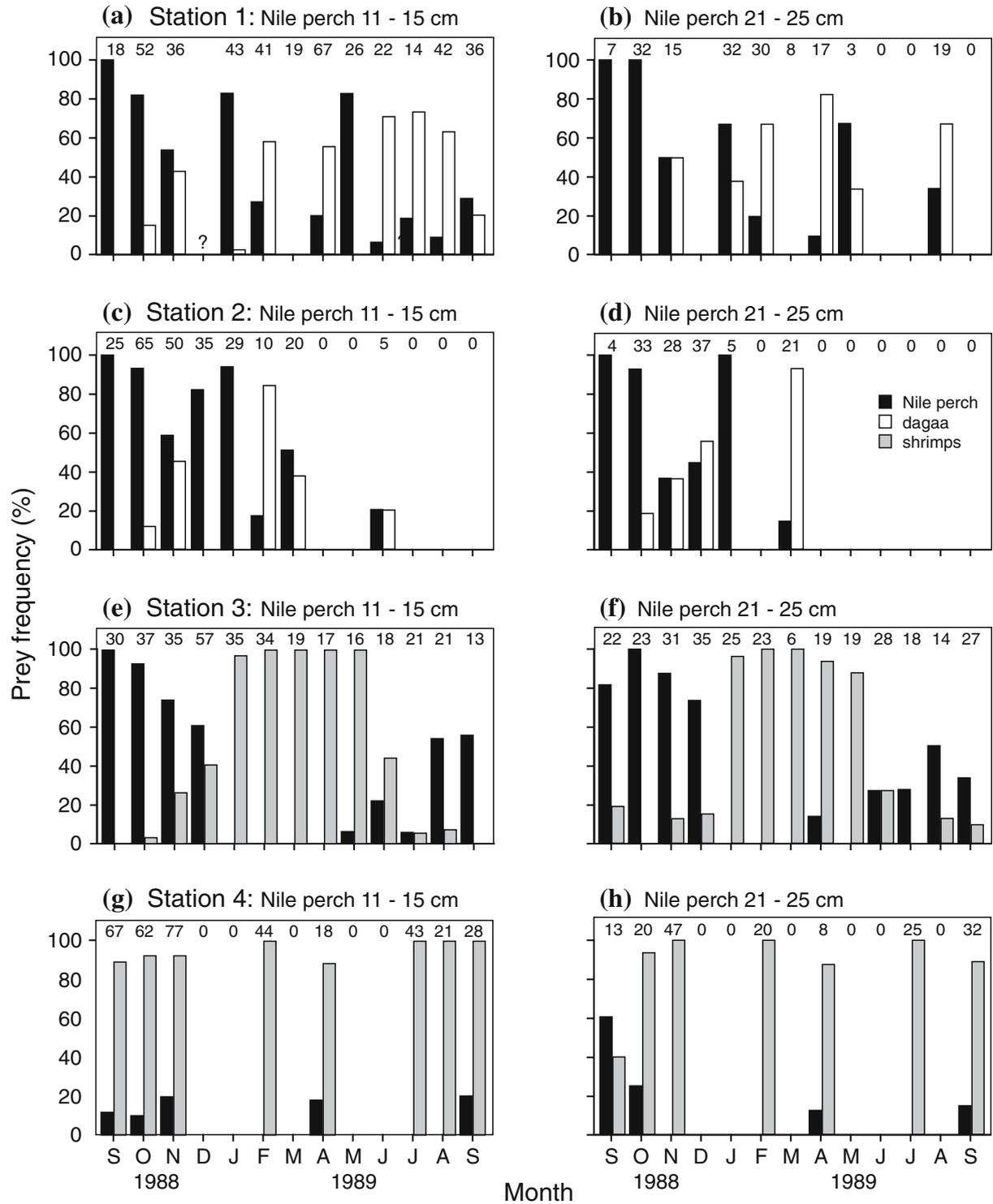
Figure 5. Frequency of occurrence of the main prey types (Nile perch ≤ 5 cm, dagaa and shrimps) of Nile perch of 11–15 and 21–25 cm at stations 1–4. Numbers above bars indicate numbers of fish investigated; a zero indicates that no fish of that size class were present. At station 1 no catch was made in December 1988. Note that similar patterns were observed in the length ranges of 16–20 and 25–30 cm.

Table 3. Correlation coefficients (*R*) and one-tailed *p*-values for the numbers per month of 1–5 cm Nile perch in the trawl catches and their frequency of occurrence in stomachs of larger size classes (11–15 and 21–25 cm; Fig. 5) from the same catches

Station	Nile perch (cm)	*R*	*p*	*n*
1	11–15	0.715	**0.007**	11
	21–25	0.758	**0.015**	8
2	11–15	0.690	0.029	8
	21–25	0.203	0.350	6
3	11–15	−0.197	0.260	13
	21–25	−0.185	0.273	13
4	11–15	0.452	0.131	8
	21–25	−0.330	0.165	7

For station 2, Spearman's rank correlation coefficient was computed, as the numbers of Nile perch ≤ 5 cm were not normally distributed. For the other station *R* refers to the Pearson correlation coefficient. Bold *p*-values are significant (Bonferroni corrected per station).

To investigate if cannibalism depended on the abundance of 1–5 cm Nile perch, we calculated correlations between the number of 1–5 cm Nile perch in the catch (Table 1) and their frequency of occurrence in stomachs of larger size classes (11–15 and 21–25 cm) of Nile perch (Fig. 5). For station 1 a significant correlation was found, whereas for the other stations the correlations were not significant (Table 3).

Discussion

Spatial distribution of juvenile Nile perch

In lakes Chad, Albert and Turkana, Nile perch seem to spawn at shallow, sheltered and vegetated sites and juveniles up to a length ca. 20–30 cm lived in the vicinity of submerged vegetation (Hamblyn, 1962; Hopson, 1972; Arunga 1981). In contrast, Nile perch as small as 10 cm were caught in the open waters of Lake Nabugabo, approximately 700 m from the shore (Schofield & Chapman, 1999). Ogari (1985) noted that in the Nyanza Gulf of Lake Victoria post-larval Nile perch were restricted to the inshore areas. However, juveniles above 3 cm were caught at all depths (0–20 m). Our data from the Mwanza Gulf confirm Ogari's (1985) observations; Nile perch smaller than 5 cm occurred as far as 3 km offshore, at depths of more

than 20 m. Among these juveniles even individuals of only 1 cm were present. We have no explanation for this different pattern of habitat use between lakes where Nile perch are native and lakes where they have been introduced.

Ontogenetic changes in foraging patterns

Like previous investigators (Hopson, 1972; Hughes, 1986; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b, 1993, 2004; Schofield & Chapman, 1999) we found distinct ontogenetic changes in foraging patterns. Of the potential prey available in our study area, zooplankton was the smallest, followed by midge larvae. Shrimps, dragonfly nymphs, dagaa and small Nile perch occurred in wide size ranges. Zooplankton and midge larvae were only eaten by the smallest Nile perch and the other prey species by all size classes above 5 cm.

In Lake Chad, Nile perch ate zooplankton until a size of ca. 3 cm. In pelagic larvae of 4–14 mm cladocerans dominated, and in the onshore post-larvae > 1 cm, cyclopoid copepods (Hopson, 1972). Calanoid copepods were rare in the diet in this lake. In the Mwanza Gulf, zooplanktivory was confined to Nile perch < 5 cm. The proportion of cyclopoid copepods decreased and that of calanoids increased with size of the fish. Cladocerans were rare, both in the environment and in the diet. Juvenile stages of other piscivores, like pikeperch, *Stizostedion lucioperca* L., sauger, *Stizostedion canadense* Griffith & Smith and smelt, *Osmerus eperlanus* L. show a similar preference for calanoids over cyclopoids (Nelson, 1968; Tatrai & Ponyi, 1976; Van Densen, 1985). This general preference for calanoid copepods, suggests that in spite of their lower detection efficiency because of lower movement frequency (Wright & O'Brien, 1984), and lower catch efficiency due to better evasion abilities (Drenner & McComas, 1980) calanoids are more profitable prey than cyclopoids.

The stomach contents of 1–4 cm classes of Nile perch, compared with the size distribution of zooplankton in the Mwanza Gulf, revealed a distinct ontogenetic shift in selectivity for prey size. Similar size selectivity was observed for Nile perch up to 10 cm when feeding on shrimps (Goudswaard et al., 2006). In general it appears that both within and between prey types there is a positive correlation between Nile perch size and

prey size (Gee, 1969; Hopson, 1972; Ogutu-Oh-wayo, 1985, 1990b, 1993, 2004; Ogari & Dadzie, 1988; Schofield & Chapman, 1999). In the Mwanza Gulf, this selectivity appeared to be especially strong in small Nile perch (<10 cm). After the decline of the haplochromines in Lake Victoria, shrimps made up a major part of the diet of Nile perch up to at least 50 cm, and were common up to 80 cm (Ogari & Dadzie, 1988; Hughes, 1986, 1992; Ogutu-Ohwayo, 1990b; Mkumbo & Ligtvoet, 1992). Fish larger than 100 cm were mainly piscivorous, and in this size class prey size selectivity seemed to increase again (Ogutu-Ohwayo, 2004). Among other explanations, the low selectivity of Nile perch between 10 and 100 cm after the decline of the haplochromines might be caused by scarcity of prey of appropriate size. According to Hughes (1992) Nile perch larger than 67 cm will have a gill raker spacing that exceeds the mean body depth of *C. nilotica*, which could explain the decline of shrimps in their diet.

Differences in foraging patterns by habitat and season

Although an ontogenetic shift in the diet of juvenile Nile perch was obvious at all sampling stations, the contribution of each of the prey types differed. With increasing water depth the frequency of occurrence in the diet of most prey types decreased, whereas that of shrimps increased. Though our sampling design did not include replicates, data collected by Ogari (1985) in the Nyanza Gulf confirmed our observations on habitat related differences in foraging patterns. The diet composition of Nile perch in this gulf showed a comparable increase of shrimps and a decrease of dagaa and Nile perch from shallow to deep waters.

Schofield & Chapman (1999) compared the diet of 5–35 cm TL Nile perch from wetland and exposed habitats in Lake Nabugabo. In both habitats they found a shift from feeding primarily on invertebrates to a dominance of fish (mainly dagaa and juvenile Nile perch) at approximately 30 cm TL. However, in wetland transects fish were more important in the diet of smaller juveniles than in exposed areas and the shift to piscivory was less abrupt (Schofield & Chapman, 1999). No shrimps were encountered in the Lake Nabugabo

fish; they seem to be absent in this rather acid lake (Ogutu-Ohwayo, 1993; Schofield & Chapman, 1999).

The site-specific dietary shifts found in the Mwanza Gulf may have been partly caused by differential prey availability. High shrimp densities have been reported for deeper waters in the lake, including stations 3 and 4 (Budeba, 2003; Goudswaard et al., 2006; J.H.W. unpublished data), where they were important prey for juvenile Nile perch. However, dagaa biomass in the Mwanza Gulf was lowest at station 1 and peaked at station 3, with intermediate values at stations 2 and 4 (Wanink et al., 1999). No significant differences were found in the abundance of small Nile perch (≤5 cm) between stations 1 and 4. These data suggest that the decreasing contribution of dagaa and 1–5 cm Nile perch to the diet of larger juvenile Nile perch, when going from station 1 to 4, was not caused by a decrease in availability of prey fish.

A possible cause for the shift from fish prey to shrimps with increasing water depth would be a preference for shrimps over juvenile Nile perch and dagaa. At station 1, where shrimp densities are generally low (Budeba, 2003; J.H.W. unpublished data), there was a significant correlation between the abundance of small Nile perch (≤5 cm) and their presence in the diet of Nile perch >10 cm. At station 3 and 4, where shrimps are common during at least a part of the year (Budeba, 2003; J.H.W. unpublished data), the correlation was not significant. We have no quantitative data on shrimp densities from the period in which the diet study was done. Consequently, we cannot exclude that Nile perch diets only reflect the relative abundance of prey types. Nevertheless, it is remarkable that in April 1989 when small Nile perch (<5 cm) were extremely abundant at stations 3 and 4, most of their larger congeners only fed on shrimps.

The distinct seasonal patterns in diet of Nile perch at station 3 correlate with seasonal changes in the abundance of shrimps that were generally observed at this station, with high catch rates during approximately December to May (Budeba, 2003; J.H.W. unpublished data). During this period Nile perch of 11–30 cm fed almost exclusively on shrimps, irrespective of catch rates of Nile perch ≤5 cm. These seasonal patterns also might

reveal a preference for feeding on shrimps over cannibalism.

Shrimps as a key prey

From a study on 27 species of freshwater piscivores from Europe and North America, it appeared that growth during the first year of life is critical in setting the pattern for size at all subsequent ages (Mittelbach & Persson, 1998). Further, it was found that the size spectrum of food items of small piscivores determined their growth rate and the switch to piscivory and, consequently, strongly affected recruitment to the adult population (Van Densen et al., 1996). Especially the abundance of macro-invertebrates appeared important in this respect. Both the spatial and seasonal foraging patterns in the Mwanza Gulf indicate the importance of shrimps as a prey for juvenile Nile perch at the end of the 1980s. Between the 1950s and the 1980s, haplochromine cichlids were the main prey of Nile perch in Lake Victoria (Hamblyn, 1966; Gee, 1969; Ogutu-Ohwayo, 1990b, 2004). Although from this period no data are available of fish smaller than 20 cm, 20–30 cm size classes of Nile perch fed on fish (mainly haplochromines) and not on shrimps (Gee, 1969; Ogutu-Ohwayo, 1990b, 2004). In the sub-littoral areas (6–20 m) of the Mwanza Gulf, shrimps strongly increased in the 1980s, which coincided with the decline of the haplochromine cichlids in this area (Goldschmidt et al., 1993; Goudswaard et al., 2006). Our findings suggest that juvenile Nile perch predominantly fed on these shrimps, whenever available. Similar observations were made in Lake Kyoga after the decline of the cichlids due to the boom of the introduced Nile perch (Ogutu-Ohwayo, 1990b, 2004). In Lake Victoria, in the absence of haplochromine cichlids, larger Nile perch seemed to depend highly on shrimps as well; shrimps dominated the diet of fish up to at least 60 cm (Hughes, 1986, 1992; Ogari & Dadzie, 1988). In Lake Albert, which was always characterised by a paucity of cichlids (Lowe-McConnell, 1987), shrimps were important in the diet of Nile perch of 15–95 cm (Hamblyn, 1966), though for the period 1989–1992 Ogutu-Ohwayo (2004) found shrimps almost exclusively in fish <20 cm. In Lake Chad, the shrimp *Macrobrachium niloticum* (Roux) dominated the stomach contents of Nile perch up to 40 cm in inshore and up to 55 cm in offshore areas (Hopson, 1972).

Our data suggest that the preference of Nile perch for shrimps after the decline of the haplochromines reduced cannibalism. This would enhance rates of recruitment to the adult population and may partly explain the success of Nile perch in Lake Victoria. Obviously, in a system with a fish assemblage of mainly dagaa and Nile perch, shrimps should be regarded as a key prey for Nile perch. However, due to a recovery of some of the haplochromine cichlids in the course of the 1990s (Witte et al., 2000; Balirwa et al., 2003; Getabu et al., 2003) the fish assemblage is currently changing again. This may have an impact on the foraging patterns of Nile perch. Preliminary data from stomach analyses suggest that haplochromines are now becoming common again in the diet of juvenile Nile perch. Likewise, in the early 1990s the relative importance of shrimps in the diet of juvenile Nile perch (<20 cm) from Lake Kyoga decreased, while that of haplochromine cichlids increased. According to Kaufman & Schwartz (2002) Nile perch seem to prefer, and grow fastest on a haplochromine prey base. This seems to be confirmed by the above-mentioned switches in diet after resurgence of some haplochromines and by the high condition factor of Nile perch in Lake Victoria before the decline of the haplochromine cichlids (Ogutu-Ohwayo, 2004).

The original high abundance of haplochromines in Lake Victoria likely had a strongly negative impact on the shrimp population (Goudswaard et al., 2006). However, if the levels of resurging haplochromines are such that shrimps can coexist with them, shrimps will probably remain an important food source to the smaller juvenile Nile perch. A system, in which Nile perch <10 cm feed on shrimps and larger ones on haplochromines may be extremely beneficial in terms of Nile perch production.

References

Arunga, J. O., 1981. A case study of the Lake Victoria Nile perch *Lates niloticus* (Mbuta) fishery. In Proceedings of the Workshop of the Kenya Marine and Fisheries Research Institute on Aquatic Resources of Kenya, July 13–19, 1981. National Academy for the Advancement of Arts and Science, Nairobi, 165–184.

Balirwa, J. S., C. A. Chapman, L. J. Chapman, I. G. Cowx, K. Geheb, L. Kaufman, R. H. Lowe-McConnell, O. Seehausen, J. H. Wanink, R. L. Welcomme & F. Witte, 2003. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage?. BioScience 53: 703–715.

Barel, C. D. N., W. Ligtvoet, T. Goldschmidt, F. Witte & P. C. Goudswaard, 1991. The haplochromine cichlids in Lake Victoria: an assessment of biological and fisheries interests. In Keenleyside, M. H. A. (ed.), Cichlid Fishes, Behaviour, Ecology and Evolution. Chapman & Hall, London, 258–279.

Budeba, Y. L. 2003. The role of Nile shrimp, *Caridina nilotica*, in the food web of Nile perch, *Lates niloticus*, in Lake Victoria. Ph.D. thesis, University of Hull.

Drenner, R. W. & S. R. McComas, 1980. The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In Kerfoot, W. C. (ed.), Evolution and Ecology of Zooplankton Communities. University Press of New England, Hanover (NH), USA, 587–593.

Gee, J. M., 1969. A comparison of certain aspects of the biology of *Lates niloticus* (Linne) in some East African lakes. Revue de Zoologie et de Botanique Africaines 80: 244–262.

Getabu, A., R. Tumwebaze & D. N. MacLennan, 2003. Spatial distribution and temporal changes in the fish populations of Lake Victoria. Aquatic Living Resources 16: 159–165.

Goldschmidt, T., F. Witte & J. Wanink, 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. Conservation Biology 7: 686–700.

Goudswaard, P. C., J. H. Wanink, F. Witte & E. F. B. Katunzi, 2004. Diel vertical migration of major fish-species in Lake Victoria, East Africa. Hydrobiologia 513: 141–152.

Goudswaard, P. C., F. Witte & J. H. Wanink, 2006. The shrimp *Caridina nilotica* in Lake Victoria (East Africa), before and after the Nile perch increase. Hydrobiologia DOI 10.1007/s10750-005-1385-9.

Haccou, P. & E. Meelis, 1992. Statistical Analysis of Behavioural Data. Oxford University Press, Oxford.

Hamblyn, E. L., 1962. Nile perch investigation. In Annual Report 1961, East African Freshwater Fisheries Research Organisation, Jinja, 23–28.

Hamblyn, E. L., 1966. The food and feeding habits of Nile perch: *Lates niloticus* (Linné) (Pisces: Centropomidae). Revue de Zoologie et de Botanique Africaines 74: 1–28.

Hecky, R. E., 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25: 39–48.

Hecky, R. E., F. B. W. Bugenyi, P. Ochumba, J. F. Talling, R. Mugidde, M. Gophen & L. Kaufman, 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. Limnology and Oceanography 39: 1476–1481.

Hopson, A. J., 1972. A study of the Nile perch, *Lates niloticus* (L.), in Lake Chad. HMSO Overseas Research Publication 19. Foreign and Commonwealth Office, London.

Hughes, N. F., 1986. Changes in the feeding biology of the Nile perch, *Lates niloticus* (L.) (Pisces: Centropomidae), in Lake Victoria, East Africa since its introduction in 1960, and its impacts on the native fish community of the Nyanza Gulf. Journal of Fish Biology 29: 541–548.

Hughes, N. F., 1992. Nile perch, *Lates niloticus*, predation on the freshwater prawn, *Caridina nilotica*, in the Nyanza Gulf, Lake Victoria, East Africa. Environmental Biology of Fishes 33: 307–309.

Hyslop, E. J., 1980. Stomach contents analysis – a review of methods and their application. Journal of Fish Biology 17: 411–429.

Kaufman, L., 1992. Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. BioScience 42: 846–858.

Kaufman, L. & J. Schwartz, 2002. Nile perch population dynamics in Lake Victoria: implications for management and conservation. In Ruth, M. & J. Lindholm (eds), Dynamic Modeling for Marine Conservation. Springer-Verlag, New York, 257–313.

Krebs, J. R., 1978. Optimal foraging: decision rules for predators. In Krebs, J. R. & N. B. Davies (eds), Behavioural Ecology: an Evolutionary Approach. Blackwell Scientific Publications, Oxford, 23–63.

Ligtvoet, W. & O. C. Mkumbo, 1990. Synopsis on ecological and fishery research on Nile perch (*Lates niloticus*) in Lake Victoria, conducted by HEST/TAFIRI. FAO Fisheries Report 430: 35–74.

Lowe-McConnell, R. H., 1987. Ecological Studies in Tropical Fish Communities. Cambridge University Press, Cambridge.

Ludsin, S. A. & D. R. DeVries, 1997. First-year recruitment of largemouth bass: The interdependency of early life stages. Ecological Applications 7: 1024–1038.

Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454–1465.

Mkumbo, O. C. & W. Ligtvoet, 1992. Changes in the diet of Nile perch, *Lates niloticus* (L), in the Mwanza Gulf, Lake Victoria. Hydrobiologia 232: 79–83.

Mous, P. J., P. C. Goudswaard, E. F. B. Katunzi, Y. L. Budeba, F. Witte & W. Ligtvoet, 1995. Sampling and measur-

ing. In Witte, F. & W. L. T. Van Densen (eds), Fish Stocks and Fisheries of Lake Victoria. Samara Publishing, Cardigan, UK, 55–82.

Mugidde, R., 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). Internationale Vereinigung für Theoretische und Angewandte Limnologie. Verhandlungen Limnologie 25: 846–849.

Nelson, W. R., 1968. Reproduction and early life history of sauger, *Stizostedion canadense*, in Lewis Clarke Lake. Transactions of the American Fisheries Society 97: 159–166.

Ochumba, P. B. O. & D. I. Kibaara, 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. African Journal of Ecology 27: 23–34.

Ogari, J., 1985. Distribution, food and feeding habits of *Lates niloticus* in Nyanza Gulf of Lake Victoria (Kenya). FAO Fisheries Report 335: 68–80.

Ogari, J. & S. Dadzie, 1988. The food of the Nile perch, *Lates niloticus* (L.) after the disappearance of the haplochromine cichlids in the Nyanza Gulf of Lake Victoria (Kenya). Journal of Fish Biology 32: 571–577.

Ogutu-Ohwayo, R., 1985. The effects of predation by Nile perch, *Lates niloticus* (Linné) introduced into Lake Kyoga (Uganda) in relation to the fisheries of Lake Kyoga and Lake Victoria. FAO Fisheries Report 335: 18–41.

Ogutu-Ohwayo, R., 1990a. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus* and the Nile tilapia, *Oreochromis niloticus*. Environmental Biology of Fishes 27: 81–96.

Ogutu-Ohwayo, R., 1990b. Changes in the prey ingested and the variations in the Nile perch and other fish stocks of Lake Kyoga and the northern waters of Lake Victoria (Uganda). Journal of Fish Biology 37: 55–63.

Ogutu-Ohwayo, R., 1993. The effects of predation by Nile perch, *Lates niloticus*, on the fish of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 3: 701–711.

Ogutu-Ohwayo, R., 2004. Management of the Nile perch, *Lates niloticus* fishery in Lake Victoria in light of the changes in its life history characteristics. African Journal of Ecology 42: 306–314.

Olson, M. H., 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77: 179–190.

Post, D. M., 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. Ecology 84: 1298–1310.

Pringle, R. M., 2005. The origins of the Nile perch in Lake Victoria. BioScience 55: 780–787.

Salminen, M., E. Erkamo & J. Salmi, 2001. Diet of post-smolt and one-sea-winter Atlantic salmon in the Bothnian Sea, Northern Baltic. Journal of Fish Biology 58: 16–35.

Schofield, P. J. & L. J. Chapman, 1999. Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. Environmental Biology of Fishes 55: 343–358.

Seehausen, O., J. J. M. Van Alphen & F. Witte, 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277: 1808–1811.

Tatrai, I. & J. E. Ponyi, 1976. On the food of pike-perch fry (*Stizostedion lucioperca* L.) in Lake Balaton in 1970. Annales Instituti Biologici (Tihany) 43: 93–104.

Van Densen, W. L. T., 1985. Feeding behaviour of major 0 + fish species in a shallow, eutrophic lake (Tjeukemeer, the Netherlands). Zeitschrift für angewandte Ichthyologie 1: 49–70.

Van Densen, W. L. T., W. Ligtvoet & R. W. M. Roozen, 1996. Intra-cohort variation in the individual size of juvenile pike perch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Annales Zoologici Fennici 33: 495–506.

Wanink, J. H., 1991. Survival in a perturbed environment: the effects of Nile perch introduction on the zooplanktivorous fish community of Lake Victoria. In Ravera, O. (ed.), Terrestrial and Aquatic Ecosystems: Perturbation and Recovery. Ellis Horwood Ltd, Chichester, UK, 269–275.

Wanink, J. H., 1999. Prospects for the fishery on the small pelagic *Rastrineobola argentea* in Lake Victoria. Hydrobiologia 407: 183–189.

Wanink, J. H., P. C. Goudswaard & M. R. Berger, 1999. *Rastrineobola argentea*, a major resource in the ecosystem of Lake Victoria. In Van Densen, W. L. T. & M. J. Morris (eds), Fish and Fisheries of Lakes and Reservoirs in Southeast Asia and Africa. Westbury Publishing, Otley, UK, 295–309.

Wanink, J. H., J. J. Kashindye, P. C. Goudswaard & F. Witte, 2001. Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*?. Freshwater Biology 46: 75–85.

Welcomme, R. L., 1988. International introductions of inland aquatic species. FAO Fisheries Technical Paper 294: 1–318.

Witte, F. & W. de Winter, 1995. Biology of the major fish species of Lake Victoria. In Witte, F. & W. L. T. Van Densen (eds), Fish Stocks and Fisheries of Lake Victoria. Samara Publishing, Cardigan, UK, 301–320.

Witte, F., J. H. Wanink, H. A. Rutjes, H. J. van der Meer & G. E. E. J. M. van den Thillart, 2005. Eutrophication and its influences on the fish fauna of Lake Victoria. In Reddy, M. V. (ed.), Restoration and Management of Tropical Eutrophic Lakes. Science Publishers, Inc, Enfield (NH), USA, 301–338.

Witte, F., T. Goldschmidt, J. Wanink, M. Van Oijen, K. Goudswaard, E. Witte-Maas & N. Bouton, 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34: 1–28.

Witte, F., B. S. Msuku, J. H. Wanink, O. Seehausen, E. F. B. Katunzi, P. C. Goudswaard & T. Goldschmidt, 2000. Recovery of cichlid species in Lake Victoria: an examination of factors leading to differential extinction. Reviews in Fish Biology and Fisheries 10: 233–241.

Wright, D. I. & W. J. O'Brien, 1984. The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). Ecological Monographs 54: 65–98.