Causes and effects of the Lake Victoria ecological revolution

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Citation

Goudswaard, P. C. (2006, September 6). *Causes and effects of the Lake Victoria ecological revolution*. Retrieved from https://hdl.handle.net/1887/4545

CHAPTER 5

The shrimp *Caridina nilotica* in Lake Victoria (East Africa), before and after the Nile perch increase

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Published in: Hydrobiologia: 563:31-44, 2006

Abstract

The shrimp *Caridina nilotica* is a major prey of the introduced Nile perch in Lake Victoria. In spite of heavy predation, the density of shrimps increased after the Nile perch boom and the concomitant disappearance of the haplochromine cichlids. In the same period, the mean size of gravid shrimps and the size at first maturity declined. This seems to indicate an increased predation pressure on adult shrimps. Before the Nile perch upsurge, specialised shrimp eaters and piscivores, among the haplochromine cichlids, only took adult shrimps, whereas we assume that most haplochromines used to include juvenile shrimps into their diet. Another important predator on adult shrimps was *Bagrus docmak.* The combined density of predators on adult shrimps in the pre-Nile perch era was estimated at 10 kg ha^{-1} and the potential predators on juveniles were estimated at 170 kg ha^{-1}. After the Nile perch upsurge, only Nile perch up to 10 cm TL and *Rastrineobola argentea* fed on juvenile shrimps (ca. 36 kg ha^{-1}) and Nile perch from 10 to 50 cm TL (ca. 13 kg ha^{-1}) fed on adults. These rough estimates of the biomass of predators on shrimps before and after the Nile perch upsurge indicate a reduced predation pressure on juvenile shrimps. The disappearance of the haplochromines may have released competition with small Nile perch for juvenile shrimps, thus enhancing the recruitment of Nile perch.

Introduction

From the frigid polar seas to the warm tropical waters, shrimps (or prawns) often form a vital link in marine and freshwater ecosystems, both as consumers of phytoplankton, detritus and zooplankton, and as prey for fish, birds and mammals (Sahrhage, 1989; Coulter, 1991).

The atyid shrimp *Caridina nilotica* (Roux) is widely distributed throughout African rivers and lakes, from the River Nile in Egypt (Hussein & Obuid-allah, 1992) to Lake Sibaya in South Africa (Hart, 1981), but it is absent in West Africa (Holthuis, 1951). It is the only shrimp species known from Lake Victoria, East Africa (Fryer, 1960).

During the increase of the introduced Nile perch (*Lates niloticus*, Linné) and the concomitant decline of haplochromine cichlids in the 1980s (Ogutu-Ohwayo, 1990a; Witte et al., 1992b), the stock of *C. nilotica* in Lake Victoria increased suddenly (Kaufman, 1992; Witte et al., 1992a; Goldschmidt et al., 1993). These changes did not occur simultaneously throughout the lake. In the Mwanza Gulf, the Nile perch upsurge and the decline of the haplochromines occurred between 1984 and 1987, which was several years later than in the Northern part of the lake (Witte et al., 1995; Chapter 2).

After the disappearance of the haplochromine cichlids, which had been the preferred prey of Nile perch, shrimps became an important prey species of this predator up to a total length of at least 50 cm (Hughes, 1986, 1992; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990b; Mkumbo & Ligtvoet, 1992; Katunzi et al., 2006). In the Mwanza Gulf this prey shift occurred in 1987 (Mkumbo & Ligtvoet, 1992). In spite of the apparent heavy predation on *C. nilotica* by Nile perch, shrimp densities remained high (pers. obs.). From 1986 onwards, algal blooms, decreased water transparency and decreased oxygen levels near the bottom were observed for the first time in the Mwanza Gulf (for an overview see Table 3).

Several suggestions have been made in literature to explain the increase of the *C. nilotica* stock. It might for instance be related to: 1) its ability to use hypoxic refugia to avoid Nile perch predation (Kaufman, 1992; Kaufman & Ochumba 1993; Branstrator & Mwebaza-Ndawula, 1998); 2) the increased availability of algae and detritus as food sources (Kaufman, 1992); 3) reduced predation pressure on juvenile shrimps caused by the disappearance of the haplochromines (Goldschmidt et al., 1993).

So far, the biology of *C. nilotica* in Lake Victoria has been studied in the 1950s by Fryer (1960) and after the Nile perch upsurge by Branstator & Mwebaza-Ndawula (1998), Mbahinzireki et al. (1998), Budeba (2003) and Sætveit (2003). In these studies no comparisons were made between the status of the shrimps before, during and after the Nile perch upsurge. Consequently the necessary data to test the hypotheses above were lacking.

As by-catch during fishery research in southern Lake Victoria, we collected large amounts of shrimps between 1986 and 1990 and in 2001 and 2002. The samples provided data on abundance of shrimps, their length frequency distribution, and data on sizes and fecundity of gravid females. We try to elucidate if predation pressures on juveniles and adults differed in the pre- and post-Nile perch era. For this purpose we used data from the literature and unpublished reports on densities of shrimp eating fish and their stomach contents.

Material and techniques

Study area

Data were collected in the southern part of Lake Victoria (Fig. 5.1) between 1977 and 2002. Most data were collected with bottom trawlers in and just north of the Mwanza Gulf (Fig. 5.1). The Mwanza Gulf is one of the larger gulfs at the southern end of the lake. It extends southward for some 60 km, has an average width of 5 km, and a surface area of approximately 500 km^2. The numbers 1 to 5 in Fig. 5.1 indicate the main sampling areas. Especially at station 3 many data used in the present study were collected. Depths of stations 1 to 5 are: 1-2 m, 2-4 m, 12-16 m, 20-25 m and 30-35 m respectively. A transect with 11 sampling stations, crossing the Mwanza Gulf from the Butimba Bay to the Kissenda Bay was sampled as well. Four stations (F to I; Fig. 5.1) with depths ranging from 10-15 m were focussed on during this study. Additional data were collected near Nyamikoma (3-20 m deep) in the Speke Gulf and near Igusa Island (43 m deep) in June 1985 (Fig. 5.1). All stations have a soft

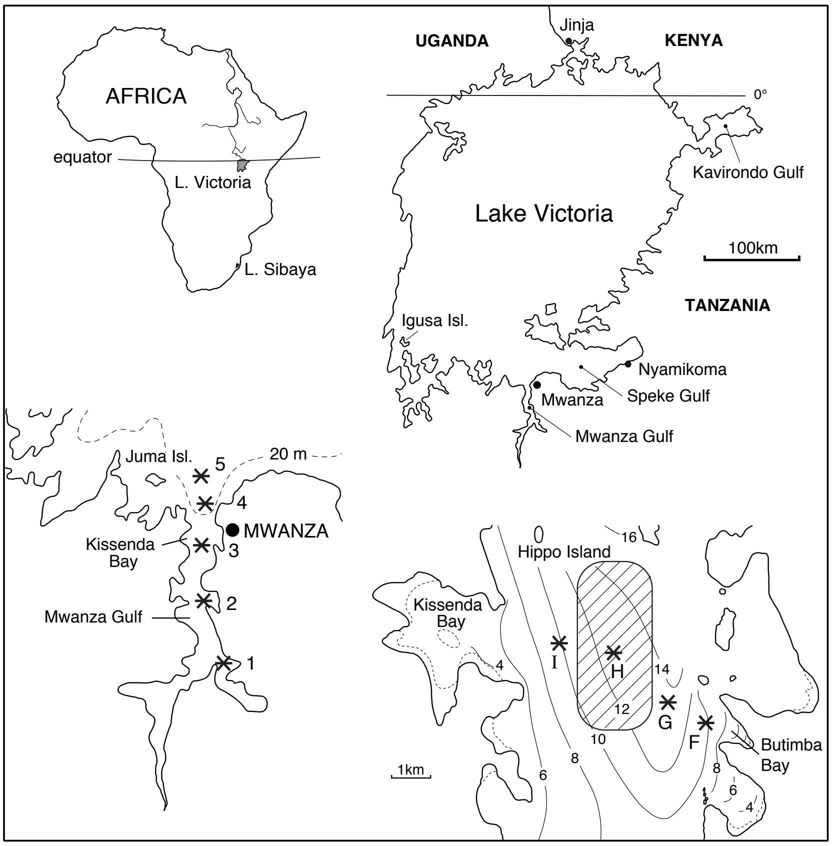

Fig. 5.1. *Sampling stations in the Mwanza Gulf of Lake Victoria. Hatched area in right bottom panel indicates station 3.*

muddy bottom. At the deeper stations (3-5) oxygen concentrations at 1 meter above the bottom, were low (< 2 mg l^{-1}) during the months December–May in 1985-87. Average temperature at 1 m above the bottom at stations 1-5 ranged from 21.3–24.0°C.

Inconsistency of sampling

Samples that were used in the present study were originally meant for other research purposes. Therefore, sampling designs and the data that were collected are inconsistent. For instance, in some cases abundance of fishes was expressed as kg h^{-1} and in others in numbers h^{-1}. Density of shrimps was either given in number or in volume. To enable comparisons, we converted lengths of fishes to weights, and volumes of shrimps to numbers.

Densities of shrimps

In 1983 most shrimps present in the fish catches were preserved, whereas from 1986 onwards when densities increased, random samples were frequently taken. The objectives of these collections were investigations of length frequency distributions and size at maturity.

Bottom trawls with 20 mm codend mesh (all mesh sizes refer to stretched meshes) were made by MV Mdiria and MV Kiboko. Trawl shots by MV Mdiria lasted 45 minutes to two hours and by MV Kiboko half an hour. The effective horizontal opening of the trawl net of MV Kiboko was estimated at 33.3% of the head rope length. The same ratio was applied to MV Mdiria. This ship fished with a head rope of 25 m and a speed of 3.5 nautical miles (1 nautical mile = 1852 m) h^{-1} resulting in a swept area of 5.3 ha h^{-1}. MV Kiboko fished with a head rope of 18 m and a speed of 3 nautical miles h^{-1}, thus covering 3.3 ha h^{-1}. From 1984 to 1990 four stations in the Mwanza Gulf and one just north of it were fished monthly with MV Kiboko.

Besides MV Mdiria and MV Kiboko, a small trawler, towing either a bottom trawl net (head rope 4.6 m, codend mesh 5 mm) or a surface trawl net (beam 5 m, codend mesh 5 mm) was used (Goudswaard et al., 1995). Trawl shots by the small trawler lasted 10 minutes and were made frequently on the research transect across the Mwanza Gulf (Stations F- I; Fig. 5.1) from 1979 to 1992 and 2001 to 2002.

Sampling directly aiming at shrimps was done with a lift net (110 x 110 cm, 8 mm mesh), at station G (depth 12-14 m and close to station 3; Fig. 5.1) in the Mwanza Gulf during the period 1986–1989. Shrimps were stored in 5% formaldehyde solution immediately after catching, and were analysed in the laboratory.

Densities of shrimp predators

The contribution of shrimps to the diet of Nile perch was studied from fishes caught in the Mwanza Gulf between 1986 and 1990. Fishes were stored in 5% formaldehyde solution and stomach and intestine contents were investigated in the laboratory under a stereo microscope with magnifications up to 50 x. Data of shrimps in the diet of other fishes were obtained from literature and unpublished data.

Biomass of shrimp eating fish (i.e. haplochromines and the catfish *Bagrus docmak* Forsskåll) before 1980 was calculated from the average catch rate (kg h^{-1}) of MV Mdiria in 1978/79. Though this trawler fished throughout the Mwanza Gulf, most of the catches in 1978/79 were made at station 3. Based on literature (Ogutu-Ohwayo, 1990b; Hughes, 1986, 1992: Ogari & Dadzie, 1988; Mkumbo & Ligtvoet, 1992), Nile perch biomass after the boom was split into shrimp eaters (<50 cm Total Length = TL) and fish eaters (>50cm TL). The former group was divided into fish feeding on juvenile and adult shrimps. Calculation of the biomasses of these groups was done by means of their length-weight relationship and length frequency distributions in the bottom trawl catches of MV Kiboko at station 3 in 1987 and 1989. These were years with the highest and lowest Nile perch catch rates respectively during the period 1987-1990.

Numbers of juvenile Nile perch ($\leq$10 cm Tl) were transferred to weight via $\ln DW = 3.349 \ln SL - 6.777$ and $DW = 0.22 FW$ (DW= Dry Weight in mg, SL= Standard Length in mm, FW = fresh weight; (Wanink & Goudswaard, 1994; Wanink et al., 2002).

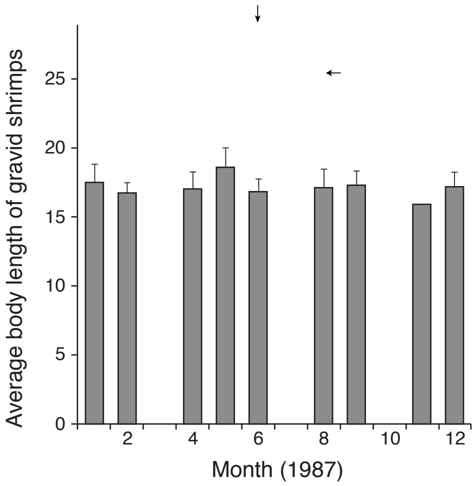

Fig. 5.2. *Average size of gravid females per month in 1987. Arrows indicate points used in measuring body length. Before measuring the body was straightened.*

The weight of Nile perch ($\geq$11cm TL) was calculated as FW (in kg) = $6 \times 10^{-6} . TL^{3.17}$ (in cm; Ligtvoet & Mkumbo, 1990).

Life history parameters of shrimps

The length of the shrimps was measured, following Hart (1980a), as the distance in lateral view from the anterior margin of the carapace behind the insertion of the eyestalk to the most posterior margin of the abdomen (Fig. 5.2). The body of the shrimps was straightened before measuring. Lengths were measured to the nearest .5 mm below, except for the sample from 2001 that was measured to the nearest mm. Shrimps were classified as gravid females when eggs or larvae were found attached to the pleopods. It is possible to distinguish males and females on basis of the form and size of the appendix on the second pleopod, but it is time consuming and was therefore not done in the present study.

Sætveit (2003) found that *C. nilotica* males mature at a smaller size than females. In this study we classified all shrimps of 12.0 mm body length and above as mature, as the smallest gravid female collected was 12 mm. To compare the size distributions of adult shrimps over different years, we used only gravid females, as this was the most convenient method to determine adulthood. As the sample sizes were too small to study size distributions per station the samples of gravid shrimps were lumped into two categories: those of the stations 1 to 3 (1-16 m), and those of the stations 4-5 (20-35 m). In 1983 only 13 gravid shrimps were collected at station 1 to 3 (Table 1). Because we considered this amount too low for a reliable length-frequency distribution, we omitted 1983 from the statistical tests for size decrease over the years. In most years

Table 5.1 *Smallest, largest and average size (± standard deviation), and number (N) of gravid shrimps. Largest of all shrimps (gravid and non-gravid), total number and number of samples over the period 1983-2001. Years and months of sampling are given in the first two columns. Shallow stations (1-3) in upper section of table and deep stations (4 and 5) in lower section.*

		Gravid shrimps				All shrimps		
Year	Months	Smallest mm	Largest mm	Average ± std mm	N	Largest	Total N	N samples
Station 1-3 (1-16m)								
1983	5,11	15.0	21.5	17.9 ± 1.5	13	21.5	56	3
1986	7,12	16.0	20.5	18.8 ± 0.9	41	25.5	177	3
1987	1,2,4,5,6,11	15.0	20.0	17.0 ± 0.8	620	21.0	4230	15
1988	1	15.0	19.0	16.7 ± 0.8	76	19.0	961	2
1989	4,12	14.0	22.0	16.7 ± 1.3	173	22.0	1399	3
1990	1,2	13.5	23.5	17.6 ± 1.1	1330	23.5	6551	2
2001	6	12	18	14.3 ± 1.2	46	18	199	1
Station 4-5 (20-35m)								
1986	8,9,10,11	14.5	25.0	18.4 ± 1.5	493	25.0	1528	10
1987	4,6,8,9,12	13.0	20.0	17.2 ± 1.2	233	21.5	2832	7
1988	2,3,4,6,7,12	14.5	20.5	17.0 ± 1.3	319	20.5	2380	6

sampling of *C. nilotica* was restricted to only a few months (Table 1). The exception was 1987 when samples were collected during 9 months equally distributed over the year. In order to check for potential bias due to sampling in different periods of the year, the length distribution of gravid females from 1987 was tested for seasonal differences.

For 307 shrimps, the number of eggs, carried by gravid females, were counted with a stereomicroscope at a magnification of 12 x. Females with larvae were rarely encountered and were excluded. A regression was computed for body length and the number of eggs in gravid females.

Statistics

All data were tested for normal distribution with a Kolmogorov-Smirnov test. Non parametric tests were used when data were not normally distributed. The Kruskal-Wallis test and Jonckheere-Terpstra test (Hollander & Wolfe, 1973) were used to test for differences between more than two independent samples; the Spearman Rank Correlation test was used to test for correlation between the length of Nile perch and the body size of shrimps. A General Linear Model (GLM) with year as factor and body length as covariate was used to test for differences in fecundity between the different years. The GLM was performed on log-transformed data. Residuals were

Table 5.2 *Maximum number of shrimps caught in a bottom trawl shot of 10 minutes at stations F – I (10-15 m deep) along the research transect in the first quarter of the year (January-March) and total number of catches that were made in the period.*

Year	Max. N shrimps	N catches
1979	0	7
1980	0	8
1982	0	1
1983	0	1
1984	0	2
1987	436	3
1988	200 000	2
1992	100 000	2
2002	400 000	12

tested with a Kolmogorov-Smirnov test for normality. Statistical tests were performed with SPSS 10.0 for Windows.

Results

Densities of shrimps

Until the middle of the 1980s, shrimps were rarely caught in the Mwanza Gulf. Catches of for instance 3 shrimps in August 1981 in a bottom trawl by MV Mdiria in the Mwanza Gulf, and 8 shrimps in December 1981 in a surface trawl in the Butimba Bay (Fig. 5.1), were exceptionally high. In May and November 1983 a total of 56 shrimps was collected in three bottom trawl shots in the Mwanza Gulf by MV Mdiria.

In 1986 the numbers of *C. nilotica* increased, and samples up to a few hundred shrimps could be collected from each bottom trawl catch by MV Kiboko in the southern part of Lake Victoria. In 1987 shrimps were abundant and it was easy to collect thousands in a single bottom trawl catch. Even though, with their slender bodies, the shrimps could easily pass the 20 mm codend meshes, occasionally a few hundred kilos of shrimps were caught.

To get a better indication of the time and magnitude of increase of shrimps in the Mwanza Gulf, we scored the maximum catch rate with the small trawl at stations F to I, during the first quarter of each year (Table 2). During this period catch rates were generally high. From 1979 till 1984 no shrimps were caught. In 1987 the maximum number of shrimps in one of the three catches amounted to 436. In all subsequent years when the stations F to I were sampled, during the period January to March, at least one of the catches contained a huge amount of shrimps (Table 2). Sampling with a lift net at station G in June 1987 revealed a mean density of 793 (± 486) shrimps m^{-2}.

Densities of shrimp predators

Before the Nile perch upsurge, the mean catch rate of haplochromines in the bottom trawls of MV Mdiria in the central part (station 3) of the Mwanza Gulf in 1978/79 was 1138 kg h^{-1}, which corresponded to 213 kg ha^{-1}. The shrimp eating haplochromines, mainly taking adult *C. nilotica*, comprised 0.2% of the demersal haplochromine stock, which corresponded to 0.4 kg ha^{-1}. The piscivorous haplochromines made up 2.8% of the stock, which was 6 kg ha^{-1}.

Among the predatory catfishes (*Bagrus docmak*, *Clarias gariepinus* (Burchell), *Synodontis* spec., *Schilbe intermedius* (Linné) formerly *S. mystus*), *B.*

docmak was the only one for which shrimps made up an important component of the diet before the Nile perch upsurge (Corbet, 1961; Chilvers & Gee, 1974; Mwebaza-Ndawula, 1984; Okach & Dadzie, 1988).

Although no information is given in literature on the size of the shrimps eaten by *B. docmak*, we assume that they mainly fed on adult shrimps. The catch rate of *B. docmak* by MV Mdiria in 1978/79 was 18.5 kg h^{-1}, which corresponded to 3.5 kg ha^{-1}. Combining the foregoing densities of potential predators on adult shrimps results in a density of approximately 10 kg ha^{-1}.

After the Nile perch upsurge in the Mwanza Gulf, *C. nilotica* was found in the stomachs of Nile perch from 1 cm to 65 cm TL (Fig. 5.4). Body size of *C. nilotica* correlated significantly (Spearman R= 0.714, P= 0.000, N= 115) with Nile perch length up to 10 cm. Nile perch above this size fed on adult shrimps (Fig. 5.4). Shrimps <10 mm were mainly eaten by the small Nile perches (<10 cm; Fig. 5.4) and were also found in zooplanktivorous and detritivorous haplochromines, which survived the Nile perch predation (JHW, pers. obs.).

For Nile perch of 10-50 cm feeding on *adult* shrimps at station 3, we found annual averages of 118 fishes ha^{-1} in 1987 and 57 fishes ha^{-1} in 1989. This corresponded to weights of respectively 14.8 kg ha^{-1} and 11.9 kg ha^{-1}.

Life history parameters of shrimps

The number of eggs increased with body length (BL): 50 eggs were found in the smallest gravid shrimp (12.5 mm), and 521 eggs in the largest (23 mm). The relation between body length in mm (0.5 mm length classes) and number of eggs was: N_{eggs}= 0.0072 $BL^{3.54}$ (R^2 = 0.540; N= 307). A GLM analysis revealed that there was a significant difference in fecundity between years (P= 0.008) and that the fecundity increased significantly with shrimp length (P= 0.000). The interaction between the factor year and the covariate length was also significant (P= 0.008), implying yearly differences in the relations between fecundity and length. In spite of these differences there was no clear

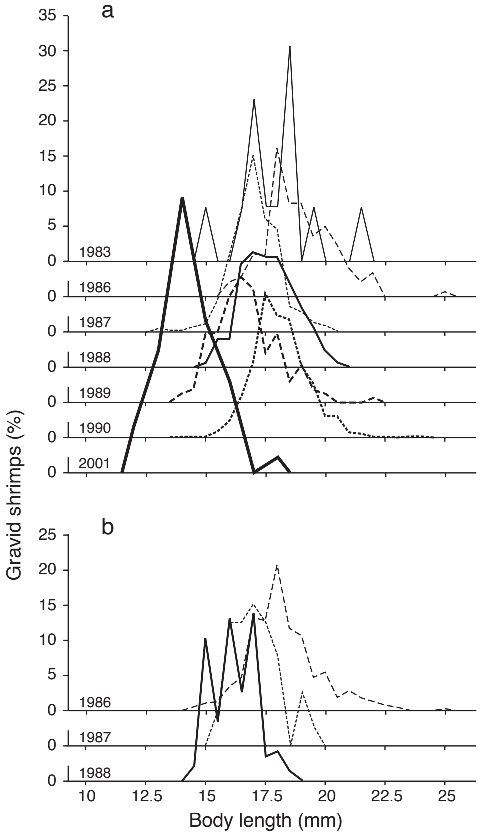

Fig. 5.3. *Length frequency distribution of gravid C. nilotica between 1983 and 2001:*
a) in shallow water (1-16 m) and
b) in deep water (20-35 m).

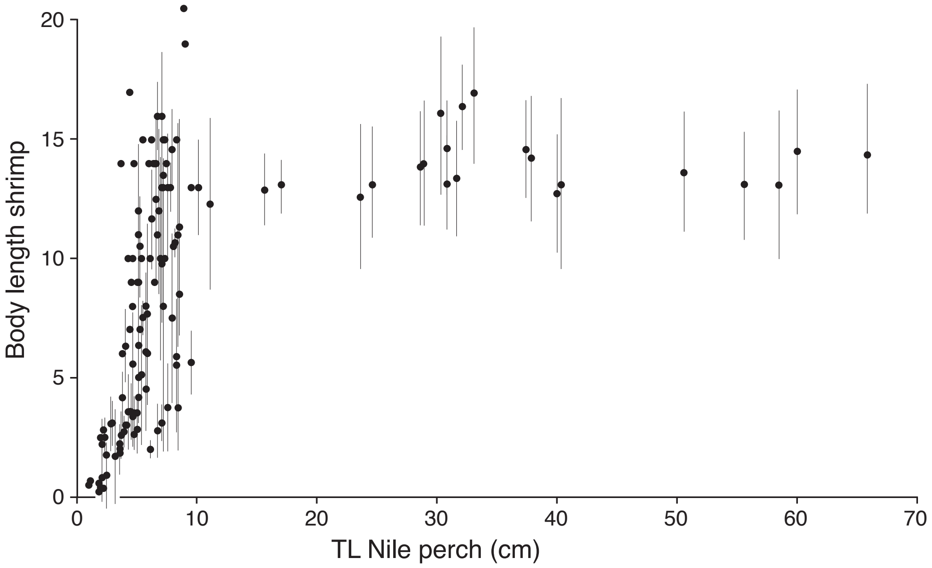

Fig. 5.4. *Relation between total length of Nile perch and average body length of C. nilotica in stomach contents. Bars indicate standard deviations.*

trend showing an increase or decrease of fecundity over the years.

The largest *C. nilotica*, 25.5 mm, was caught in July 1986 at station 1 in the Mwanza Gulf (Table 1). The largest gravid females were 25 mm and were caught at station 5 in 1986. The smallest gravid female was found in 2001 at station G and was 12 mm (Table 1). The largest juvenile shrimp still attached to the pleopods of a female measured 2 mm. The smallest free-living shrimp that was caught was 5 mm. Free-swimming stages of intermediate sizes were never observed, despite intensive sampling for zooplankton with different gears (Goldschmidt et al., 1990; Mous et al., 1995). Nevertheless, shrimps of 2-5 mm were present in stomachs of juvenile Nile perch (see below).

In gravid shrimps from shallow water (1-16 m) a decline in average size from 18.8 to14.3 mm was found for the period 1986-2001 (Spearman Rank Correlation for average length per year, R= -0.657, $P_{\text{1-tailed}}$ = 0.078, N= 6; Jonckheere-Terpstra test for the frequencies of length classes, P= 0.000; N= 601; Fig. 5.3a; Table 1). In deep water over the period 1986 to 1988 the average size of gravid shrimps declined from 18.4 to 17.0 mm (Spearman Rank Correlation for average length per year, R= -1.000, $P_{\text{1-tailed}}$ = 0.000, N= 3; Jonckheere-Terpstra test for the frequencies of length classes, P = 0.000, N= 298; Fig. 5.3b; Table 1). In most years sampling of *C. nilotica* was restricted to only a few months (Table 1). The exception was 1987 when samples were collected during 9 months equally distributed over the year. There were significant differences in body lengths of gravid shrimps between the months in 1987, but there was no consistent trend throughout the year (Fig. 5.2; Kruskal-Wallis test; P= 0.000, N= 853). The greatest average length (18.7 mm) was found in May;

the smallest average length (16.8 mm) was found in February. To check if the decrease in size over the years could not have been caused by the sampling of only a few months in the years after 1987, we tested the frequencies of length classes in the samples from 2001 against those from the month with the lowest average size in 1987, viz. February. Even in this case the decline in size was significant (Mann-Whitney U test P= 0.000).

The size of the smallest gravid shrimps, which is considered the size at first maturity, also decreased significantly between 1986 and 2001 (Table 1; Spearman Rank Correlation test, R= -0.986, $P_{1\text{-tailed}}$ = 0.000, N= 6).

Discussion

Densities of shrimps

The density of *C. nilotica* before the Nile perch boom in the 1980s in Lake Victoria is difficult to assess due to a lack of sufficient quantitative data. Shrimps were found from littoral areas to deep water (>60 m). Fryer (1960) distinguished two ecotypes, of which one was found in the littoral region, wherever there were beds of submerged vegetation. Of this group he stated that they were “extremely abundant”, but he did not quantify this. The other ecotype was a slender and benthic form that was most common in the deep waters (Fryer, 1960). Based on the habitats that we fished during our surveys, we probably dealt with this deep-water ecotype.

Graham (1929) stated that shrimps (prawns) were the second most important food item for the catfishes from deep water: *B. docmak* and *S. intermedius*. However, the extensive work of Corbet (1961) showed that shrimps were insignificant in the diet of *S. intermedius*, as well as in the other catfishes with the exception of *B. docmak*. This was confirmed by other studies (Chilvers & Gee, 1974; Mwebaza & Ndawula, 1984; Okach & Dadzie, 1988).

Despite Fryer’s (1960) remark about the abundance of shrimps in the littoral region, at our sampling stations in the Mwanza Gulf, with depths ranging from 1-25 m, shrimps were found only incidentally in bottom trawl catches between 1977 and 1982. Moreover, when present, the numbers were extremely low (FW, pers. obs.; M.J.P. Van Oijen, pers. com.). The main occurrence of the specialised shrimp eating haplochromines in deep (>20 m) water outside the Mwanza Gulf (Greenwood & Barel; 1978; Greenwood, 1981), suggests that before the Nile perch increase shrimps were most abundant at these depths.

Budeba (2003) confirmed our observations, indicating relatively high densities of shrimps in the Mwanza Gulf after the Nile perch upsurge. In a monthly sampling programme from May 2001 to April 2002 he caught considerable amounts of shrimps with lift nets, mainly at depths >10 m. From 11 to 25 m deep, the average catches increased from 3 to 30 g m^{-3} (Budeba, 2003). We converted these weights to numbers of shrimps via ln Dry Weight (mg) = 2.700 ln Body Length - 4.876 (mm) and Dry Weight = 0.2 Fresh Weight (Wanink, 1998). When using a body length of 15 mm, which approximated the average length of gravid shrimps in the Mwanza Gulf in 2001 (Fig. 5.3a), 3-30 g corresponds with 50-520 individuals. Such densities were never found in this area before the Nile perch upsurge.

Stomach content analysis of juvenile Nile perch (0-30 cm TL) in 1988/89 at stations 1-4 revealed that shrimps were the dominant prey at the deeper stations 3 and 4, while they were insignificant at the shallowest stations 1 and 2 (Katunzi et al., 2006). This agrees with the distribution pattern observed by Budeba (2003). Further, the latter author noticed seasonal fluctuations, with an increased abundance in the first quarter of the year. Similar seasonal fluctuations were observed in stomach contents of 0-group Nile perch at station 3, where shrimps dominated the diet from January to June (Katunzi et al., 2006). In Ugandan waters of Lake Victoria in 1994, Mbahinzireki et al. (1998) found densities from 0 to 3231 shrimps m^{-2} in shallow (<25m) and 33 to 2206 shrimps m^{-2} in deep (60m) water. Obviously, in the past decades the number of shrimps rose with several orders of magnitude, but the variation in catch rate was huge, which may indicate a patchy distribution and seasonal migrations.

Densities of shrimp predators before the Nile perch upsurge

Before the Nile perch upsurge in the early 1980s, the main predators of shrimps were haplochromine cichlids and *B. docmak* (Corbet, 1961; Chilvers & Gee, 1974; Greenwood, 1974; Okach & Dadzie, 1988). Stomachs of up to 2000 haplochromine cichlids, covering different trophic groups and collected between 1977 and 1984, have been analysed by several researchers. At least 13 specialised shrimp eating haplochromines are known from Lake Victoria (Greenwood, 1981; Witte & Van Oijen, 1990) of which two species were common enough for stomach analysis. *Haplochromis* (*Tridontochromis*) “erythrocryptogramma”, was collected in 1978-1980 in sub-littoral waters (6-20 m) of the Mwanza Gulf and fed almost exclusively on adult shrimps (M.J.P. Van Oijen, pers. com.). Stomach content analysis from a sample of *Haplochromis (T.) sulphurius*, Greenwood & Barel that was collected in June 1985 at deep (32-43 m) stations, showed that this species predominantly fed on adult shrimps (PCG, pers. obs.)

Of the over 114 piscivorous haplochromine species of Lake Victoria several included adult shrimps in their diet. The major food items of these piscivorous species were juvenile cichlids. Most of the piscivorous species that included shrimps in their diet had an adult size <10 cm, or were juveniles of larger growing species (Greenwood, 1981; Van Oijen, 1982, 1989; 1991, pers. com.). Over 400 stomachs of common molluscivorous and insectivorous species did not reveal any shrimp (Hoogerhoud et al., 1983; Hoogerhoud, 1986). In several hundreds of stomachs of zooplanktivorous species, no shrimps were found either (Goldschmidt et al., 1990; FW, pers. obs.). Neither were shrimps observed as food of detritivorous haplochromines (Goldschmidt et al., 1993; FW, pers.obs.).

Juvenile shrimps were not found in the stomachs before 1985. Because shrimps were mainly occurring in deeper water before the Nile perch upsurge, we expect that at that time, especially deepwater haplochromines were the potential predators of juvenile shrimps. Unfortunately, deepwater haplochromines were only incidentally included in our research on diets. Further, it should be noted that especially juvenile shrimps might have been overlooked among insect remains and zooplankton in stomach analyses when shrimp densities were low. Nevertheless, we assume that all haplochromines would eat juvenile shrimps when available. Zooplanktivorous haplochromines in 1987 included juvenile shrimps in their diet. The same was found for both zooplanktivores and detritivores in 2001/2002 (JHW, pers. obs.). This suggests that these small sized (± 8 cm SL) haplochromines, which before 1985 made up more than 80 % of the demersal haplochromine biomass (Witte & Van Oijen, 1990; Goldschmidt et al., 1993), at that time also fed on juvenile shrimps when available. If our assumptions are correct, it would imply that the biomass of predators, potentially feeding on juvenile shrimps, was at least 80% of the demersal haplochromine stock, i.e. 170 kg ha^{-1}.

Densities of shrimp predators after the Nile perch upsurge

After the Nile perch upsurge the haplochromines and *B. docmak* declined strongly, making their predation on shrimps insignificant (Witte et al., 1992a; Goudswaard & Witte, 1997). For Nile perch of 10-50 cm TL feeding on *adult* shrimps at station 3, we found annual averages of 14.8 kg ha^{-1} in 1987 and 11.9 kg ha^{-1} in 1989, and an average of 13.4 kg ha^{-1} over both years.

At station 3 the density of juvenile Nile perch was highest in the Mwanza Gulf (Katunzi et al., 2006). At this station, the number of Nile perch <10 cm TL, feeding on *juvenile* shrimps, increased from almost zero in 1984 to an annual average of 1325 fishes ha^{-1} in 1987 (PCG & FW, Chapter 3-unpublished data). This corresponded to 8.4 kg ha^{-1}. In 1989 the number declined to194 fishes which corresponded to 1.2 kg ha^{-1}. The small cyprinid *Rastrineobola argentea* Pellegrin invaded the demersal habitat after the collapse of the haplochromines and started to include juvenile shrimps in its diet (Wanink, 1998). During the period 1987-1989 the average biomass of this species at station 3 was 31.5 kg ha^{-1} (Wanink et al., in press). So, between 1987 and 1989 biomass of fish feeding on juvenile shrimps at station 3 ranged from 40 to 33 kg ha^{-1} and was 36.5 kg ha^{-1} on average**.**

Predation and life history aspects

The gravid shrimps in Lake Victoria showed a decline in body size over the period 1986-2001 (Fig. 5.3). Mbahinzireki et al. (1998) reported a body size range of 12 to 18 mm in 1993/94, at one deep- and 10 shallow-water stations at the Ugandan side of the lake. Based on their data, we calculated an average body size of 15.3 mm for that period. At the same deep-water station in Uganda, Sætveit (2003) found carapace lengths ranging from 3.87 to 4.99 mm in 2001, which was recalculated by us to a body size of 12-16 mm, and an average size of 13.4 mm. The size decline in the North over a period of 7 years confirms our observations in the South. Moreover, our data showed that length at first maturity of the shrimps also decreased.

Before the Nile perch upsurge the biomass of predators potentially feeding on adult shrimps was estimated at 10 kg ha^{-1}. In the same period, the total potential predator density on juvenile shrimps was 170 kg ha^{-1}. After 1985, this picture changed, as the biomass of Nile perch (<10 cm TL) plus that of *R. argentea* feeding on juvenile shrimps was on average 36 kg ha^{-1}, and the biomass of Nile perch of 10-50 cm TL, preying upon adult shrimps, was on average 13 kg ha^{-1}. Thus, before the Nile perch boom the biomass of predators on juvenile shrimps was approximately 17 times higher than that of predators on adult shrimps, and after the boom only 3 times. The biomass of potential predators on adult shrimps remained approximately the same and that on juvenile shrimps declined, whereas the biomass of shrimps increased manifold. Therefore, after the Nile perch upsurge, the biomass of predators in relation to the biomass of shrimps, especially juveniles, was relatively low compared to the pre-Nile perch period. It is likely that this allowed a strong recruitment of shrimps to the reproductive stage.

A decrease in maximum body size and size at maturity is a common response to increased mortality of adult organisms. Such a decrease in body size and size at maturity was observed in *C. nilotica*. However, although the estimated ratio of predators on juvenile and adult shrimps decreased from 17 : 1 to 3 : 1, our data do not indicate an absolute increase in predation pressure on adult shrimps.

Increased relative fecundity and a reduced generation time, resulting in an increased total reproductive output (Noakes & Balon, 1982; Roff, 1992; Stearns, 1992) may also compensate adult mortality. However, we have no indications that the relative fecundity of *C. nilotica* changed consistently over the years 1986-1990. Mbahinzireki (1998) neither found a change in relative fecundity between June 1992 and September 1994. Sætveit (2003) found a minimum of 59 eggs for an 11.9 mm long shrimp and a maximum of 234 eggs for a shrimp of 15.6 mm in 2001 in Uganda (carapace length recalculated to body length by us). These data fit perfectly within the range that we found for the second half of the 1980s.

Decreases in body size and size at maturity were observed in *R. argentea* in Lake Victoria, where the impact of fishing methods and Nile perch shifted the predation pressure from juveniles to adults in the 1980s (Wanink, 1998). The relative fecundity of the dwarfed *R. argentea* did not change either (Wanink, 1998). However, the fish increased their reproductive output by a combination of increased growth rate and decreased age at maturity. Unfortunately, we have no data on growth rate of *C. nilotica.*

Apart from the suggested effect of predation pressure by Nile perch on adult shrimps, other factors such as increased environmental stress (e.g. hypoxia, food availability and quality) also might affect size at maturity (Videler, pers. com.). For instance, an increase in oxygen demand by increased body size was shown by Hart (1980b).

In conclusion we have no unequivocal explanation for the size decline of the shrimps, but the increase of the population may be explained by the strong decrease in predation on juvenile shrimps.

The role of increased primary production and hypoxic refugia

Other explanations for the increase of shrimps in Lake Victoria than reduction in juvenile mortality have been suggested. Kaufman (1992) mentioned the increased availability of algae and detritus. Primary production and the availability of detritus have increased during the past decades, due to increased eutrophication (Hecky, 1993).

Table 5.3. *Main ecological changes in the Mwanza Gulf between 1983 and 2001*

Period	Observations	References
1977-1985	Shrimps only occasionally found in low densities	This paper
1983-1984	Invasion of sub-adult Nile perch	This thesis
1983-1987	Strong growth of Nile perch population	This thesis
1985	First juvenile Nile perch in trawl catches	Goudswaard & Witte 1985
1984-1987	Decline of the haplochromine stock	Witte et al., 1992b
1986-1987	Start of growth of the shrimp stock	This paper; JHW, pers. obs.
1986-1987	First observation of severe algal blooms; prolonged low dissolved oxygen levels and decrease water transparency	Witte et al., 1992a, 2005; Wanink et al., 2001
Sept. 1987	Catches of haplochromines reach zero level	Ligtvoet & Mkumbo, 1990; Witte et al., 1992b
1987	Diet switch of Nile perch from haplochromines to other fish and shrimps	Ligtvoet & Mkumbo, 1990
1987-2001	Decline in body size of *Caridina nilotica*	This paper

Eutrophication started already in the 1920s and intensified in the 1960s (Hecky, 1993; Verschuren et al., 2002) though severe algal blooms were only observed in the 1980s (Table 3; Ocumba & Kibaara, 1989; Mugidde, 1993). However, it should be noticed that detritus was also abundantly available before the Nile perch increase during the 1980s. For this reason we do not regard the increase of detritus a key factor for the increase of the shrimp population. Moreover, not only the quantity of detritus is important, also the quality plays a role. Due to the changes in the phytoplankton composition (Hecky, 1993; Mugidde, 1993; Gophen et al., 1995) the majority of the bottom debris in the past was mainly made up of decaying diatoms (in particular *Aulacoseira* spp.), whereas after the Nile perch boom it mainly consisted of decaying cyanophyta. It is as yet unknown if this qualitative difference had any effect.

According to several studies, the increased hypoxia in the lower part of the water column for prolonged periods (Table 3; Hecky, 1993), might provide a refugium to *C. nilotica* to avoid Nile perch predation (Kaufman & Ochumba, 1993; Branstrator & Mwebaza-Ndawula, 1998). However, Kaufman & Ochumba (1993) also observed on several occasions, large sonar targets in strata bearing only 1-2 mg O_2 l^{-1}. Trawling on these occasions suggested that these targets were Nile perch, which had been feeding heavily on shrimps (Kaufman & Ochumba, 1993). Similar observations were made during hypoxia in the Mwanza Gulf (Wanink et al., 2001). Unlike Kaufman &

Ochumba, Wanink et al. (unpublished data) observed *C. nilotica* near the surface under conditions of oxygen stratification. In both cases it seems that the hypoxic layer does not provide an adequate refugium. The same was concluded for *R. argentea* by Wanink et al. (2001).

Cascading effects

Our data suggest that the decline of the haplochromine stock, through a decrease in predation pressure, has been beneficial to juvenile shrimps. On its turn the increase of juvenile shrimps may have had a positive impact on juvenile Nile perch. Before 1985 hardly any juvenile Nile perch were present in the Mwanza Gulf. The area was first colonised by sub-adult and adult Nile perch (Table 3; Goudswaard & Witte, 1985). A tentative scenario for the changes in the Mwanza Gulf could be the following: (1) High presence of potential predators (viz. zooplanktivorous and detritivorous haplochromines) on shrimp larvae might have been a factor that limited the abundance of *C. nilotica* before the decline of the haplochromine stock. (2) The invasion of adult and sub-adult Nile perch in 1983/84 resulted in a reduction of the haplochromines. (3) This led to a reduced predation on juvenile shrimps causing an increase of *C. nilotica* stock. 4) On their turn, juvenile shrimps appeared an important food source of juvenile Nile perch that first appeared in the Mwanza Gulf in 1985. 5) Adult shrimps replaced the haplochromines in the diet of larger Nile perch (Ligvoet & Mkumbo, 1990; Mkumbo & Ligtvoet, 1992; Katunzi et al., 2006).

It appears that both the stock of *C. nilotica* and that of Nile perch can flourish under these conditions. Because, in the absence of haplochromines, shrimps are a key prey to Nile perch (Katunzi et al., 2006), they played a crucial role in the ecological changes in Lake Victoria during the past decades.

Acknowledgements

Our thank goes to the staff of the Tanzania Fisheries Research Institute and in particular to the crews of MV Kiboko and the small trawler, who fished to collect many of the data upon which this paper is based. J.J. Videler and C.D.N. Barel are thanked for their comments on the draft of this paper. The HEST project was financially supported by the section Research and Technology of the Netherlands Minister of Development Co-operation and by the Organization for the Advancement of Tropical Research (WOTRO) grants W87-129, W87-161, W87-189 and W84-488. The Leiden University Fund, the Schure-Beijerinck-Popping Fund, the Van Tienhoven Foundation and Yellow Springs Instruments are thanked for additional funding.