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# Cascading Effects of the Introduced Nile Perch on the Detritivorous/Phytoplanktivorous Species in the Sublittoral Areas of Lake Victoria

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**Abstract:** *In the 1980s an explosive increase of the introduced Nile perch (Lates sp.; Harrison 1991) in Lake Victoria caused the destruction of approximately 65% of the endemic haplochromine cichlids. The eradication of approximately 200 vertebrate species in less than a decade may well represent the largest extinction event among vertebrates during this century. The introduction of the Nile perch can be considered as a large-scale, albeit unintended, experiment. Far-reaching changes in the food web are taking place. We present data on the importance of haplochromines in the ecosystem prior to the Nile perch boom. An analysis of the pelagic community in the sublittoral area of the Mwanza Gulf revealed that the phytoplanktivores formed 18% of the biomass of the total haplochromine community. In the benthic community, the detritivores that frequently included phytoplankton in their diet comprised 31% of the biomass. We examine the hypothesis that algal grazing was reduced by the disappearance of haplochromine phytoplanktivores and detritivores. The disappearance of these groups may have contributed to the recent algal blooms. To investigate this hypothesis we consider a second major change in the system. Coinciding with the decrease of the haplochromines, the number of atyid prawns, *Caridina nilotica*, has strongly increased. We present preliminary evidence that the stock of the detritivorous haplochromines that formerly comprised most of the demersal ichthyomass has (partially?) been replaced by the prawn. We discuss the possible mechanisms underlying this major change in the food web. With respect*

Efectos en cascada por la introducción de la perca del Nilo sobre las especies detritívoras/fitoplanctívoras en las áreas subtidales del lago Victoria

**Resumen:** *Durante la década del 80 un incremento explosivo de la perca del Nilo (Lates spp., Harrison 1991) en el lago Victoria causó la destrucción de aproximadamente el 65% de los cíclidos haplocromínidos endémicos. La erradicación de aproximadamente doscientas especies de vertebrados en menos de una década representa seguramente el mayor evento de extinción de esta centuria entre los vertebrados. La introducción de la perca del Nilo, si bien no intencional, puede ser considerada como un experimento a gran escala. Están ocurriendo cambios de largo alcance en la red trófica. Nosotros presentamos datos sobre la importancia de haplocromínidos en el ecosistema antes de la explosión demográfica de la perca del Nilo. Un análisis de la comunidad pelágica en el área sublitoral del golfo Mwanza reveló que los fitoplanctívoros formaron un 18% de la biomasa total de la comunidad de haplocromínidos. En las comunidades bentónicas, los detritívoros que incluyeron frecuentemente en sus dietas fitoplancton comprendieron un 31% de la biomasa. Nosotros examinamos la hipótesis de que el pastoreo de algas fue reducido por la desaparición de haplocromínidos fitoplanctívoros y detritívoros. La desaparición de estos grupos puede haber contribuido al bloom algal reciente. Para investigar esta hipótesis, nosotros consideramos un segundo cambio de importancia en el sistema.*

to the conservation of the Great African Lakes, the collapse of Lake Victoria's ecosystem should serve as an example of how easily a complex ecosystem can be irreversibly destroyed.

Coincidente con el descenso de los haplocromínidos, el número de camarones, *Caridina nilotica*, aumentó fuertemente. Nosotros presentamos evidencia preliminar que indica que el stock de haplocromínidos detritívoros, que con anterioridad comprendió la mayor parte de la ictiomasa demersal, ha sido (¿parcialmente?) reemplazado por el camarón. Nosotros discutimos los posibles mecanismos subyacentes a este importante cambio en la red trófica. Con respecto a la conservación de los Grandes Lagos Africanos, el colapso del ecosistema del lago Victoria debe servir como ejemplo de cuán fácilmente puede ser destruido en forma irreversible un ecosistema.

## Introduction

The Great Lakes of East Africa are invaluable to the Africans who depend on them, as well as for their inherent interest for scientists, naturalists, and environmentalists worldwide. Besides their significance for the well-being of the people who are directly dependent on the resources provided by them, these lakes represent a unique heritage that offers scientists opportunities to study a wide spectrum of geological, hydrological, and biological phenomena (Coulter 1991).

Lake Victoria, with a surface area of 69,000 km<sup>2</sup>, is the world's largest tropical lake. The lake is approximately 750,000 years old and may have dried up more recently (Stager et al. 1986). The fish fauna of Lake Victoria was dominated by a diversified, presumably monophyletic (Meyer et al. 1990) species flock of haplochromine cichlids.

The explosive speciation and adaptive radiation displayed by these endemics remains unrivalled among vertebrates, the cichlid species flock of Lake Malawi being the only possible exception (Barel et al. 1991; Goldschmidt & Witte 1992). However, no other group of vertebrates is known in which such an extensive adaptive radiation was realized with so little anatomical diversity (Greenwood 1974; Barel et al. 1991). According to our most recent counts, Lake Victoria's pre-Nile perch species flock was comprised of 300+ species that occupied a great variety of niches in the lake (Witte et al. 1992b). Each habitat contained its own community of haplochromine cichlids (Greenwood 1974; van Oijen et al. 1981; van Oijen 1982; Hoogerhoud et al. 1983; Witte 1984; Witte & van Oijen 1990; Witte et al. 1992b; Goldschmidt et al. 1990; Goldschmidt & Witte 1990; Goldschmidt 1991; Barel et al. 1991).

To boost fisheries, Nile perch (*Lates* sp.; Harrison 1991) was introduced into the lake in the 1950s. Only much later, in the early 1980s, was an explosive increase of this predator observed. Within a decade, the complex ecosystem of Lake Victoria has been irreversibly

destroyed by the irruption of the introduced perch (Hughes 1983; Barel et al. 1985; Ogutu-Ohwayo 1990a, 1990b; Witte et al. 1992a, 1992b). In spite of this, many fisheries biologists regard the introduction as a great success. This is not surprising since the fish yield in recent years has increased three- to four-fold (CIFA 1988; Greboval 1990). In view of the present instability of the system, however, it is in our opinion too early to judge the ultimate impact of the induced changes on the fisheries.

In this paper we demonstrate that prior to the Nile perch boom the demersal detritivorous haplochromines were the dominant trophic group near the lake bottom and that the pelagic community of haplochromines represented a large biomass. Previous studies emphasize the importance of the pelagic zooplanktivores in contributing to the total biomass of the haplochromines (Witte 1981; Witte & Goudswaard 1985). However, the importance of the pelagic phytoplanktivores has been overlooked. We suggest that the disappearance of the haplochromines that fed on phytoplankton may partially explain the recent blooms of blue-green algae (Ochumba 1987; Ochumba & Kibaara 1989; personal observation). We argue that the bottom-dwelling detritivorous haplochromines have (partially?) been replaced by the native atyid prawn *Caridina nilotica*.

We use the term "replacement," see Daan (1980): "Replacement of one stock by another implies that, within a geographical area and within a particular time span, one stock has gone down and another has increased . . . Replacement requires that there be some functional relationship between the two events." To detect a possible functional relationship between the fall of the (detritivorous) haplochromines and the rise of the atyid prawn, we describe spatial distributions, diets, and a number of crucial life-history characteristics of the most abundant detritivorous haplochromines and the atyid prawn. We conclude that replacement of the detritivorous haplochromines by the prawn is likely to have taken place and discuss the possible mechanism(s) involved.

## Material and Methods

Species that have not been described bear temporary names, indicated by quotation marks. Samples of all species have been deposited at the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands. Haplochromine species were classified into trophic groups following Witte and van Oijen (1990). The group of detritivorous/phytoplanktivorous species (Witte 1981) was split into the detritivorous and the phytoplanktivores in this paper. The curved head group is an assemblage of species (mainly *H. "75"* and *H. cinctus*), for which we could

usually only identify males that have reproductive coloration. Descriptions of the research area and fishing techniques can be found in Witte (1981) and van Oijen et al. (1981).

Estimates of fish biomass were based on the lakewide UNDP survey by Kudhongania and Cordone (1974) made between January 1969 and May 1971. The biomass data for the various trophic groups of haplochromines were collected in sublittoral waters of the Mwanza Gulf (6–20 m) between 1977 and 1990. Eleven stations along a transect (2–14 m deep) across the Mwanza Gulf were sampled with a small bottom trawl, a surface trawl,

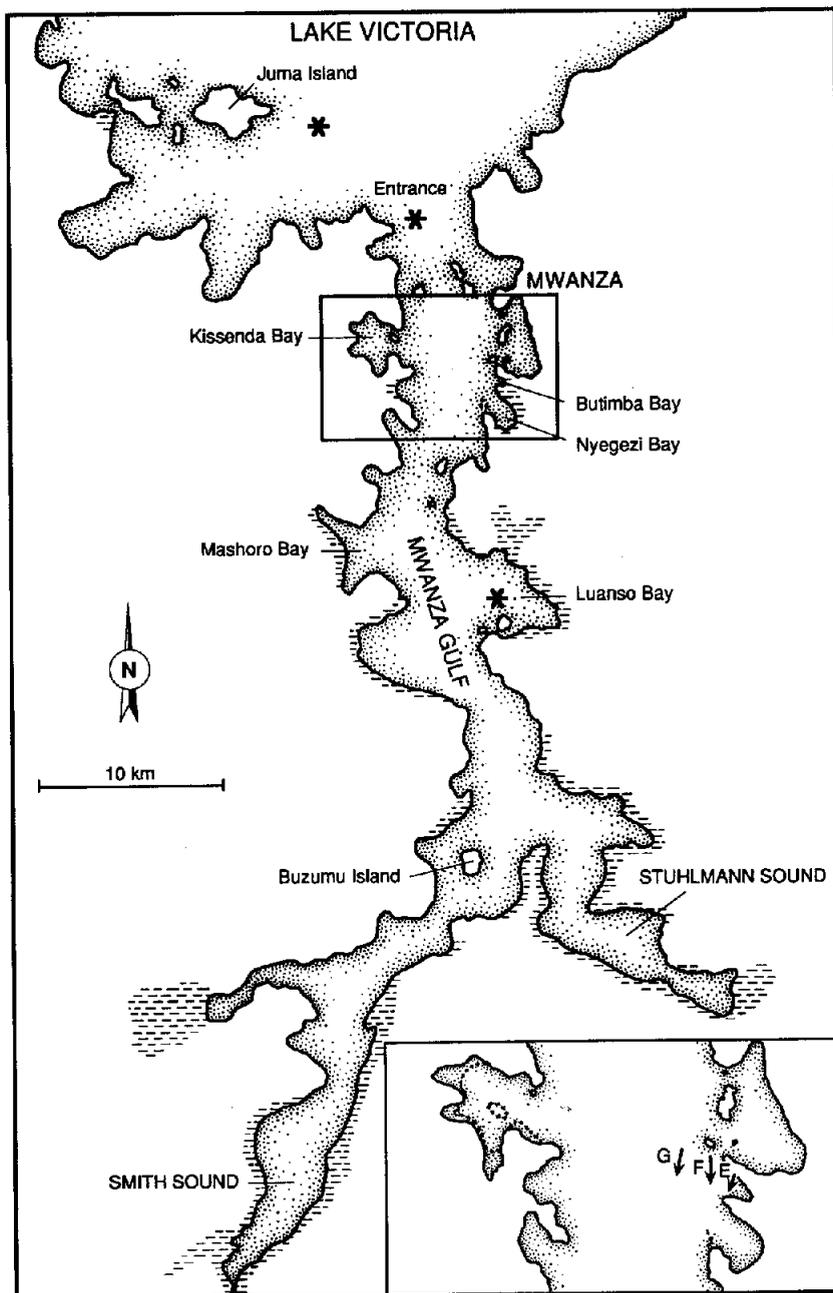


Figure 1. Map of the Mwanza Gulf and surroundings. Sampling stations of *Haplochromis* Ecology Survey Team are indicated.

Table 1. Estimates of standing stocks of demersal fishes in Lake Victoria prior to the Nile perch upsurge.

Species	Metric Tons	%
Haplochromine spp. (300+)	536,568	83.0
Tilapiine spp. (5)	13,888	2.0
<i>Bagrus docmak</i>	39,685	5.8
Clariidae spp. (6)	27,406	4.0
<i>Synodontis</i> spp. (2)	23,260	3.4
<i>Schilbe mystus</i>	646	0.1
<i>Protopterus aethiopicus</i>	9543	1.4
<i>Lates</i> sp.	402	0.1
<i>Barbus altianalis</i>	213	0.0
<i>Labeo victorianus</i>	68	0.0
<i>Mormyrus kannume</i>	181	0.1

Adapted from Kudhonganika and Cordone, 1974.

and gill nets (Witte 1981; Goldschmidt et al. 1990; Witte et al. 1992b). Most of the stations were sampled between 1979 and 1982 and between 1987 and 1990. Station G (14 m) was sampled at regular intervals throughout the whole period. Samples were also taken at a 6-m deep station in the Luanso Bay and at a 20-m deep station at the entrance of the Mwanza Gulf (Fig. 1).

Vertical distributions of adult fishes were determined with gill nets (2.5 cm stretched mesh size, 5 m in width, and as deep as the column, 6–20 m) marked horizontally each meter. At the Luanso Bay station (6 m), five day and four night catches were made between August 15 and August 20, 1984. At station G, 33 day and 43 night catches were made between August 17, 1981, and July 21, 1984. Occasionally, conventional gill nets were set in the top, middle, and bottom layer (mesh sizes 25, 38, and 51 mm). At the entrance of the Mwanza Gulf (20 m), four day and three night catches were made between August 29 and September 4, 1984. Gill nets were left in the water for periods of five to six hours. Day catches are those between 10.00 and 17.00 hours, and night catches those between 22.00 and 05.00 hours.

At Station G, eight surface trawls and eight bottom trawls were made during the day as well as during the night between August 17, 1981, and June 18, 1982. Haplochromines from these trawl catches were used for the diet analysis. Stomach and intestine fullness was esti-

Table 2. Trophic composition of the haplochromines in diurnal bottom trawl catches ( $n = 30$ ) in the sublittoral area of the Mwanza Gulf in 1978–1979.

Trophic Group	% of Number	Estimated % of Weight
Detritivores	61.3	54.5
Phytoplanktivores	0.2	0.2
Zooplanktivores	30.4	27.0
Insectivores	3.1	9.7
Molluscivores	0.7	2.2
Piscivores	0.9	2.8
Prawn Eaters	0.1	0.2
Rest	3.8	3.4

Table 3. Trophic composition of the haplochromines in the water column ( $n = 16$  catches) in the sublittoral area of the Mwanza Gulf (Station G) in 1981–1982.

Trophic Group	% of Number	Estimated % of Weight
Detritivores	37.7	31.3
Phytoplanktivores	21.5	17.7
Zooplanktivores	30.1	24.8
Insectivores	5.1	14.7
Molluscivores	0.9	2.6
Piscivores	1.9	5.5
Prawn Eaters	1.3	2.1
Rest	1.6	1.3

Gill nets were set by day and by night.

mated. Stomachs and intestines estimated to be less than 20% full were discarded. Estimates of the food volume of the particular food items as a percentage of the total volume of ingested food were made and weighed to the degree of fullness.

From March 1983 through October 1984, samples were usually taken twice a month at Station G. Fishes were preserved in formaldehyde (4–8%). Females were dissected and the developmental stage of their gonads was scored. In order to estimate fecundity, the number of eggs in the ovaries of ripe females was determined.

Diurnal and nocturnal vertical distributions of the prawn *Caridina nilotica* were determined on June 10–11 and 25–26, 1987. A small lift net (110 × 110 cm; 8 mm stretched mesh size) was hauled from three different water depths at Station G: 14 m (total water column), 9.4 m (upper two thirds sampled), and 4.7 m (top one third sampled). Nets were held at the selected depth for 10 min before lifting to prevent sampling in a recently disturbed habitat. Samples were stored in a 4% formaldehyde solution before being analyzed. Length of the prawns was measured from between the eyes to the origin of the telson.

The stomach contents of small Nile perch (<100 mm), caught in 1986–1988, were examined. Most fish were caught at Station G and at the entrance to the Gulf. Additional samples were taken at Station E (7 m) on the transect, in the Luansa Bay, and near Juma Island. The standard length of the fishes and the size of the prawns in their stomach were measured.

Following Greenwood (1974), three depth ranges are used in evaluating survey results: littoral (0–6 m), sublittoral (6–20 m), and deep water (>20 m).

## Results

### The Ichthyomass of Lake Victoria Before the Nile Perch Boom

#### DEMERSAL FISHES

Cichlid fishes dominated the demersal fish faunal biomass (Kudhonganika & Cordone 1974; Table 1). Haplochromines that occurred in the littoral, sublittoral,

and deep water were by far the most important group, representing 83% of the demersal ichthyomass. Tilapiines were mainly restricted to the littoral waters and comprised only 2% of the demersal ichthyomass. The only noncichlid groups notably contributing to the demersal ichthyomass were the catfishes *Bagrus*, *Clarias*, and *Synodontis*, and the lungfish *Protopterus* (together 14.6%).

A closer look at the demersal haplochromine community in the sublittoral area of the Mwanza Gulf (Table 2) revealed that the detritivores (13+ species) were the most abundant group, constituting of 54.5% of the biomass, followed by the zooplanktivores at 27%. The only other trophic groups contributing more than 5% to the haplochromine biomass were the insectivores, with 9.7%.

#### PELAGIC FISHES

Lake-wide standing stock estimates of the pelagic ichthyomass are lacking. Information on the composition of the haplochromine community, however, including the pelagic species, is available for the sublittoral area of the Mwanza Gulf. An analysis of gill net catches revealed that the pelagic fish community contributed substantially to the biomass of the haplochromines (Table 3). It is significant that the phytoplanktivores that were rare in the bottom catches (0.2% of the haplochromine biomass) comprised 18% of the total biomass of the haplochromines in the gill net samples (Tables 2 and 3; Fig. 1). The number of pelagic phytoplanktivorous haplochromine species in Lake Victoria was surprisingly low—only three species (Witte & van Oijen 1990), of which *H. "kribensis"* was by far the most abundant. The zooplanktivores that made a diurnal migration throughout the column were also an important group comprised of 21+ species (Table 2 and 3; Goldschmidt et al. 1990; Witte & van Oijen 1990). Few data are available on the standing stock of the pelagic cyprinid *Rastrineobola argentea* in the pre-Nile perch system. In surface-trawl catches, the biomass of this species amounted to approximately one third of the zooplanktivorous haplochromine biomass.

#### Detritivorous and Phytoplanktivorous Haplochromines: Bulk Species Before the Collapse

#### HORIZONTAL DISTRIBUTIONS

Both adults and juveniles of the "curved head" group (mainly *H. "75"* and *H. cinctus*) occurred in all sublittoral areas of the Mwanza Gulf. In general, *H. cinctus* occurred in deeper water than *H. "75"* (van Oijen et al. 1981). *H. "nigrofasciatus"* and *H. "kribensis"* also occurred mainly in the sublittoral area of the Mwanza Gulf. Juveniles of *H. "nigrofasciatus"* occurred in sheltered

bays, while juveniles of *H. "kribensis"* were found in the shallow southern part of the Mwanza Gulf (<5 m deep).

#### VERTICAL DISTRIBUTIONS

Species of the "curved head" group typically occurred close to the bottom, while *H. "nigrofasciatus"* dwelled slightly higher in the column (Fig. 2). *H. "kribensis"* was a surface-bound species. After sunset all species migrated upwards to a greater or lesser extent (Fig. 2). These patterns were consistent throughout the year and at stations of different depth.

#### DIETS

All species foraged mainly during the daytime, although nighttime feeding did occur (Fig. 3). Species of the "curved head" group fed mainly on detritus, both during the day and the night. Some insect larvae, copepods, and phytoplankton were also observed in their digestive tracts.

During the daytime, the diet of *H. "nigrofasciatus"* was similar to that of the "curved head" group, but *H. "nigrofasciatus"* did not feed on insect larvae. By night, foraging individuals of *H. "nigrofasciatus"* included a large fraction of the diatom *Melosira* in their stomachs (Fig. 3). Predation on algae by bottom-dwelling bulk species was presumably important. The pelagic *H. "kribensis"* had a diet strikingly different from the bottom-bound detritivores. Both by day and night, blue-green algae were the dominant food. During the daytime, *Melosira* (and occasionally other small diatoms such as *Nitzschia*) were also consumed. By night *H. kribensis* fed on adult insects and pupae at the water surface.

#### REPRODUCTIVE CHARACTERISTICS

Ripe females (presumably mainly *H. cinctus*) of the "curved head" group had a higher fecundity than similarly sized females of *H. "kribensis"* and smaller females of *H. "nigrofasciatus"*. Conversely, egg size was considerably smaller in the "curved head" group and *H. "nigrofasciatus"* than in *H. "kribensis"* (Table 4).

#### TIMING OF THE BREEDING PERIOD

The "curved head" group and *H. "nigrofasciatus"* had a distinct breeding period. The highest fraction of females with ripe or ripening ovaries and of brightly colored males was found at the end of the long rainy season (April and May; Fig. 4). This seasonality of breeding has been observed during several years (Witte 1981; Goldschmidt 1986). In contrast, ripe females and brightly

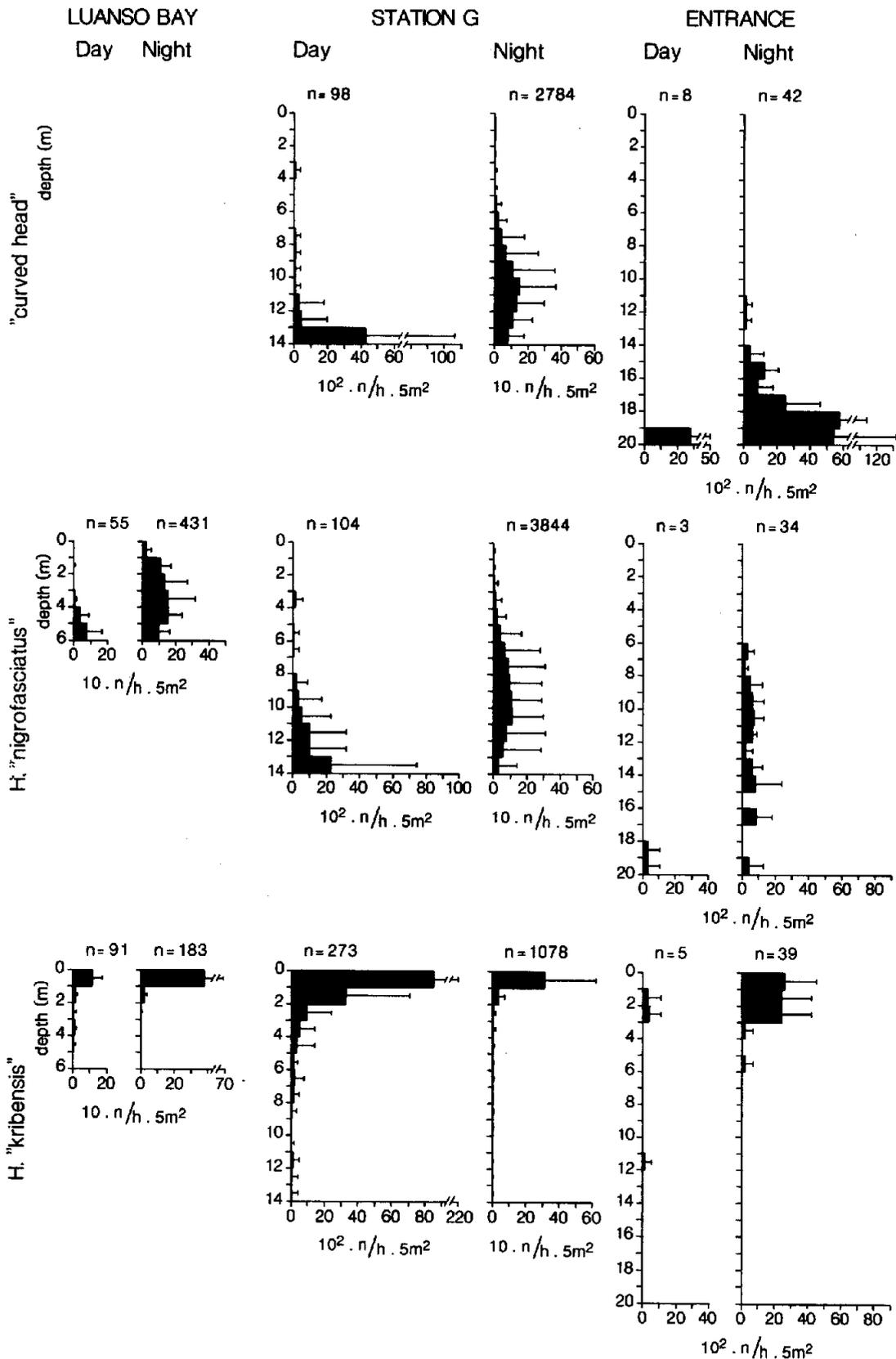


Figure 2. Diurnal and nocturnal vertical distributions of the detritivorous "curved head" group, *H. "nigrofasciatus"*, and the phytoplanktivorous *H. "kribensis"* at a 6-m (Luanso Bay), 14-m (Station G), and 20-m (entrance) deep station in the Mwanza Gulf. Plotted are average number of fishes per 5 m<sup>2</sup> of gill net (and one standard deviation) for every meter in depth. In total, 42 day and 50 night catches were made from 1981 through 1984. n = number of individuals.

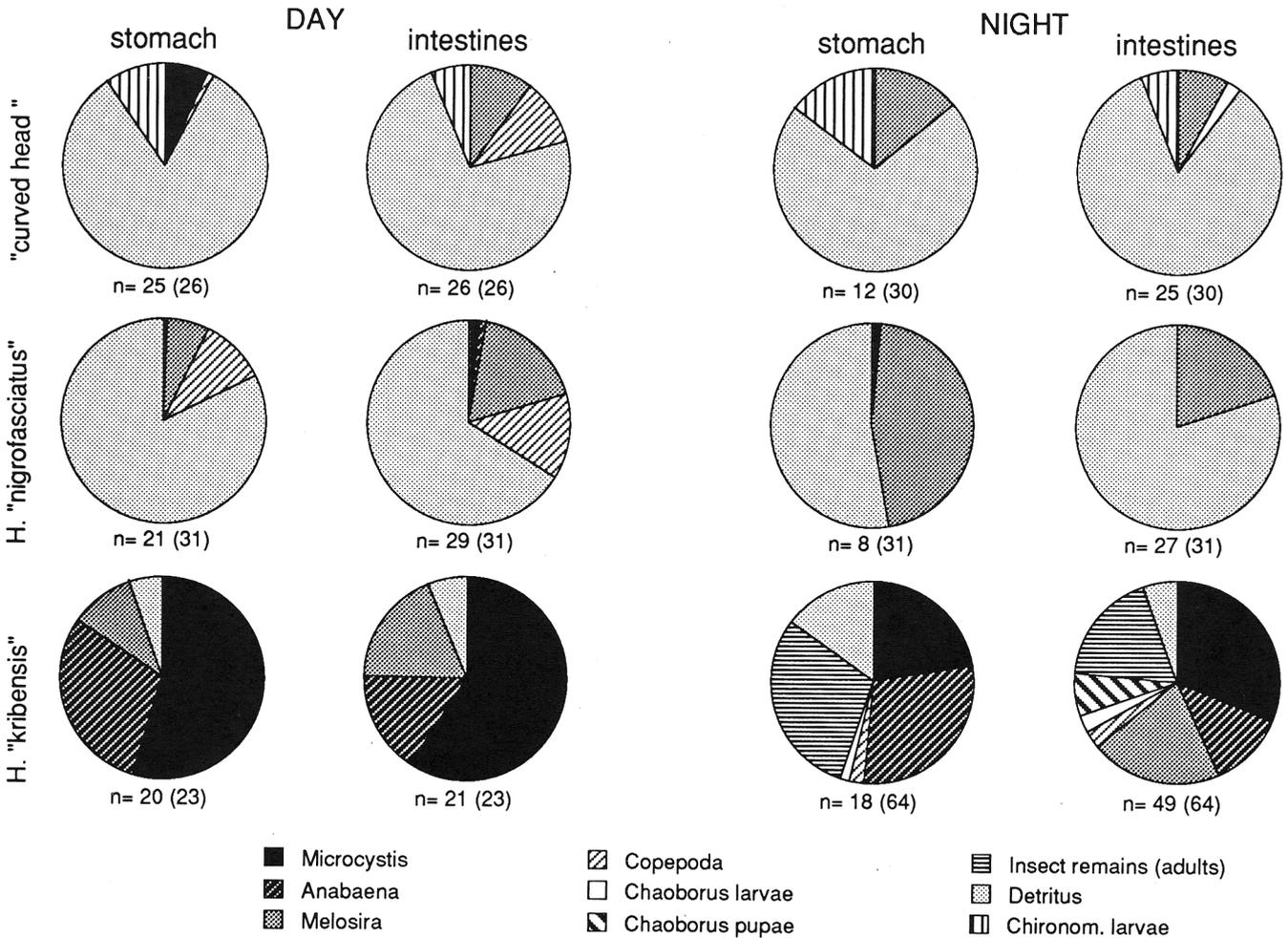


Figure 3. Diet composition (mean volume percentages) by day and night of the "curved head" group, H. "nigrofasciatus" and H. "kribensis" at the Mwanza Gulf transect throughout the year (1981-1982). Data on stomach and intestinal contents are presented separately. Empty stomachs and intestines (or filled less than 20%) were discarded n = number of individuals used for the calculation. Total number of individuals those with empty stomachs/intestines included are in brackets. See legends for prey categories.

colored males of H. "kribensis" were present all year round.

SPAWNING SITES

Brooding females (carrying eggs or juveniles in the buccal cavity) and brightly colored males of the species belonging to the "curved head" group were common in the main body of the Mwanza Gulf. Juveniles were released from the buccal cavities in these areas. Brooding females of H. "nigrofasciatus" also occurred here, but the smallest juveniles recognized (20 mm SL) were most common in sheltered, shallow bays. After a short stay in these bays, they migrated to deeper water. Ripe females of H. "kribensis" were usually present at Station G, but brooding females were rarely caught here. Juveniles of this species were caught only at shallow-water stations (3 and 5 m deep) in the southern half of the Gulf.

GgO-rH

H. "nigrofasciatus" reached a standard length of 5-6 cm within a year. Since the adults did not become much larger and the parental population collapsed after the breeding period (Fig. 5), H. "nigrofasciatus" presumably was an annual species. No quantitative evidence is available for the "curved head" group or for H. "kribensis," but these species reached larger sizes (up to 9 cm SL) than ever observed for H. "nigrofasciatus".

The Increase of Nile Perch and the Collapse of the Haplochromines

Nile perch have been recorded from experimental trawl catches in the Mwanza Gulf since 1972, the year in which a research vessel began operating in this area. However, the mean catches were low (<10 fish/trawl). Af-

Table 4. Some ecological characteristics of the phytoplanktivorous and detritivorous haplochromines and the prawn *Caridina nilotica* in the Mwanza Gulf.

	<i>Phytoplanktivorous Haplochromines</i>	<i>Detritivorous Haplochromines</i>	<i>Prawns</i>
Horizontal Distribution	littoral, mainly sublittoral, distribution in deep water unknown	littoral, mainly sublittoral and deep water at least up to 30 m	littoral, sublittoral, and deep water, at least up to 35 m
Vertical Distribution	near the surface	near the bottom, at night slightly higher	near the bottom, at night slightly higher
Diet	mainly phytoplankton and some detritus; at night also insect pupae, adult insects, and some zooplankton	mainly detritus, also some phytoplankton, zooplankton, and insect larvae	mainly detritus, a few diatoms, and epiphytic algae
Mean Fecundity	22.2 ( <i>H. keribensis</i> ; $n = 150$ )	20.2–67.6 (four different species; $n = 924$ )	123.4 ( $n = 10$ )
Mean Egg Size	3.5 ± 0.4 mm	2.8 ± 0.2–3.0 ± 0.3 mm	?
Spawning Period	year-round spawners	mostly seasonal spawners, with peaks from April to August	year-round spawners, with peaks from June to August
Spawning Sites	probably in shallower southern half of the Mwanza Gulf	Mwanza Gulf at least up to the entrance	Mwanza Gulf, at least up to Juma Island
Brood Care	mouth brooding	mouth brooding	pouch brooding
Nurseries	shallower southern half of the Mwanza Gulf	main body of Mwanza Gulf (for <i>H. nigrofasciatus</i> , sheltered bays)	?
Age at First Maturity	?	approximately 1 year for <i>H. nigrofasciatus</i>	more than 1 year?

ter 1982, a sharp increase in Nile perch catches was observed, and in 1987 the mean catch rates were over 100 kg/hr (Barel et al. 1991; Witte et al. 1992b). Nile perch have been caught in Lake Victoria over a wide depth range (1–60 m), independent of bottom type (Goudswaard & Witte 1985; Ligetvoet & Mkumbo 1990). The highest catch rates in the Tanzanian area in 1985 were obtained from waters between 16 and 50 m deep. With decreasing depth, the Nile perch catch became smaller (Goudswaard & Ligetvoet 1988). Juveniles smaller than 10 cm SL were mainly found in littoral areas (E. F. B. Katunzi, in preparation).

The densities of the bottom-dwelling detritivores and the pelagic phytoplanktivores have declined by a factor of a thousand or more since the Nile perch explosion in the Mwanza Gulf (Witte et al. 1992b). It has been clearly demonstrated that the disappearance of the haplochromines and the Nile perch explosion were not coincidental (Witte et al. 1992a, 1992b). The Nile perch was the main cause of the eradication of the haplochromines, although in some areas fisheries may have initiated and thereby facilitated this process. Haplochromines, particularly the bottom-dwelling species, were the major prey of the Nile perch. It was only after the density of the haplochromines had declined to almost zero that the Nile perch switched to other prey such as the prawn *Caridina nilotica*, the cyprinid *Rastrineobola argentea*, and its own young (Gee 1969; Okedi 1971; Hughes 1986; Ogari & Dadzie 1988; Ligetvoet & Mkumbo 1990; Ogutu-Ohwayo, 1990c).

#### The Rise of the Prawn *Caridina nilotica*: Coincidence or Replacement?

##### HORIZONTAL DISTRIBUTION AND DIET

Unfortunately, extensive ecological studies of *C. nilotica* are not available for Lake Victoria. Fryer (1960b) described *C. nilotica* as a detritus feeder, feeding on material accumulating on the bottom and on submerged vegetation. A few diatoms and strands of presumably epiphytic filamentous algae were also observed in the gut, in addition to small fragments of rotting higher plants.

Fryer (1960b) observed two forms of *C. nilotica* in Lake Victoria, a benthic form occurring in deep water and a second form common in the littoral region wherever there were beds of submerged vegetation. In the present study, no attempt was made to distinguish between these forms.

Corbet (1961), in a study on the food habits of the noncichlid fish of Lake Victoria, found that *Caridina nilotica* was a common, but never a dominant, food item in the diet of several taxa, such as *Schilbe*, *Mormyrus*, *Barbus*, and *Alestes*, which had been collected in a variety of habitats. Graham (1929) reports that prawns are an important food for the *Bagrus* in deep water.

Whereas no noncichlid fish taxon in the pre-Nile perch system mainly fed on prawns, the haplochromine

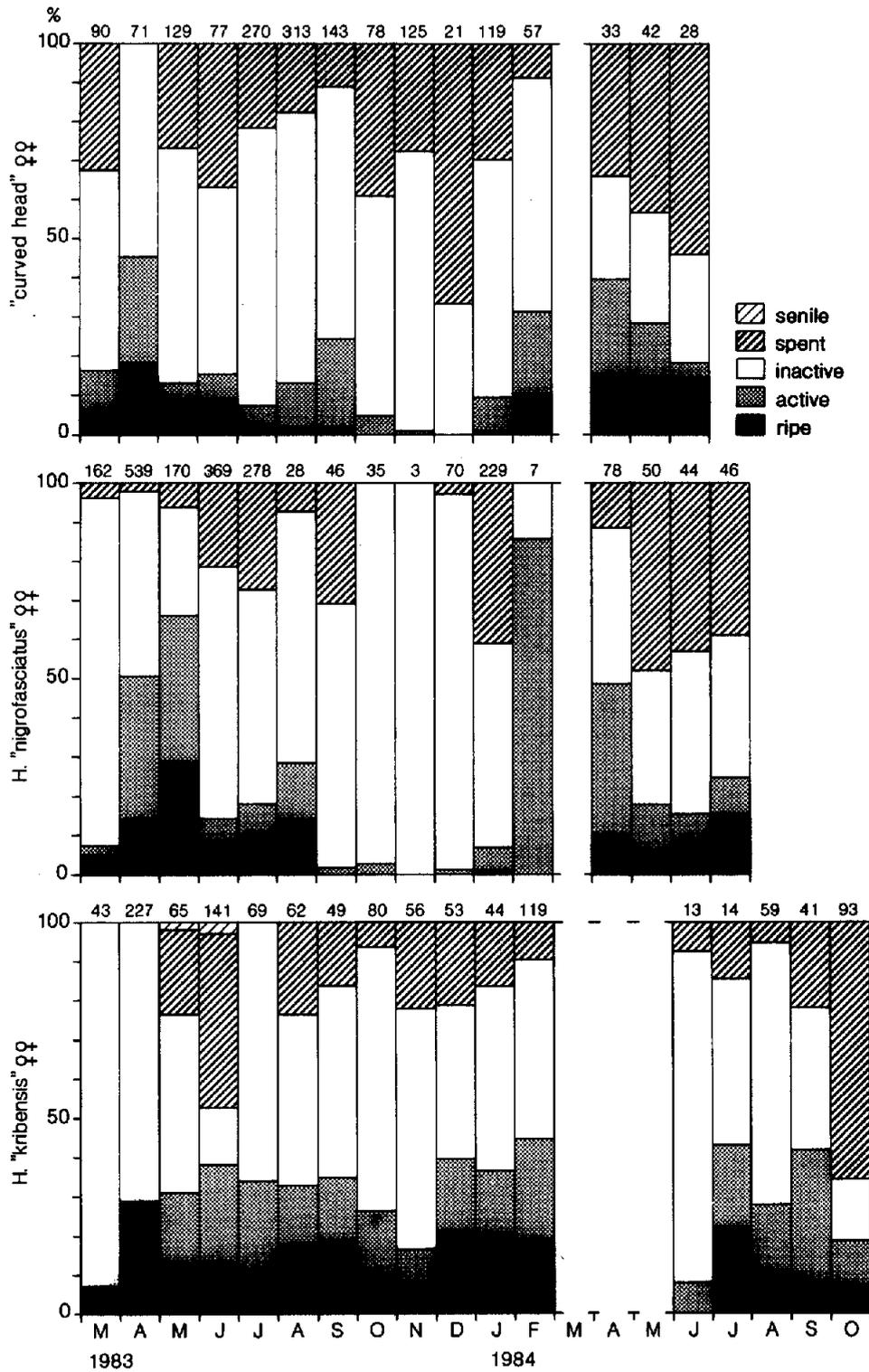


Figure 4. Breeding patterns of the "curved head" group, H. "nigrofasciatus," and H. "kribensis" in the Mwanza Gulf of Lake Victoria. Stages of gonad development of females: inactive, active (ripening), ripe, spent, senile (degenerate). Samples were collected in 1983–1984 at Station G on the Mwanza Gulf transect. Sample sizes are indicated.

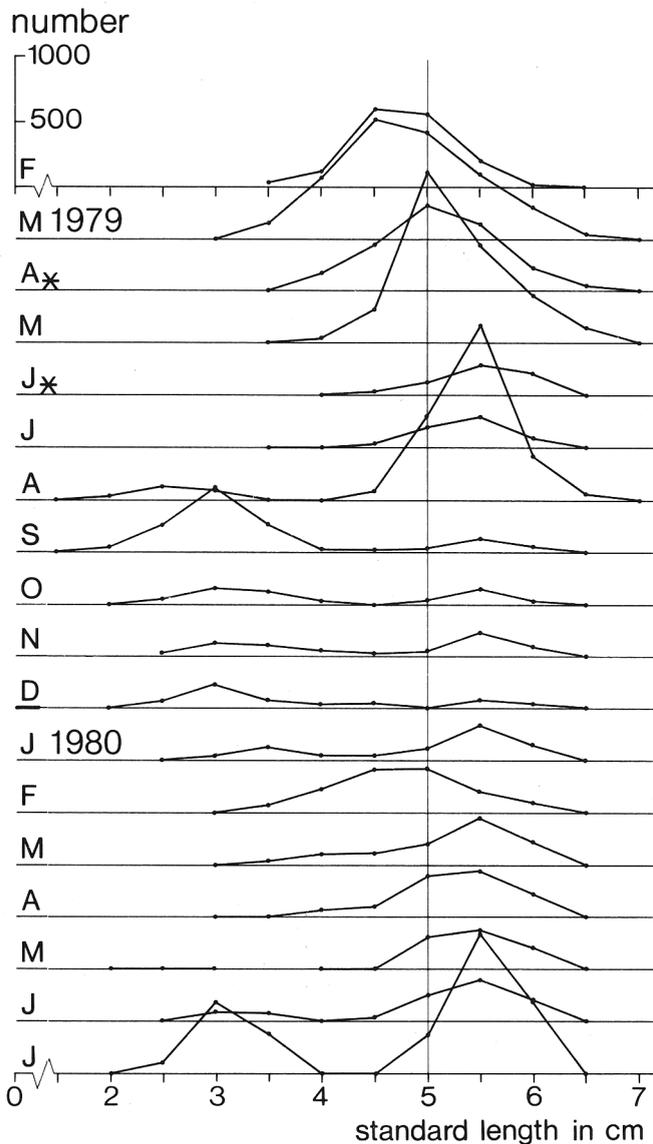


Figure 5. Length frequency of *H. nigrofasciatus*. Total number of individuals monthly caught in standard catches at Stations C, D, I-F, and G at the Mwanza Gulf transect

species flock contained the *H. tridens* group, an assemblage of at least 12 species characterized as prawn eaters (Greenwood 1974; Witte & van Oijen 1990). These species mainly occurred at depths of more than 15 m.

In the pre-Nile perch system, *Caridina nilotica* had been an insignificant element of the sub-littoral community. The first observations of large quantities of prawns in the trawl catches on the transect were made in 1986. In February 1992, with a small research boat (WiRe 1981), approximately 100,000 prawns were caught in a trawl catch of 10 min at Station F (10 m). Also, in the littoral areas along vegetated margins and rocky shores, increased densities of the prawn have been reported (Chitamwebwa & Bouton, personal communication). In

the pre-Nile perch system, bays contained little or no submerged vegetation. In recent years, however, an extensive submerged and floating vegetation of *Ceratophyllum Nymphaea* and the alien *Etchhornia* has developed in bays along the Mwanza Gulf (WiRe et al. 1992a-1992b), expanding one of the principal habits of the prawn.

DIURNAL AND NOCTURNAL VERTICAL DISTRIBUTION

In the system invaded by the Nile perch, the diurnal and nocturnal vertical distributions of the prawn were determined at Station G on the Mwanza Gulf transect (Fig. 6). During the daytime, the prawn population was concentrated in the lower part of the water column. At night, a considerable amount of prawns (27%) was caught in the middle and upper part of the column. Just as in the detritivorous haplochromines, however, the majority of the animals remained in the lower region of the column during the 24-hour day. The mean length of the prawns slightly increased with hauling depth (from 13.3 mm in the top layer to 14.0 mm near the bottom). In addition, the ratio of brooding to nonbrooding animals increased with depth from 0.0% (n = 13) at the top one third to 14.4% (n = 132) at the top two thirds to 32.9% (n = 1497) for the total column. In June 1987, large numbers of prawns were often caught in nightly surface trawls at Station G, at the station at the entrance, and near Juma Island.

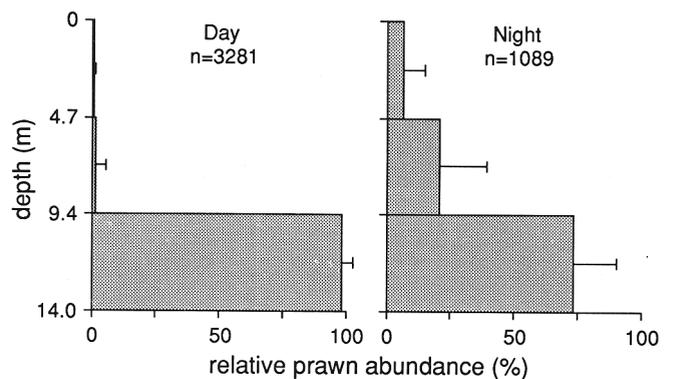


Figure 6 Diurnal and nocturnal vertical distributions of *Caridina nilotica* at Station G in the Mwanza Gulf. Plotted are relative prawn abundance (average and one standard deviation) in the top, middle and bottom parts of the column. In total 7 day and 5 night catches were made on June 10-11 and 25-26, 1987. Overall abundance (100%) per catch was estimated from the 14-m haul. The plotted values were derived from the 4.7-m haul (top), subtracting the 4.7-m haul from the 9.4-m haul (middle) and subtracting the 9.4-m haul from the 14-m haul (bottom). n = number of individuals

### REPRODUCTIVITY

In a sample taken in the Mwanza Gulf in May 1987, prawns measured from 5 mm up to 21 mm (E. H. F. M. Straetmans, unpublished data). The average fecundity of the prawns was 123.4 (Table 4). Thus, the batch fecundity of the prawns was higher than in the detritivorous haplochromines. Prawns carry the eggs and young in a brood pouch, a behavior that resembles maternal mouthbrooding, the reproductive strategy of haplochromines. Like the haplochromines, the prawns invest relatively large amounts of energy in relatively few offspring. The length of the prawns carrying eggs was determined from a large sample ( $n > 1000$ ) of brooding individuals and ranged from 13.0 mm to 22.5 mm.

### TIMING OF BREEDING AND GROWTH

A proper data set on the timing of the breeding period of *C. nilotica* is not available. Presumably, brooding females can be found all year round. Preliminary data suggest that intensified breeding occurred during the dry season (June, July, August). Stomach content investigations on juvenile Nile perch revealed a decline in the length of the prawns between the May/June and July/August sample (Fig. 7). During the same months, in 1988 and in 1989, juvenile Nile perch (<25 cm) switched from a diet dominated by prawns to one dominated by other food items (Katunzi, unpublished data). Apparently, a large part of the adult prawn population disappears from the main body of the Mwanza Gulf in July/August. A possible explanation for their disappearance is that the adults die after a breeding period. However, it is also possible that migration of adult prawns into and out of the Mwanza Gulf is involved. At the entrance, prawns remained the dominant prey for juvenile Nile perch (<25 cm) all year round.

The stomach contents of small Nile perch suggest that the juvenile prawns reach a size of 9–10 mm within a year. This is below the minimum size observed for prawns with a brood (13.0 mm), suggesting that it takes longer than a year for them to reach sexual maturity.

### Discussion

Only in the Mwanza Gulf has the haplochromine community been monitored long enough to include the Nile perch upsurge. Predation by the Nile perch, possibly facilitated by initial damage done by the fisheries, has caused the rapid eradication of the demersal and pelagic haplochromine community in the sublittoral areas of the Mwanza Gulf (Witte et al. 1992b). The rate of decline of the pelagic haplochromines was slower than that of the bottom-dwelling species, due to their smaller habitat overlap with the mainly demersal Nile perch

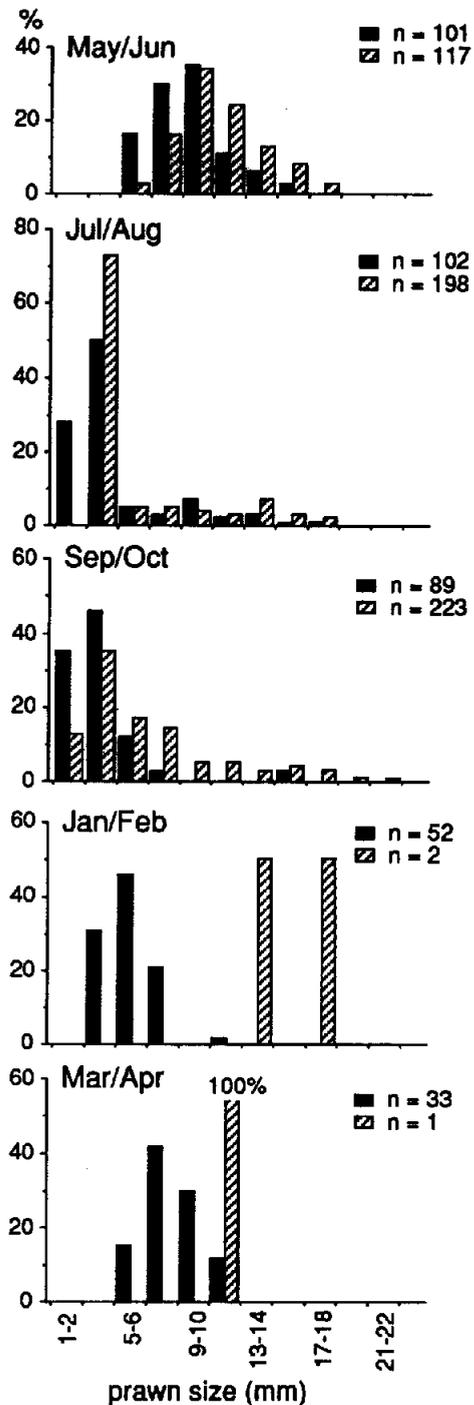


Figure 7. Length frequency histograms (%) of prawns in stomachs of juvenile Nile perches. Black bars: Nile perches 1–50 mm; hatched bars: 51–100 mm. Fish were caught in 1986–1988.

(Witte et al. 1992b). However, as a result of daily vertical migration (most zooplanktivores) and migration into shallow areas, the pelagic species were also strongly affected.

Before the explosive increase of the Nile perch in the

1980s, haplochromine cichlids were the dominant element in the demersal fish population of Lake Victoria (Kudhongania & Cordone 1974; Table 1). In this paper, we have shown that the pelagic haplochromine community represented a large ichthyomass as well. The pelagic phytoplanktivores that were restricted to the top layer constituted 18% of the haplochromine biomass in the water column. The zooplanktivores, most of which make a daily vertical migration throughout the column (Goldschmidt et al. 1990), constituted about 25% of the total haplochromine biomass. These have been replaced by the zooplanktivorous *Rastrineobola*, the catches of which increased by a factor four (Wanink 1991; Witte et al. 1992a). It is not known whether the composition of zooplankton in the diet of *Rastrineobola* is similar to that of the zooplanktivorous haplochromines. Consequently, the impact of the changes in species composition of zooplanktivores on the herbivorous zooplankton and indirectly on the phytoplankton is unknown. This makes interpretation of our data difficult, since these indirect effects on the algae may be more important than direct grazing by phytoplanktivorous fish. However, the disappearance of the pelagic phytoplanktivorous haplochromines and the detritivores, which also frequently consumed phytoplankton, has reduced grazing on the algae. In recent years, blooms of primarily blue-green algae have been reported from different areas of the lake (Ochumba & Kibaara 1989; Witte et al. 1992a). An influx of nutrients into inshore waters from upwelling and runoff may explain these blooms (Ochumba & Kibaara 1989). In our opinion, however, the disappearance of phytoplanktivorous and detritivorous haplochromines should also be considered in relation to the development of such blooms (Fig. 8).

To consider the degree to which the disappearance of the phytoplanktivorous and detritivorous haplochromines has contributed to phytoplankton blooms, we must know to what extent the atyid prawn *C. nilotica*, a potential consumer of (decaying) algae, has replaced the haplochromines feeding on detritus and phytoplankton. After the Nile perch boom in the Mwanza Gulf, which started in 1983, the haplochromines decreased; by 1986 they had virtually disappeared (Witte et al. 1992b). In the same year large quantities of prawns were observed. The current place of the prawn in the ecosystem is similar to the one previously occupied by the demersal detritivores, but it differs from that of the pelagic phytoplanktivorous (Table 4). Prawns are more benthic and feed less of phytoplankton, or possibly not at all. Whether or not the prawn has compensated for the disappearance of the detritivorous haplochromines in a quantitative sense cannot be determined because production studies are lacking.

Was the rise of the prawn functionally related to the disappearance of the detritivores? Differences in repro-

ductive strategy between haplochromines and *Caridina* presumably cannot explain the boom of the prawn (Table 4). Both apply a similar brooding strategy. The fecundity of the prawns was equal to or higher than that of the haplochromines, but never more than an order of magnitude. If it were true that prawns do not reach adult size within a year and have a restricted breeding season, they may be even slower reproducers than *H. nigrofasciatus*. In contrast to what has been suggested earlier (Ligtvoet & Witte 1991), replacement of the haplochromines by the prawn presumably does not represent a shift from slowly maturing, low-fecundity organisms to rapidly maturing, highly-fecund animals, but a more detailed study of *Caridina nilotica* is necessary to corroborate this.

It is likely that the success of the prawn is related to

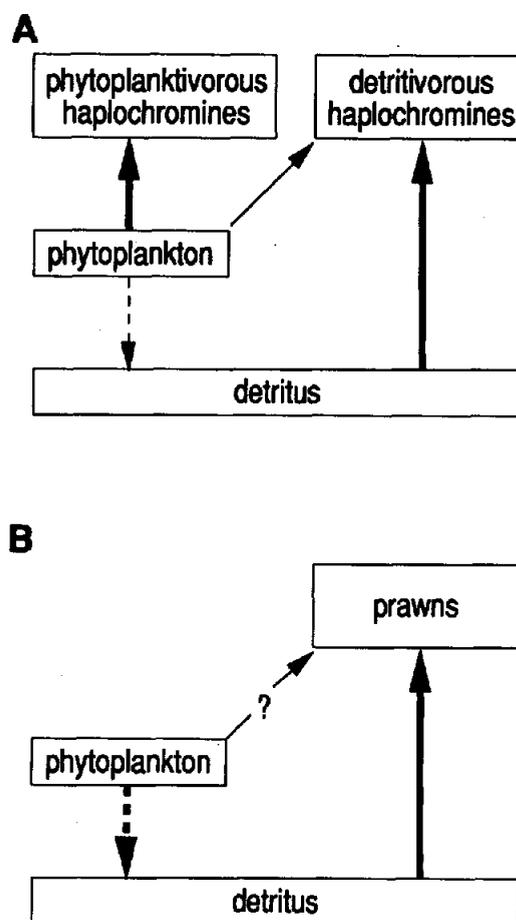


Figure 8. Hypothetical scheme illustrating the effects on phytoplankton by the disappearance of the phytoplanktivorous haplochromines and the replacement of the detritivorous haplochromines by the prawn *Caridina nilotica*. Solid lines indicate predation on phytoplankton; dashed lines indicate phytoplankton rain. The thickness of the lines suggests the importance of the flows.

extrinsic factors rather than to differences in the life histories of prawns and haplochromines. The following points deserve consideration:

- (1) When the haplochromines were still present, the Nile perch fed on them almost exclusively (Gee 1969; Okedi 1971). Only after their numbers had declined to virtually zero did Nile perch switch to other prey, among which adult prawns were important (Ligtvoet & Mkumbo 1990; Mkumbo & Ligtvoet 1992). The possible time-lag between the eradication of the former predators of the prawn and the switch of Nile perch to this food source may have provided opportunities for the prawn population to increase.
- (2) The disappearance of the detritivorous haplochromines may have had a competitive release effect. In addition, the disappearance of the pelagic phytoplanktivores may have induced a larger rain of (decaying) algae to the lake bottom, which would be available for the prawn. On the other hand, phytoplankton grazers produce detritus as well.
- (3) The eradication of the specialized haplochromine predators of the prawns, the species of the *H. tridens* group, may have diminished the mortality of both juvenile and adult prawns. But it should be emphasized that quantitatively the haplochromine prawn eaters constituted only a small fraction of the haplochromine community in the sublittoral area (0.2% of the biomass). In deep water, prawn eaters were more abundant, but never a dominant group.
- (4) In the pre-Nile perch system, the large majority of the haplochromines were potential predators of juvenile prawns, irrespective of the trophic group to which the fish belonged. The disappearance of these predators is likely to have diminished the juvenile mortality of the prawns. Juvenile prawns presently are an important prey for juvenile Nile perch. The bulk of the juvenile Nile perch are restricted to inshore water, however, while the juvenile prawns are abundant in sublittoral waters (Ligtvoet personal communication).
- (5) Submerged vegetation, a favourite habitat for *C. nilotica*, has expanded. Juveniles may be safe from predation while hidden in dense vegetation (Fryer, personal communication).

Although each of these factors may have contributed to the current abundance of the prawn, the most likely explanation, in our opinion, is a combined effect of increased availability of food for the prawns and reduced predation pressure on juvenile prawns.

Four major replacements in the Lake Victoria ecosys-

tem have been suggested (Ligtvoet & Witte 1991; Wanink 1991; Witte et al. 1992a):

- (1) Lates replaced 109+ species of haplochromine piscivores and the piscivorous catfishes (*Bagrus docmak* and *Clarias gariepinis*).
- (2) *Oreochromis niloticus* replaced the indigenous *O. esculentus* and *O. variabilis*.
- (3) The zooplanktivorous cyprinid *Rastrineobola argentea* replaced 20+ species of zooplanktivorous haplochromines.
- (4) *Caridina* replaced the detritivorous haplochromines.

This paper presents evidence for the replacement of 13+ detritivorous haplochromines by *Caridina nilotica*.

Fryer (1960a) warned of the far-reaching consequences that could be expected from the proposed introduction of the Nile perch into Lake Victoria. But ten years ago nobody could have predicted in any detail the recent cascade of effects that the Nile perch has had on the fish community, on the zoo- and phytoplankton community, and on the benthos (see Carpenter et al. 1985). The impact of the Nile perch on the Lake Victoria ecosystem is reminiscent of the effects that the introduction of the large piscivorous sea lamprey (*Petromyzon marinus*) has had on the ecosystem of Lake Michigan in North America (Kitchell & Crowder 1986). In Lake Michigan it was possible to control the sea lamprey population and also to manage the system in other respects. While we recognize that similar management of the Lake Victoria ecosystem is presently impossible, we believe that close monitoring of this rapidly changing ecosystem is essential. First, we must document this unintended large-scale experiment as carefully as possible; second, we must prevent unnecessary further damage to this and other systems. Long-term population dynamics and production studies of the dominant organisms of all trophic levels are urgently needed.

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