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Causes and effects of the Lake Victoria ecological revolution

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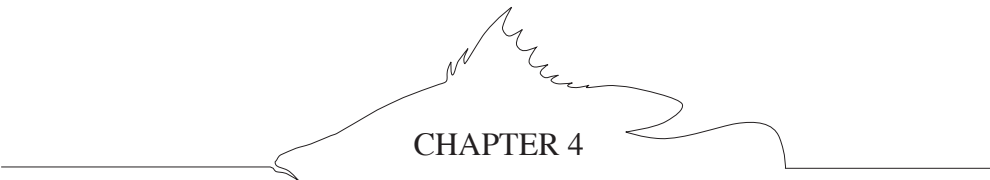
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CHAPTER 4

Diel vertical migration of major fish species in Lake Victoria, East Africa.

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Abstract

Understanding of migration patterns is essential in the interpretation of hydro-acoustic stock assessment data of partly demersal partly pelagic fish stocks. In this paper we provide this kind of information for some species that were common in the Mwanza Gulf of Lake Victoria in the 1980s, before and after the upsurge of introduced Nile perch (*Lates niloticus*). Detritivorous haplochromines and Nile tilapia (*Oreochromis niloticus*), both stay near the bottom during day and night. Feeding seems to occur predominantly during the day. The zooplanktivorous haplochromines and dagaa (*Rastrineobola argentea*) dwell near the bottom by day and migrate towards the surface during the night. They seem to follow their prey, zooplankton and lake-fly larvae. Piscivorous nembe (*Schilbe intermedius*) show similar migration patterns to zooplanktivorous fishes, but their behaviour cannot be unambiguously explained by pursuit of prey. Nile perch to some extent migrate into the column at night, though the majority remains near the bottom. Feeding takes place during day and night.

Introduction

Stock estimates of Lake Victoria fishes were until recently done by bottom trawling (Kudhongania & Cordone, 1974; Kukowski, 1978; Benda, 1981; Okemwa, 1981; Okaronon, 1994). In such estimates the vertical distribution of the species over the water column is not taken into account. Currently hydro-acoustic techniques, which do account for the vertical distribution of fish biomass, are used for stock assessments (Tumwebaze, 1997; Getabu et al., 2003). However, for a sound interpretation of the hydro-acoustic data, it is essential to have information about vertical movements of individual fish species. In this paper we provide such information for some species that were common in the Mwanza Gulf of Lake Victoria, before and after the upsurge of introduced Nile perch (*Lates niloticus* L.) in the 1980s.

The species investigated comprise: haplochromine cichlids, nembe (*Schilbe intermedius* L.), Nile perch, Nile tilapia (*Oreochromis niloticus* L.) and dagaa (*Rastrineobola argentea* Pellegrin). Phytoplanktivorous Nile tilapia and piscivorous Nile perch were both introduced into Lake Victoria during the 1950s. Landings of Nile tilapia increased gradually from 1970s onwards (Chapter 7, Goudswaard et al., 2002b), while the population of Nile perch increased explosively during the 1980s (Ogutu-Ohwayo, 1990; Barel et al., 1991). Subsequently, the majority of the original species, dominated by haplochromine cichlids, both in species number and biomass (Greenwood, 1974; Kudhongania & Cordone, 1974), disappeared from the lake and a new fish community developed (Ogutu-Ohwayo,

1990; Witte et al., 1992b). The population of dagaa, a native zooplanktivorous cyprinid, increased strongly (Wanink, 1991, 1999). Nile perch, Nile tilapia and dagaa became the three commercially most important species in the lake (Ligtvoet et al., 1995; Reynolds et al., 1995). Nembe, a piscivorous catfish, disappeared from the offshore areas. However, it remained the target species of many fishermen in the shallow waters where it maintained its population level (Chapter 6 - Goudswaard & Witte, 1997). Though almost vanished by the end of the 1980s, recently a resurgence of some detritivorous and zooplanktivorous haplochromines has been observed (Seehausen et al., 1997b), occasionally comprising 20% of the bottom trawl catches (Witte et al., 2000).

Apart from describing the vertical distribution of these species by day and night, we try to identify causal factors for their vertical migration. The species focused on in this paper represent three main trophic groups, viz. detritivores, zooplanktivores and piscivores. This enabled us to investigate the possible effects of feeding behaviour on vertical migration.

Materials and methods

Study area

All observations were made in the Mwanza Gulf (Fig. 4.1). A 3.5 km long stretch in this gulf, between Nyamatala Island and Rocky Islands, was sampled by bottom trawling with MV Kiboko, and is from here on referred to as the 'trawl area'. Station G, situated just outside the trawl area, was sampled using other techniques. Depth at the trawl area ranges from 12-16 m, while

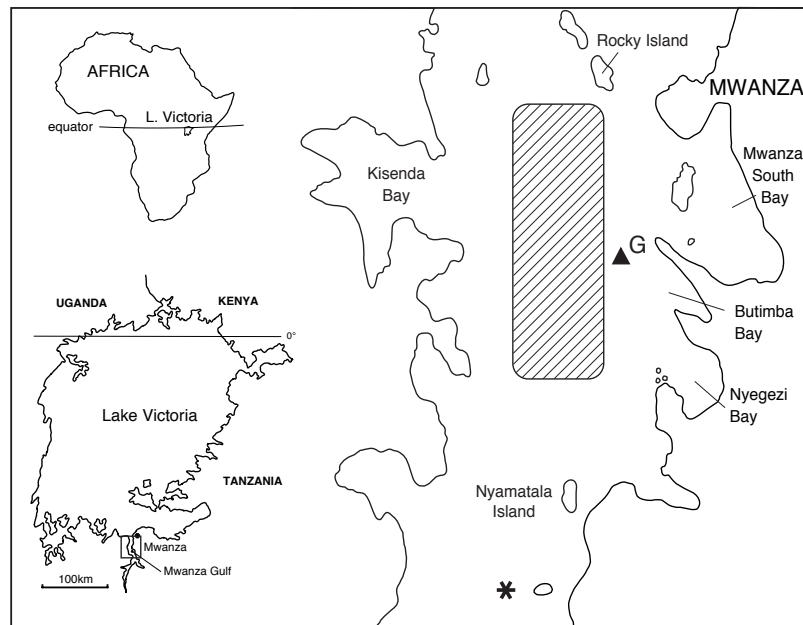


Fig. 4.1. Sampling area in the Mwanza Gulf of Lake Victoria.

station G is 13–14 m deep (Witte, 1981). The bottom of these stations is covered with a thick deposit of organic mud. Gillnet fishing for large Nile perch was done south of Nyamatala Island and to the west of a small unnamed rocky island, where the water deepens into a pit with a maximum depth of 13 m.

Trawling

MV Kiboko, a 105 hp trawler, used a bottom trawl with a head rope of 18 m and a 20 mm codend mesh. All mesh sizes given in this article are referring to stretched meshes. Seven sessions, each covering a full day and night cycle, were made on: 10–11 and 24–25 June, and 29–30 September 1987; 13–14 and 26–27 September 1988; 1–2 and 15–16 November 1989. Each session started in the morning and ended 25 h later. Trawl shots lasted 30 minutes and were made

at regular intervals. The number of trawl shots was respectively: 13, 13, 13, 17, 13, 26 and 25. The hours between 06.00 and 19.00 are defined as day and those between 19.00 and 06.00 as night. The twilight period in the study area, 2°34'S, is less than half an hour. These trawl sessions formed the basic sampling method for Nile perch, Nile tilapia and nembe. Total length of the first two species and fork length of nembe were measured to the nearest cm below. Only a small number (N=38) of Nile tilapia, ranging from 37 to 64 cm, was caught by bottom trawling. The majority of Nile tilapia occurs in shallower areas (Chapter 8 - Goudswaard et al., 2002a).

Trawling for haplochromine cichlids was done with a small boat, towing either a bottom trawl (head rope 4.6 m, codend mesh 5 mm) or a surface trawl (beam 5 m, codend mesh 5 mm) (Goudswaard et al.,

1995). Between April 1981 and July 1982 station G was sampled in this way during the day (between 13.00 and 15.00 h) and at night (between 01.00 and 03.00 h). The sizes of haplochromines caught ranged from approximately 5 to 8 cm standard length.

Gillnetting

Gillnets with a length of 15, 30 or 60 m (height 1.5 m) were set at surface, bottom and mid-water position at station G. The 60-m nets (ply 210/3) were composed of six alternating panels of 10 m, with mesh sizes of 25, 38 and 50 mm. These gillnets were used during 10 sessions of 24 h each between July 1980 and July 1982, during full and new moon. The nets were used to sample haplochromines, but nembe (size range 8 – 28 cm) were caught as by-catch.

The two other gillnet types were used at station G from April till September 1987 to sample dagaa and juvenile Nile perch. The 15-m nets had a mesh size of 12.5 mm (monofilament, knotless). These nets retain dagaa of about 5.5 cm long (range 3.3 – 6.3 cm standard length), being mainly of adult size (Wanink, 1999), and Nile perch of 5.4 cm on average (range 4.0 – 6.7 cm). The 30-m nets had a mesh size of 25 mm (ply 210/3) and caught Nile perch of 9.0 cm on average (size range 7.6 – 10.4 cm). The 15-m and 30 m gillnets were used in seven 24-h sessions.

Gillnets for Nile perch with a mesh size of 10, 15, 17 and 21 cm were set during 10 nights between March and July 1987, south of Nyamatala Island where the water is 6 to 13 m deep. Each net was 25 m long and approximately 2 m high. The estimated Nile perch length at maximal selection for the four mesh sizes used, are respectively

37, 55, 60 and 73 cm (Ligtvoet et al., 1995). Twenty-three nets were set at the bottom, and seventeen 1 m below the water surface. The nets were set shortly before sunset and lifted just after sunrise.

The same set of nets was used once near Nyamatala Island on 8 June and twice at station G in the Mwanza Gulf on 25 June and 9 July 1987 in a 24-h fishing session. In general, nets were set between noon and noon the next day. Nets were emptied around sunset, after which they were set again either for the whole night or till midnight. In the latter case the nets were checked again around dawn. The last session ran from sunrise till noon. One night session that was set too early before sunset, was eliminated from the calculations. In total, five day-sessions and three night-sessions were made. Catch rates were standardised as the number of fishes caught in 20 nets during 5 hours.

Feeding activity of Nile perch

Assessment of feeding activity of large Nile perch was done on fresh fishes. For this purpose, we did not score the degree of fullness, but only scored presence or absence of food. Fishes, either from gillnets or bottom trawls, which were recognised as having regurgitated their food, were omitted. Nevertheless, some fishes that had regurgitated their food may not have been recognised and thus erroneously been classified as 'empty'.

Hydro-acoustics

A Lowrange Mach 1 echo-sounder, using a frequency of 192 Khz and a 1192 transducer (8") fitted under MV Kiboko at 1.2 m below the surface, could detect all objects >8 mm

present in the water column. Twice a 24-h recording was done while the ship was moored at station G. Dates of recording were 30–31 October 1989 (one day after new moon) and 13–14 November 1989 (at full moon).

Data analysis

Nile perch in bottom trawls were divided into three size classes: <26 cm (the bulk of the catches), 26 – 50 cm and >50 cm. Nile perch up to 25 cm long mainly fed on zooplankton, insect larvae, shrimps and small fish. Nile perch from 26 to 50 cm long fed on shrimps and fish, whereas fishes above 50 cm were mainly piscivorous (Hughes, 1986; Ogari & Dadzie, 1988; Ogutu-Ohwayo, 1990; Mkumbo & Ligetvoet, 1992; EFBK, pers. obs.).

For comparing distributions in bottom-, mid- and top-set gillnets, we calculated the relative frequencies as percentages of the total catch per day or night. Data were tested for normal distribution with the Kolmogorov-Smirnov test. To compare differences in bottom trawl catches during day and night, we used the T-test when the distributions were normal. The Mann-Whitney U test was used when the data were not normally distributed or when sample sizes were small. To test for differences in vertical distributions during the night we used the Kruskal-Wallis test.

Results

The bottom-trawl catches of Nile perch in the trawl area were generally higher during daytime than at night, although variation in the yield of individual trawl shots was large (Fig. 4.2). The difference is significant

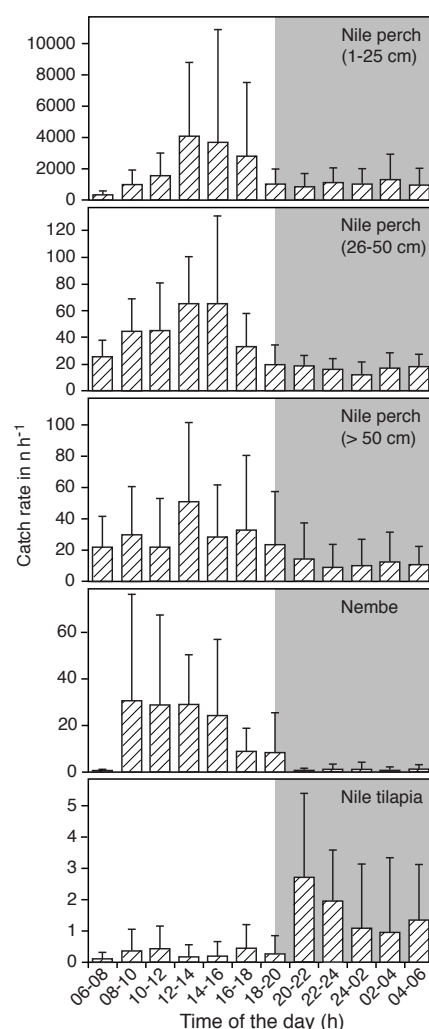


Fig. 4.2. Average number of Nile perch, nembe and Nile tilapia (and standard deviation) per hour bottom trawling, for seven 24-h periods between 1987 and 1989 in the Mwanza Gulf. The shaded area represents the dark period. Samples were lumped in classes of two hours. Statistical tests were done on the original catch data per half hour.

for the size groups 26 – 50 cm and >50 cm, but not for juvenile Nile perch up to 25 cm (Table 4.1). Also catches of nembe were higher during the day than at night. In

Table 4.1. Tests for differences in mean numbers of fish in trawls during day and night. Mann-Whitney tests were used except for Nile perch 26-50 cm where a T-test was used. *P* = two-tailed significance level, *N* = number of fishing session. haplo = haplochromines, float. = floating trawling, bot = bottom trawl, D = day, N = night.

Species (group)	Gear type	Mean number ($\pm$ std)		<i>P</i>	<i>N</i>
		Day	Night		
Nile perch < 26 cm	bot.	1062 (1972)	483 (533)	0.599	D 71, N 48
Nile perch 26-50 cm	bot.	22.3 (18.5)	7.9 (4.5)	0.000	D 71, N 48
Nile perch > 50 cm	bot.	15.8 (18.4)	5.2 (8.1)	0.000	D 71, N 48
Nembe	bot.	10.6 (15.7)	0.4 (0.9)	0.000	D 71, N 48
Nile tilapia	bot.	0.07 (0.26)	0.81 (1.16)	0.000	D 71, N 48
Detritivorous haplo.	float.	0	0	-	-
Detritivorous haplo.	bot.	754 (614)	1380 (1462)	0.453	D 9, N 9
Zooplanktivorous haplo.	float.	1.6 (2.0)	149 (155)	0.001	D 9, N 9
Zooplanktivorous haplo.	bot.	207 (263)	51.7 (54.9)	0.070	D 9, N 9

contrast, tilapia were caught mainly at night in the bottom trawl catches, although the total number caught is low (*N* = 38).

Surface- and bottom-trawl catches at station G in 1981–1982 provide data on haplochromine cichlids (Fig. 4.3). Though, like in Nile tilapia, bottom-trawl catches of detritivores seemed higher at night than during the day, the difference was not significant due to high standard deviations (Table 4.1). For the same reason, the bottom trawl catch rates of zooplanktivores during daytime were not significantly higher than at night (Fig. 4.3, Table 4.1). No detritivores were caught in the surface trawls, whereas zooplanktivores were caught significantly more at night than by day with this gear.

Gillnet catches at station G revealed that neither detritivorous nor zooplanktivorous haplochromines were evenly distributed over the water column

(Table 4.2). Virtually all detritivores were caught in the bottom and mid-water nets and were most abundant near the bottom during the day (Fig. 4.4, Table 4.3). No significant difference was found for the mid-water nets. Zooplanktivores were found all over the column, but dominated in the bottom and mid-water nets during the day and in the surface nets at night (Fig. 4.4, Table 4.3). Juvenile Nile perch, up to 11 cm, were unevenly distributed over the water column during the day, with catches decreasing towards the surface. No indication for an uneven distribution in the water column during the night was found (Table 4.2). In mid water, catches of juvenile Nile perch were higher at night than by day (Fig. 4.4, Table 4.3). No data are available for mid-water catches of large Nile perch. However, bottom catches were always higher than top catches (Fig. 4.4). Top and bottom set

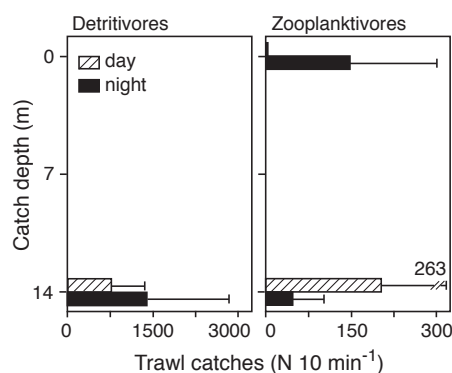


Fig. 4.3. Average number (and standard deviation) of detritivorous and zooplanktivorous haplochromines in surface- and bottom-trawl catches of ten minutes each. Trawls were made during day and night at station G in the Mwanza Gulf in 1981-1982. Number indicates standard deviation too long to be depicted.

gillnets placed at station G and south of Nyamatala Island, during 24-h sessions, produced more, large Nile perch during the night than during the day, both in pelagic and bottom set position (Table 4.3).

A series of 10 nightly gillnet catches for large Nile perch (>30 cm), with nets of four different mesh sizes, show that for 10 and 15 cm meshes, the bottom set nets produce more fish than the top set nets (Fig. 4.5; Mann-Whitney U test, $P = 0.000$ for 10 cm and $P = 0.000$ for 15 cm mesh). For 17 and 21 cm meshed nets the differences are not significant (Mann-Whitney U test $P = 0.399$ for 17 cm and $P = 0.112$ for 21 cm mesh). The mean number of Nile perch in the bottom net decreased with increasing mesh size (Kruskal-Wallis Test $P = 0.000$; Spearman rank correlation for means $R = 1$, $P = 0.000$) but not in the top set nets (Kruskal-Wallis Test $P = 0.138$).

Fig. 4.4. Distribution in percentage (and standard deviation) of detritivorous and zooplanktivorous haplochromines, nembe, dagaa and Nile perch from surface-, mid- and bottom-set gillnets. Nets were set at station G (13m deep) during day and night. Data for Nile perch above 30 cm were collected at station G and south of Nyamatala Island (6-13 m deep) with top and bottom nets only. Data for haplochromines and nembe are from 1981-1982, and for dagaa and Nile perch from 1987-1989. Numbers indicate standard deviations too long to be depicted.

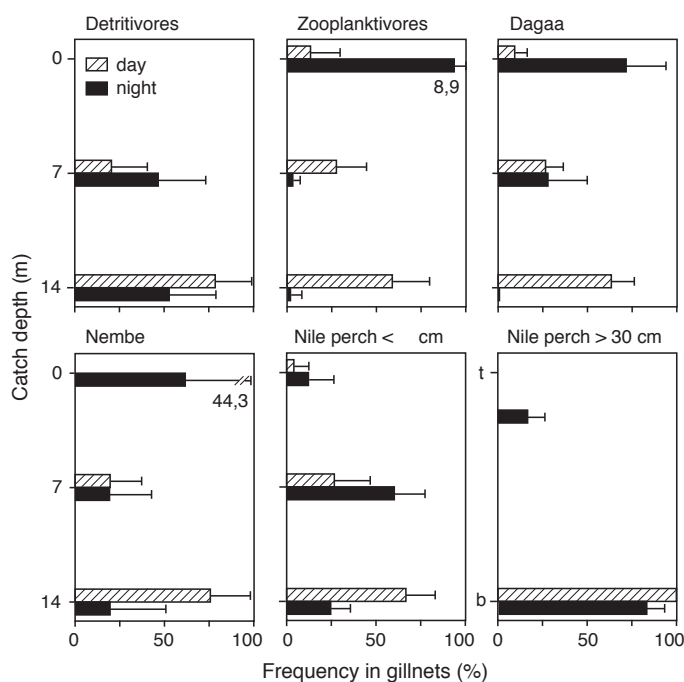


Table 4.2. Kruskal-Wallis test for equal distribution of fish in gillnets, set at different levels in the water column, by day (D) and night (N). *P* is two-tailed significance level; *N* is number of fishing sessions. haplo. = haplochromines.

Species (group)	Period	<i>P</i>	<i>N</i>	Mean Rank		
				Top	Mid.	Bot.
Detritivorous	D	0.000	10	5.0	16.2	22.8
Haplochromines	N	0.000	10	5.5	19.9	18.7
Zooplanktivorous	D	0.003	10	8.2	14.5	21.7
Haplochromines	N	0.000	10	25.0	12.8	8.3
Nembe	D	0.001	6	4.0	9.7	14.8
”	N	0.131	6	13.0	7.5	8.0
Dagaa	D	0.010	7	5.9	11.3	15.9
”	N	0.004	5	12.2	8.8	3.0
Nile perch < 11 cm	D	0.019	5	3.9	8.4	11.7
”	N	0.085	5	5.2	11.4	7.4

Like in juvenile Nile perch, the daytime catches of nembe decreased towards the surface, while no significant difference between depth levels was found at night (Table 4.2). When comparing day and night catches at the same level in the water column, the catches of nembe in mid water showed no differences between day and night. Bottom catches were higher during daytime than at night and the reverse was found for the surface catches (4.4, Table 4.3). The pattern of the zooplanktivorous dagaa is similar to that of the zooplanktivorous haplochromines (Fig. 4.4, Tables 4.2 and 4.3).

Hydro-acoustic recordings reveal a clear difference in the presence of objects in the water column between day and night (Fig. 4.6). Before sunset, single objects, probably large fish are found in mid-water position. At the same time, small aggregations, probably shoals of small fish are present near the

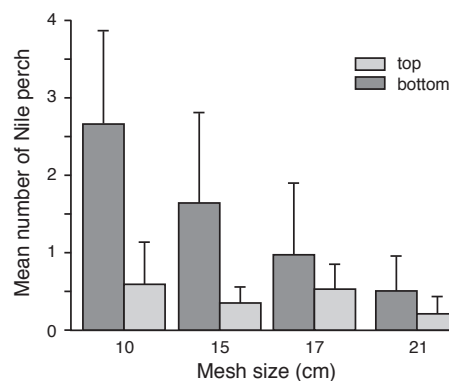


Fig. 4.5. Mean number of Nile perch per net per night caught in gillnets of 10, 15, 17 and 21 cm mesh size, south of Nyamatala Island. Nets of 25m were set at the bottom (6-10m deep) or one meter below the surface (top) just before sunset and lifted after sunrise the next day. All data are based upon 10 sessions, except for the 17cm nets, which were set seven times. (lines indicate standard deviations).

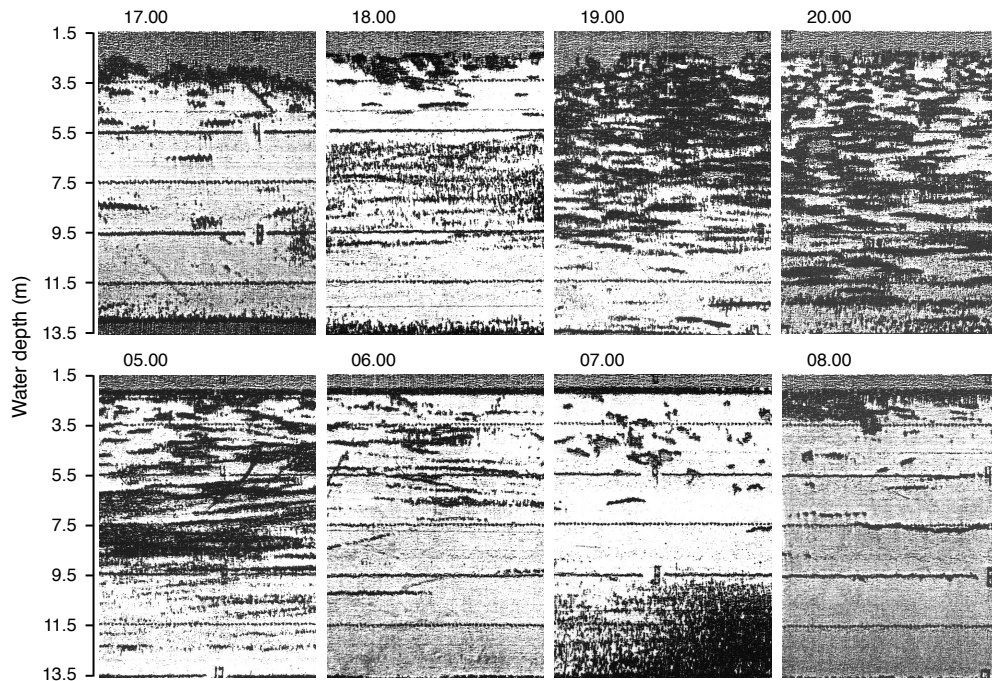


Fig. 4.6. Hydro-acoustic recordings made on 30-31 October 1989 at station G. Each panel shows a record of 2.5 minutes. Top-row recordings were made around sunset (ca. 19.00 h) and bottom row recordings around sunrise (ca. 06.00 h). The depth range covers the whole water column except for the upper 1.5 m, because of the draught of the ship.

surface. During sunset, the whole column is filled with objects, probably small fish, shrimps and insect larvae, obscuring any other detail in these records. At sunrise, most objects disappear into the bottom and the situation of the previous day is restored (Fig. 4.6). The recordings taken during new moon do not differ in appearance from those taken during full moon. We also did not find any influence of the lunar period in the trawl catches of each of the studied fish species.

Discussion

Diel vertical migration and trophic guild

The 24-h bottom-trawl and gillnet catches suggest that active hunters, like piscivorous nembe, zooplanktivorous haplochromines, and zooplanktivorous dagaa, migrated higher into the water column at night. The migration of dagaa is complex. At night the major part of the population dwells in the upper part of the water column, though adults seem to stay closer to the surface than juveniles. During daytime, adult fish dwell near the bottom, whereas juveniles and tapeworm-infested adults stay near the surface (Wanink, 1992; Wanink & Goudswaard, 1994).

Catches of detritivorous haplochromines in bottom-set gillnets

Table 4.3. Mann-Whitney test for differences in mean numbers of fish in gillnet catches during day (D) and night (N) at different levels in the water column. Generally only one net was set per depth level. However, data of Nile perch > 30 cm represent the mean number per 5 hours in 20 nets (23 nets were set at the bottom and 17 at the top). *P* is two-tailed significance level; *N* is number of fishing sessions.

Species (group)	Level	Mean number ($\pm$ std)		<i>N</i>	<i>P</i>
		Day	Night		
Detritivorous	Top	0.1 (0.3)	0	D 9, N 9	0.317
Haplochromines	Middle	51.0 (57.6)	27.1 (21.1)	D 10, N 10	0.569
	Bottom	131.3 (67.8)	22.7 (22.4)	D 10, N 10	0.000
Zooplanktivorous	Top	4.2 (6.0)	30.8 (16.0)	D 9, N 9	0.001
Haplochromines	Middle	17.9 (27.5)	1.2 (1.5)	D 10, N 10	0.003
	Bottom	36.8 (31.4)	0.5 (1.6)	D 10, N 10	0.001
Nembe	Top	0	14.7 (13.7)	D 6, N 6	0.007
	Middle	1.8 (1.3)	3.3 (5.3)	D 6, N 6	0.679
	Bottom	12.7 (14.1)	1.8 (1.6)	D 6, N 6	0.030
Dagaa	Top	28.7 (31.3)	399.1 (130.2)	D 7, N 5	0.003
	Middle	135.1 (164.5)	186.9 (171.4)	D 7, N 5	0.755
	Bottom	268.2 (197.5)	6.2 (3.7)	D 7, N 5	0.003
Nile perch < 11 cm	Top	0.4 (0.6)	3.9 (4.3)	D 5, N 5	0.066
	Middle	5.9 (8.8)	28.1 (32.9)	D 5, N 5	0.045
	Bottom	10.3 (9.1)	15.4 (22.3)	D 5, N 5	0.465
Nile perch > 30 cm	Top	0 (-)	3.6 (1.4)	D 5, N 4	0.007
	Bottom	4.5 (2.6)	21.0 (18.7)	D 5, N 3	0.036

declined significantly at night, but no increase in the mid-and top-set nets was observed (Table 4.3). Research of Goldschmidt et al. (1993) revealed that at least a part of the detritivorous haplochromines do rise 2–4 m into the water column at night. Our mid-water nets were set above that level. In spite of this upward migration, our bottom-trawl catches, which only cover the lower 2 m of the column, did not decline during the night. Active fish have a greater chance being caught by gillnets than passive fish, while the reverse is true for trawl nets. Therefore, the combination of low gillnet catches and relatively high trawl catches near the bottom at night

(Tables 4.1 and 4.3) suggests inactivity of the detritivorous haplochromines during the night. This suggestion is further supported by a high percentage of empty stomachs in detritivorous haplochromines at night (Goldschmidt et al., 1993).

The bottom-trawl catches of Nile tilapia increased during the night. Though this originally phytoplanktivorous species has recently extended its diet with especially macrobenthic invertebrates (Gophen et al., 1993; Mwebaza-Ndawula, 1994; Balirwa, 1998), its feeding behaviour is likely to be still comparable to that of the detritivorous haplochromines. The pattern found in our tilapia catches was confirmed by the catches

of a commercial bottom trawler, operating in the southern part of the Mwanza Gulf during 1985. Those catches amounted to 0.05 kg h^{-1} during daytime (97 h trawling) and 1.29 kg h^{-1} at night (131 h trawling). Unfortunately, we have no information of the vertical distribution of Nile tilapia. Field observations of stomach contents have shown that intense feeding activity in tilapiines, including Nile tilapia, is almost entirely restricted to daytime (Moriarty, 1973; Beverage & Baird, 2000). Consequently, as in detritivorous haplochromines, nocturnal inactivity rather than downward migration may explain the higher presence of Nile tilapia in bottom trawl catches at night.

The results of 25-mm gillnets for small Nile perch (Fig. 4.4) show that the majority of the juveniles occur, both during day and night, in the lower half of the water column, although there is a slight migration during the night into mid water. A survey by Katunzi (pers. obs.) revealed that 78.8% of the stomachs of 6000 juvenile Nile perch (1–30 cm), caught in bottom trawls during the day, contained food. This implies that juveniles feed during daytime. The observation of full stomachs in juvenile Nile perch that were caught with gillnets during the night in mid water may indicate that they feed also during the night.

Although the bottom-trawl catches at night decreased, we observed an increase in catches of large Nile perch (>30 cm) in bottom set gillnets during the night (Table 4.3). This indicates that large Nile perch are more active at night than by day. Catches also increased at night in the top set nets. As we have no surface trawls for these fishes it cannot be concluded whether this increase is due to increased activity or to migration

towards the surface at night. Catches of top set gillnets at night show a remarkable pattern as compared to bottom set nets. In contrast to the expectation, because of higher abundance of smaller fish in a population, there was no decrease in number of fish per net with increasing mesh size in the top set nets. In bottom set nets this decrease was present (Fig. 4.5). The relatively low catches of Nile perch in top set gillnets of 10 and 15 cm mesh as compared to those in bottom set nets of the same mesh sizes, cannot be explained unambiguously. It could either imply that Nile perch <60 cm are less inclined to migrate into the water column, or that they are less active in the top layers. Considering all Nile perch >30 cm caught in top and bottom set gillnets, there was no significant difference in the percentage of stomachs containing prey during day and night (respectively 52%, $N=48$ and 48%, $N=658$). However, Nile perch caught by bottom trawl during the day appeared to have a higher percentage of stomachs containing food than those caught at night (respectively 84%, $N=283$ and 62%, $N=225$; recalculated from: Ligetvoet & Mkumbo, 1990). In conclusion, both juvenile and adult Nile perch feed during the day as well as at night. After the decline of the haplochromines in the second half of the 1980s, shrimps were mainly taken during the day while fish, dagaa and juvenile Nile perch, dominated the diet during the night (Ligetvoet & Mkumbo, 1990; Mkumbo & Ligetvoet, 1992).

The gillnet catches suggest that piscivorous nembe and zooplanktivorous dagaa are active during the day at the bottom and at the surface at night. The occurrence of dagaa near the bottom has been observed for the first time in the second half of the 1980s.

Before the decline of the zooplanktivorous haplochromines, dagaa was not caught in the lowest part of the water column (Witte et al., 1999; Wanink & Witte, 2000).

Possible causes of vertical migration

Diel variation in light condition may influence foraging efficiency, predator detection and mate attraction (Wootton, 1990). Many pelagic species stay near the bottom during daylight and move to the surface at sunset. These fish may be following the vertical movement of their prey (Allison et al., 1996). Another possibility is that they move into darker water during daytime to reduce the chance of being detected by predators (Clark & Levy, 1988). A third hypothesis is that they move into deeper, cooler, waters after feeding near the surface, to minimize energy expenditure (Brett, 1971; Wanink, 1998). Diel variation in abiotic factors such as hypoxia may also play a role in certain water bodies (Junk et al., 1997). In the Mwanza Gulf, however, we never observed distinct day and night patterns in oxygen concentration within the period of our research.

Predator avoidance and vertical migration

Prior to the Nile perch upsurge, the main piscivorous fish in the Mwanza Gulf were the catfishes *Bagrus docmak* (Forsskäll), *Clarias gariepinus* (Burchell), nembe, and fish-eating haplochromines. Piscivorous haplochromines were hunting all over the water column, though most species were found near the bottom and only a few in mid water and near the surface (Van Oijen, 1982). Probably most piscivorous haplochromines were hunting during the day, but gillnet catches suggested that

some species were active during night (Van Oijen, 1982). *B. docmak* and *C. gariepinus* were mainly demersal nocturnal hunters on haplochromines (Bruton, 1979a, b; Okach & Dadzie, 1988). If predator avoidance was a major factor determining migration of haplochromines in pre-Nile perch era, one would have expected all haplochromines to migrate to the surface waters. In spite of this, only the zooplanktivorous haplochromines did so, while a large part of the detritivores and other trophic groups remained at the bottom (Witte, 1984).

After the Nile perch boom, *B. docmak* and *C. gariepinus* declined strongly, while the piscivorous haplochromines disappeared completely. Predation pressure on fish strongly increased with the increase of Nile perch. Initially the piscivorous biomass made up less than 10% of the total fish stock, while after the Nile perch boom this rose to ca. 90% (Witte et al., 1999). During daytime Nile perch were mainly caught at the bottom. If predation would be a causal factor for vertical migration of dagaa, both, presence of piscivorous birds during daytime at the surface (Wanink, 1992) as well as presence of high Nile perch densities near the bottom would play a role. Indeed, avoiding predation by birds may explain the evasion of the surface layers during the day. However, it does not explain why after the Nile perch upsurge, the daily downward migration extended towards the bottom, while previously dagaa dwelled at intermediate depths.

Neither for dagaa, nor for haplochromines, can predation avoidance fully explain their vertical migration. In the following section we will explore the availability of food as a causal factor.

Food and vertical migration

The large numbers of objects observed on the hydro-acoustic recordings made during the night are most likely larvae and pupae of chaoborid species and pupae of chironomids. The third and fourth instar larvae of chaoborids dwell in the bottom during the day and migrate to the surface every night, where they feed on zooplankton. Migration of chaoborids into the bottom substrate during the day is possibly a move to avoid predation by fish (Dawidowicz et al., 1990). This suggests that chaoborid larvae are most easily available as prey during the night. Pupae of chaoborids and chironomids migrate to the surface around new moon where they emerge as lake flies or midges and form large clouds (MacDonald, 1956; Tjønneland, 1958). During such nights, many haplochromine species included these pupae in their diet (Goldschmidt et al., 1990, 1993). Goldschmidt et al. (1993) observed that a quarter of the shrimp population migrated into the middle and upper part of the column at night. In periods with low oxygen concentrations near the bottom, they were caught massively in nightly surface trawls (Wanink & Goudswaard, unpublished). In offshore areas in Ugandan waters, Lehman et al. (1996) also noticed migration to mid water and surface water during the night.

Copepods, the dominant zooplankton in the Mwanza Gulf (Akiyama, 1977; Goldschmidt et al., 1990; Witte et al., 1995) showed signs of diel vertical migration. At night the densities at the surface generally increased (W. Hoogenboezem, pers. com.). Ringelberg et al. (1991) found that the zooplankter *Daphnia hyalina* in Lake Maarseveen (The

Netherlands) moved into deeper water just before sunrise and migrated into the water column at sunset. They proved that vertical migration coincided with 'maximal relative increases in light intensity' and was induced by the presence of juvenile perch. Dawidowicz et al. (1990) showed that, under experimental conditions, *Chaoborus* larvae were able to detect the presence of fish. This induced migration into the mud by day to avoid predation. The foregoing studies indicate the induction of vertical migration of invertebrate prey by fish. Alternatively, fish migration might be induced by prey migration.

Dagaa, zooplanktivorous haplochromines and, to some extent, juvenile Nile perch, may follow zooplankton and larvae, pupae of chaoborids and chironomids to the surface at night. Zooplanktivorous haplochromines, which fed on cyclopoid copepods near the bottom during the day, migrated towards the surface at night, and switched to *Chaoborus* larvae (Goldschmidt et al., 1990). Wanink (1998) found that adult dagaa, after eating emerging lake flies at the water surface, moved to lower water levels. This seems to support the theory that fish move to deeper water after feeding, to reduce their rate of energy expenditure in cooler water (Wootton, 1990). However, as Wanink (1998) noticed, the supposed benefit in energy expenditure from moving into a cooler environment may have been marginal, since temperature showed little variation over the water column in the Mwanza Gulf. A similar pattern of feeding and migration was found for *Engraulicypris sardella* in Lake Malawi (Allison et al., 1995). These cases suggest that diel vertical migration in zooplanktivorous fish is driven

by factors related to feeding. This suggestion is supported by the fact that detritivorous haplochromines and Nile tilapia, which mainly feed on bottom debris, do not show vertical migration. Another support for food as a causal factor comes from the downward migration to the bottom of dagaa after the Nile perch upsurge. It has been shown (Wanink & Witte, 2000) that after the disappearance of the bottom-dwelling haplochromines, dagaa occupied this habitat and included macrobenthic invertebrates in their diet, formerly a major food item for haplochromines. Thus it seems that dagaa migrates into a habitat rich in food, in spite of high predation pressure. Feeding cannot explain unambiguously why piscivorous nembe moves to the surface at night. Stomach contents of nembe predominantly caught in gillnets set overnight, were dominated by haplochromine cichlids, though dagaa and terrestrial insects made up an important component (Corbet, 1961). The latter two prey items occurred at the surface during the night. The availability of large quantities of haplochromines near the bottom would make vertical migration useless, unless nembe was outcompeted by *Bagrus* and *Clarias* or piscivorous haplochromines. Irrespective of the causes, our study clearly shows differences in vertical distribution and diel vertical migration in major fish species of Lake Victoria. These data are important for the interpretation of the currently undertaken hydro-acoustic surveys as they may help partitioning the hydro-acoustic records into species groups, and thus result into more precise stock estimates.

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