

**FOOD AND FEEDING HABITS OF *HAPLOCHROMIS*
(TELEOSTEI : CICHLIDAE) FROM LAKE KIVU
(CENTRAL AFRICA)**

**II. Daily feeding periodicity and dietary changes
of some *Haplochromis* species under natural conditions**

by

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SUMMARY

The feeding periodicity and dietary changes of *Haplochromis graueri*, *H. olivaceus*, *H. nigroides* and *H. kamiranzovu*, 4 endemic species from lake Kivu, were investigated by determining the stomach fullness index at intervals of 3 hours over a 24-hour cycle. These 4 species showed 2 types of daily feeding activity rhythm both characterised by a major food intake at daytime. A first type of bimodal feeding rhythm with the first peak situated in the morning between 6.00 a.m. and 12.00 a.m. and a second one in the evening between 3.00 and 9.00 p.m. characterizes *H. graueri*, and *H. olivaceus*. *H. kamiranzovu* and *H. nigroides* on the other hand showed a unimodal feeding rhythm with a single peak situated in the afternoon between 3.00 and 6.00 p.m.

The beginning of each period of active foraging is rather easily detected in catches by a rapid rise in number of fish captured. The highest degree of stomach fullness appears almost invariably about 3 hours after the beginning of such a foraging peak.

The variation of the coefficient of vacuity in the various *Haplochromis* species studied is not only related to the dial feeding rhythm but also to the items ingested : it is higher in carnivorous species and lower in omnivorous, detritivorous and phytophagous ones.

The relation between the uptake of various prey types and feeding time over the 24 h period indicates that some prey items are more accessible at specific hours of the day. These *Haplochromis* species have developed a strategy for cropping potential food items at specific periods of the day. This probably leads to a further reduction or in some cases to a complete absence of interspecific food competition.

Keywords : Feeding periodicity, food and feeding habits, *Haplochromis*, Cichlidae, lake Kivu.

INTRODUCTION

Haplochromis is one of the largest and most widespread genera of cichlids in lake Kivu (Central Africa). The genus is represented by at least 13 species which are all endemic to the lake. In 1977, attention was drawn to their ecology and several field missions have been organized by the « Musée Royal de l'Afrique Centrale » (MRAC, Tervuren-Belgium) in collaboration with the « Institut National de la Recherche Scientifique » (INRS, Butare-Rwanda) in order to investigate the biology of various species of *Haplochromis*. Several aspects of their biology are under investigation (systematics, reproduction, growth, food and feeding habits) and several papers have been recently published on their systematics (COENEN *et al.*, 1984; SNOEKS, 1986, 1988; SNOEKS *et al.*, 1984, 1987 and 1990) while only a few on their food and feeding ecology (VERBEKE, 1957, Ulyel *et al.*, 1990).

Although it is known that fish species differ widely in their food and daily feeding pattern, these aspects have received little attention in the *Haplochromis* species of lake Kivu. THYS VAN DEN AUDENAERDE (1986) observed that *Haplochromis* species from lake Kivu were active during the day, but asleep at night. DE VOS *et al.* (1987) concluded that some *Haplochromis* species such as *Haplochromis kamiranzovu* showed vertical food migration during the night while some others species like *H. graueri*, *H. gracilior* seemed to be strictly benthic and inactive.

Those studies did not take into account, even partially, the food, feeding habits, nor stomach fullness which are the most important ways to investigate food availability and abundance, ecological separation of fish assemblages and the utilisation of food under natural conditions.

The present paper deals with the daily feeding periodicity of 4 *Haplochromis* species. The ecological significance of the diet in relation to different kinds of food items eaten during the 24-hour period is also discussed.

MATERIAL AND METHODS

Fieldwork was carried out at Gisenyi and Kibuye Bay in lake Kivu (Rwanda, 1.500 m altitude), one of the smallest lakes of the East-African Rift Valley with a total water surface of about 2.370 km² and with a mean depth of 240 m. Lake Kivu (Fig. 1) is located south of the Equator (1°34'30"-2°30' Latitude South and 28°50'-29°23' Longitude East). It is surrounded by several active volcanoes (Nyamulagira, Nyiragongo...) and geothermal springs. It is characterized by a very high concentration of dissolved gas (CH₄, 370 ml/l; CO₂, 1400 ml/l) in the deeper layers. The temperature of water at the surface ranges between 24 to 25.5 °C (DEGENS *et al.*, 1973; DEUSER *et al.*, 1973; DE JONGH and SPLIETHOFF, 1980).

The study was based on six 24-hour periods of capture at intervals of 3 hours on August 18-31, 1981 (Murakoze mission IV) and on February 12-17, 1987.

Fishing periods cover the whole interval of 3 hours and were given as the time the nets were emptied (*e.g.* the 9.00 a.m. sample covered 6.00 to 9.00 a.m. fishing).

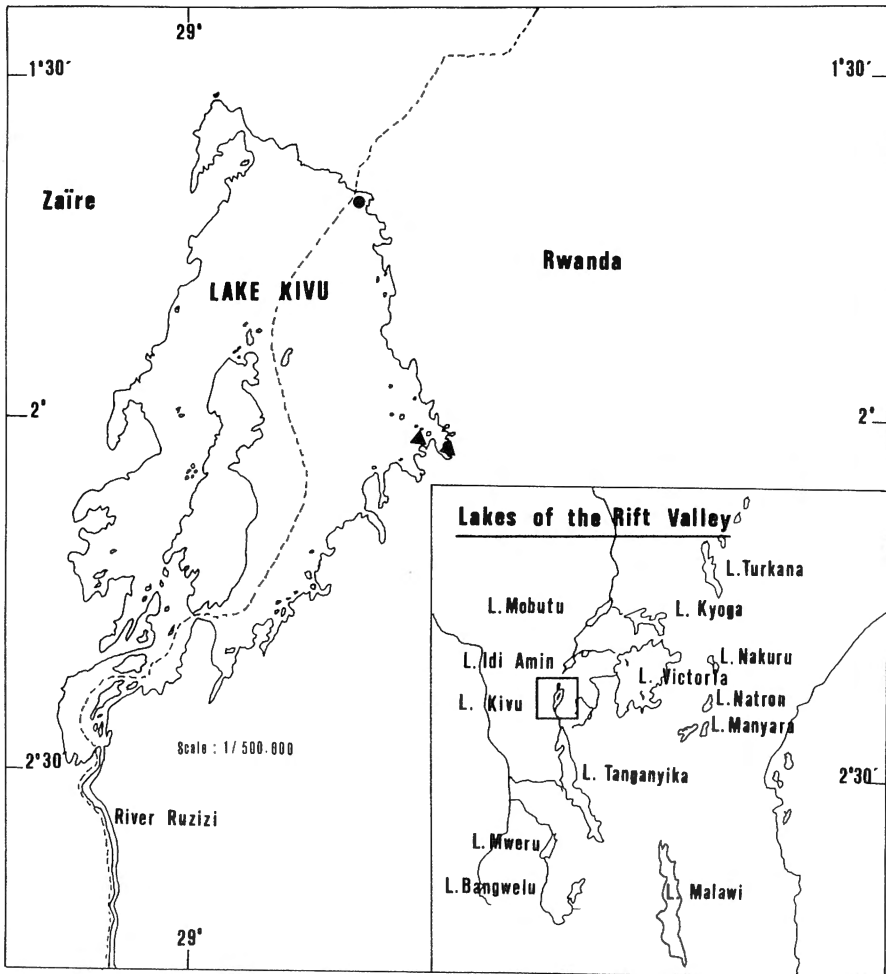


Fig. 1. — Map of lake Kivu showing geographical location and study area. Fishing stations — (▲) Kibuye bay; (●) Gisenyi bay.

Fish were collected at two sites using monofilament bottom gill-nets of :

(a) 15-10-40-30-20-20-12 and 10 mm ktk,

(b) 12-15-12-40-30-20-20 and 15 mm ktk mesh-size at Kibuye Bay between 0 and 70 m depth (see THYS VAN DEN AUDENAERDE, 1986) and bottom gill-nets of 10-12-15-20 and 25 mm mesh-size at Gisenyi Bay (0-45 m depth).

A 24-hours experimental fishing protocol was organized at Kibuye Bay by the Murakoze IV group.

A first series (a) of gill-nets was first placed in the water at 6.00 a.m.; at 9.00 a.m., series (b) was set at some distance, and 3 hours later on, the set of net

(a) was taken out of the water. At 12.00 a.m., set (b) was taken out and the series of the net (a) was set again but at some distance with a switching of the two first nets to the end of the series and so on. In this way, each net of each different mesh-size was fishing at various depths and during one or more of various periods of the day (THYS VAN DEN AUDENAERDE, 1986).

After the capture, the fishes were immediately injected intraperitoneally with 10 % buffered formaldehyde in order to stop digestion, and later on, they were transferred to 70 % ethanol to preserve gut contents for subsequent analysis. In the laboratory, the stomach and gut contents were removed and kept separately in microtubes in 70 % ethanol. Only stomach contents were examined for the purpose of this study.

For the estimation of the « fullness index » and the quantification of each food item, the numerical method and point methods (HYNES, 1950 ; WINDELL, 1968 ; HYSLOP, 1980) were used. A defined number of points depending on the visually estimated volume was awarded to each stomach content and food item. Although the point method (HYNES 1950 ; WINDEL, 1968) is considered to be a « subjective allotment of points », it has the advantage of being easy, fast and adapted to any kind of food items such as soft animal tissues, detritus, hard invertebrate remnants and plant materials that can not be numerically or gravimetrically quantified (WINDELL, 1968 ; HYSLOP, 1980 ; JANSSENS DE BISTHOVEN *et al.*, 1990). The visual estimate of the stomach fullness was made using the scale of HYNES (1950), modified by WINDELL, 1968) and OLATUNDE (1978) (Table I).

TABLE I

Visual estimate of stomach fullness

Stomach replenishment	Points
Full (distended stomach)	100
3/4 full	75
1/2 full	50
1/4 full	25
trace	1-5
Empty	0

Mean stomach fullness index (MFI) with respect to capture time and food items categories was calculated using the following formula :

$$\text{MFI} = \Sigma \text{Vc} / \text{Ne}$$

$$\text{VC} = (\text{Nv} / \text{Ne}) \cdot 100$$

where V_c is the estimated fullness of the stomach (points-method); N_e = total number of stomachs examined; N_v = total number of empty stomachs and VC = coefficient of empty stomachs (or the percentage of occurrence of fish with empty stomachs).

A one way analysis of variance has been used to compare different mean values of the stomach fullness indices (MFI) and prey items according to the time of the day.

RESULTS

General aspects of food and feeding habits

A total number of 689 fish ranging from 43 to 126 mm standard length (SL) were collected on 6 sampling days (Table II).

TABLE II

Numbers and size range of fish examined as collected from Kibuye and Gisenyi Baies

	(n)	size range (SL in mm)
<i>Haplochromis graueri</i> BOULENGER, 1914	159	48-126
<i>Haplochromis nigroides</i> PELLEGRIN, 1939	182	47-80
<i>Haplochromis olivaceus</i> SNOEKS, DE VOS, COENEN and THYS, 1990	184	43-90
<i>Haplochromis kamiranzovu</i> SNOEKS, COENEN and THYS, 1984	164	49-76

The food of these *Haplochromis* species consists of at least 21 different major prey items. As indicated by the gut content analysis, 3 major trophic groups were recognized, namely detritivorous (mud-feeder), microherbivorous or microphytophagous and insectivorous (Table III).

(1) *Mud-feeder* : this group is represented by *H. nigroides*. The gut content of this species consists almost entirely of microbenthic material, silts and detritus. The stomach of *H. nigroides* contains typically a mass of grey-black materials which after examination in suspension, revealed detritus and benthic organisms ranging from diatoms, protozoans, insect remains, ostracods and substantial amounts of grey-green mud which characterizes mud-feeder fishes.

(2) *Microphytophagous* : the group includes two species : *H. kamiranzovu* and *H. olivaceus*. Gut contents were dominated by substantial quantities of algae of benthic, epiphytic, epilithic and pelagic origin. The diet of *H. kamiranzovu* was mainly composed of the pelagic algae *Microcystis flos aquae* and a small quantity

of zooplankton especially copepods and cladocerans. The stomach of *H. olivaceus* contained significantly more periphyton, diatoms, epiphytic algae and a larger proportion of detritus. *Cladophora* sp. was frequently ingested by *H. olivaceus* in Gisenyi Bay while at Kibuye Bay the stomach content is dominated by *Callothrix*

TABLE III

Mean volume (MÆ) and percentage (%) in points-volume of various food items recorded in the stomach of 4 Haplochromis species from lake Kivu

	Species							
	<i>H. olivaceus</i>		<i>H. kamiranzovu</i>		<i>H. graueri</i>		<i>H. nigroides</i>	
Food items	MÆ	%	MÆ	%	MÆ	%	MÆ	%
Fish remains	0.05	0.08	0.09	0.13	—	—	0.03	6.61
Detritus	14.74	22.25	4.13	1.59	1.41	3.13	17.04	27.95
Sediments	4.64	7.00	0.77	1.08	1.99	4.41	0.33	0.54
Diatoms	4.72	7.12	0.26	0.37	0.15	0.33	1.17	1.92
Chironomids (larvae)	0.75	1.13	0.28	0.39	34.77	77.10	1.83	3.00
Nematodes (P)	0.34	0.51	0.08	0.11	—	—	0.13	0.21
Rotifera	0.04	0.06	0.02	0.03	—	—	0.14	0.23
Cladocera	0.03	0.05	3.36	4.79	0.63	1.40	5.73	9.4
Copepods	3.47	5.24	6.59	9.26	3.20	7.10	8.63	14.15
Eggs (unidentified)	0.99	1.49	0.16	0.22	1.08	2.39	1.69	2.77
Ostracods	0.07	0.11	0.09	0.13	0.26	0.58	0.13	0.21
Macrophyt remains	0.43	0.65	0.38	0.53	0.55	1.22	0.82	1.34
Algae	33.64	50.78	54.01	80.07	0.03	0.07	9.20	15.09
Acanthocephala (P)	0.02	0.03	0.02	0.03	—	—	0.02	0.03
Acarina (P)	—	—	—	—	0.01	0.02	0.13	0.21
Diptera (pupae)	0.23	0.35	0.15	0.21	0.45	1.00	2.67	4.38
Plecoptera (nymphs)	—	—	—	—	—	—	0.49	0.80
Ephemeroptera (nymphs)	0.41	0.62	—	—	—	—	1.85	3.05
Insect remains	—	—	—	—	—	—	0.27	0.44
Hymenoptera	—	—	—	—	—	—	0.16	0.26
Unidentified animal remains	1.68	2.54	0.81	1.14	0.57	1.26	4.93	8.09

(—) represents different item categories which are not recorded in the stomach.

(P) = intestinal parasites

epiphytica and *Schizothrix* sp. Considering the internal teeth composed of 4 to 9 rows, *H. olivaceus* shows « scraper » and « browser » characteristics.

(3) *Carnivorous* : *H. graueri* represents this group. It is a bottom feeder in which the main food is composed of dipteran larvae and pupae, especially chironomid larvae with variable quantities of other insects (terrestrial and aquatic), ephemeropterans, anisopterans and hemipterans. A very small quantity of copepods, cladocerans, detritus and sediments is also registered in the stomach of *H. graueri*.

Catch rates (Gisenyi Bay, February 12 and 17, 1987)

The catch rates showed 2 major peaks, when taking into account all 4 species studied together. The first peak appears almost invariably in the morning between 6.00 and 9.00 a.m., and the second in the afternoon between 3.00 and 6.00 p.m. (Fig 2). It is lower at noon and the lowest catch rate is recorded during the night. The mean number of fish captured during daytime appeared highly significantly different from the night catch rate ($P \leq 0.001$).

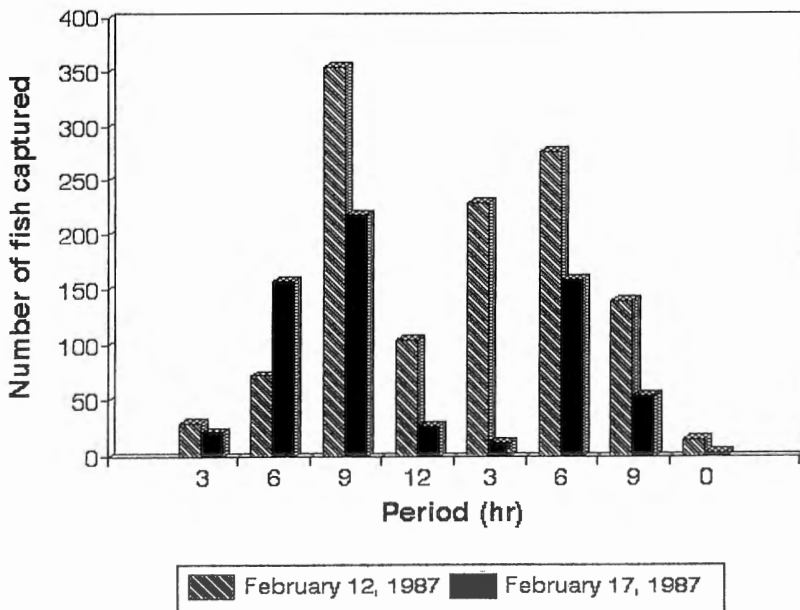


Fig. 2. — Catch-rates of *Haplochromis* species expressed as the total number of fish captured in Gisenyi Bay, February 12 and 17, 1987. (hr = hour)

Considering the catch rate for each species separately as represented in Fig. 3, the highest capture of *Haplochromis kamiranzovu* occurred in the afternoon from 3.00 to 9.00 p.m. This may indicate a vertical migration to search for food after

sunset. In the morning and during the day (between 9.00 a.m. and 9.00 p.m.), the rate of capture of *H. kamiranzovu* is significantly higher ($P \leq 0.05$) than of the others three species (*H. graueri*, *H. olivaceus* and *H. nigroides*). It can be hypothesized that *H. kamiranzovu* presents an active locomotory and feeding activity throughout the day till 9.00 p.m.

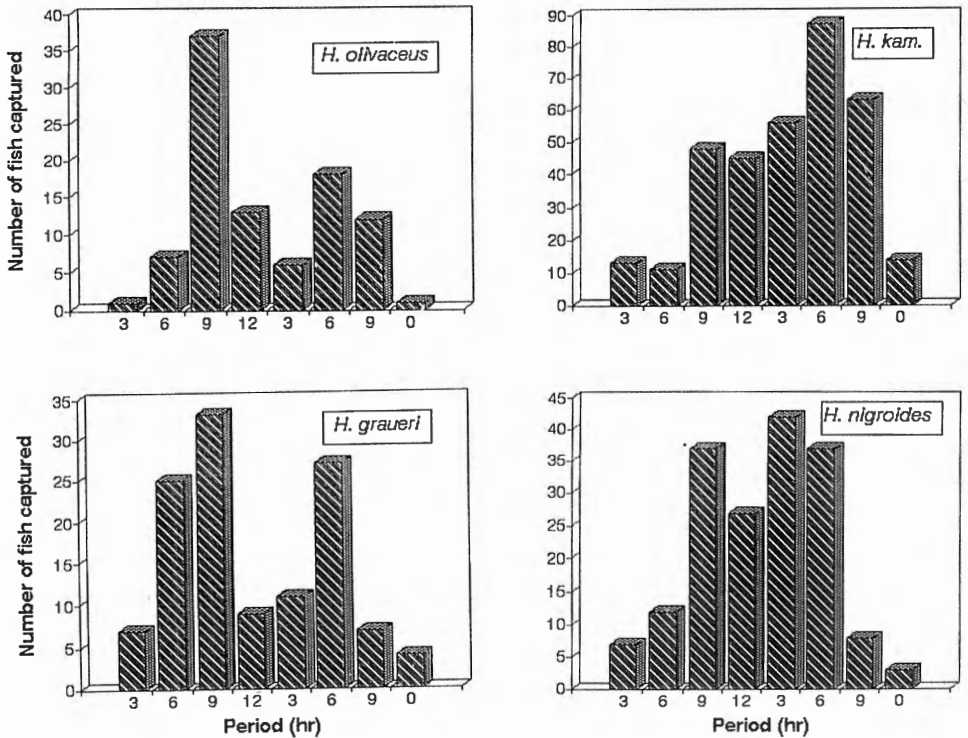


Fig. 3. — Catch-rates of four different *Haplochromis* species (*Haplochromis olivaceus*, *H. graueri*, *H. kamiranzovu* and *H. nigroides*), given as the total number of fishes captured during 3 cumulated 24-hour cycles. Abbreviation in the figure : *H. kamir.* = *H. kamiranzovu*.

Daily feeding rhythm

The analysis of the daily feeding activity pattern in the *Haplochromis* species of lake Kivu suggests that food uptake occurred mainly during daytime ($P \leq 0.01$) (Fig. 4, (a) and (b); Fig. 5 (a) and (b)). *H. graueri* and *H. olivaceus* indicate a bimodal feeding activity rhythm with the first peak situated in the morning between 6.00 and 12.00 a.m. and the second peak in the evening between 3.00 and 9.00 p.m.

In *H. graueri*, the means which characterize the major feeding peaks (9.00 a.m., $\text{MFI} = 21.7 \pm 7.3$ and 9.00 p.m., $\text{MFI} = 24.3 \pm 13.8$) show a highly significant difference with the means of all others periods ($P \leq 0.01$) (Fig. 4 (a)).

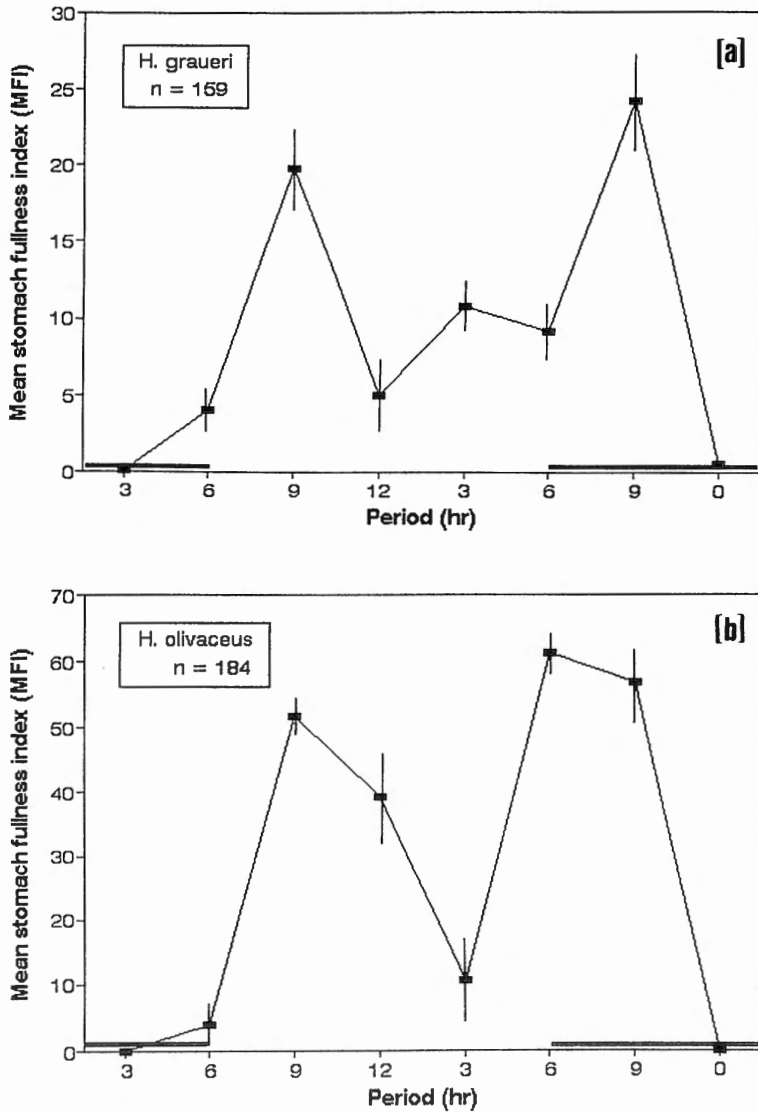


Fig. 4. — Daily feeding periodicity (in points-volume) of *H. graueri* (a), *H. olivaceus* (b). Fine curve (—) represents the mean points-volume of fullness index of the stomach at intervals of 3 hours of capture. Dotted solid bar (—) indicates hours of darkness. Vertical lines (|) represents the standard error on means (\pm SE).

The results obtained with *H. olivaceus* reveal like in *H. graueri* two daily feeding peaks, the first peak is observed in the morning at 9.00 a.m. (MFI = 51. \pm 8.3) and the second at 6.00 p.m. (MFI = 61.1 \pm 6.4) (Fig. 4 (b)) and continues till 9.00 p.m.

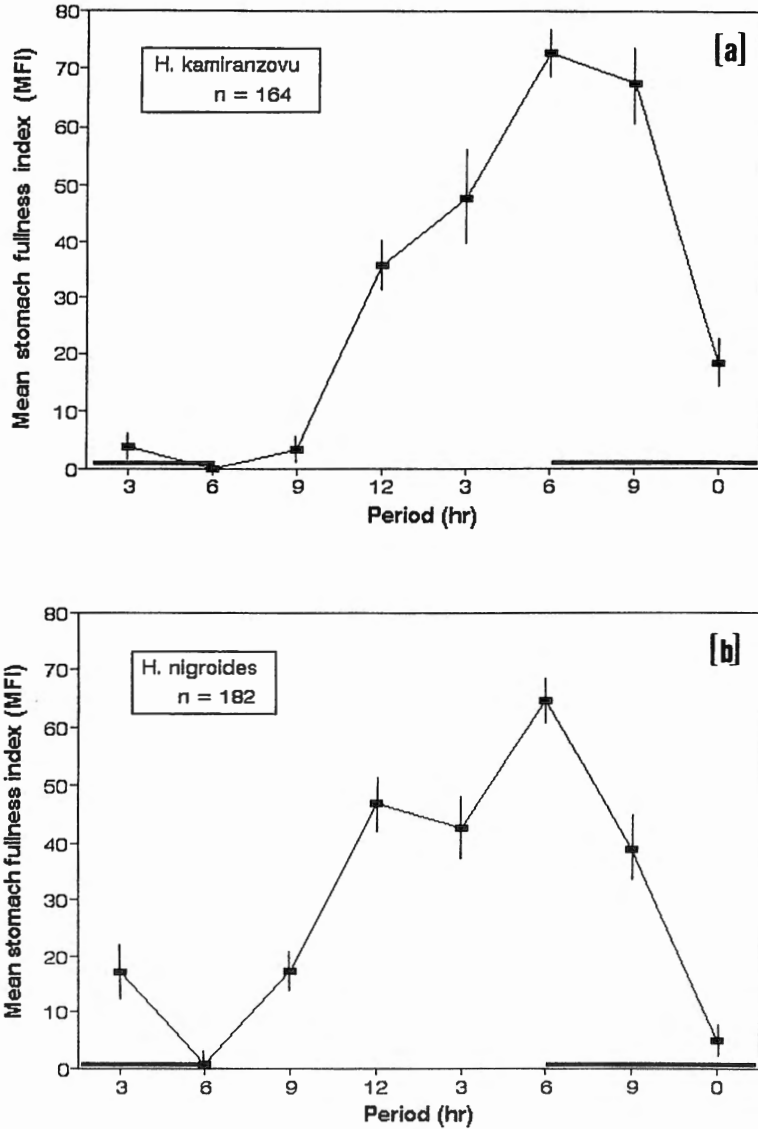


Fig. 5. — Daily feeding periodicity (in points-volume) of *H. kamiranzovu* (a) and *H. nigroides* (b). Fine curve (—) represents the mean points-volume of fullness index of the stomach at intervals of 3 hours of capture. Dotted solid bar (—) indicates hours of darkness. Vertical lines (|) represents the standard error on means (\pm SE).

Both mean volumes of feeding intensity are highly significantly different of the means of 3.00 and 6.00 a.m. ($P \leq 0.01$) and with 3.00 and 12.00 p.m. periods

($P \leq 0.001$) but not with the means of the feeding intensity of 9.00 p.m. (MFI = 56.7 ± 12.4 , $P > 0.05$).

In both species, accelerated feeding activities started at about 6.00 a.m. and continued until 9.00 a.m. The stomach emptied slowly from that time onwards until around 12.00 a.m. in *H. graueri* and 3.00 p.m. in *H. olivaceus*. A low replenishment of the stomach is observed in most fish between 12.00 a.m. and 3.00 p.m.

In *H. graueri* for example, intermittent feeding occurred for a long period ranging between 12.00 a.m. to 6.00 p.m. during daytime. A high degree of variation of the degree of stomach fullness has been observed varying in some fish from empty stomachs up to full stomachs.

In contrast to this, *H. kamiranzovu* and *H. nigroides* show a single peak of feeding activity situated at 6.00 p.m. Active feeding started at about 6.00 a.m. and stomachs reach their maximum fullness at around 3.00 to 6.00 p.m. Thereafter, the stomachs remained nearly full until about 9.00 p.m. ($P \leq 0.05$) in *H. kamiranzovu*, but decreased rapidly in *H. nigroides* (Fig. 5 (a) and (b)).

Coefficient of vacuity (CV)

The highest percentages of empty stomachs were observed during the night-time while lower percentages were seen during the day ($P \leq 0.01$). The variation of the average vacuity coefficient in the various *Haplochromis* species studied here seems not only to be related with the diel feeding rhythm but also with the food items ingested (Table IV). It indicates that these *Haplochromis* species do not feed during the night. It can also be postulated that the highest capacity of stomach and intestinal storage must occur in daytime, while *Haplochromis* are inactive at night (THYS VAN DEN AUDENAERDE, 1986 and DE VOS *et al.*, 1987).

TABLE IV

Variations of coefficient of vacuity (CV) of 4 *Haplochromis* species calculated as the percentage of occurrence of empty stomachs over a 24-hour cycle in lake Kivu

Hour (hr)	3 a.m.	6 a.m.	9 a.m.	12 a.m.	3 p.m.	6 p.m.	9 p.m.	0 p.m.
<i>H. kamiranzovu</i>	92.3	100.0	35.71	7.6	4.1	5.8	10.8	57.1
<i>H. nigroides</i>	40.0	80.0	40.9	16.3	14.3	14.8	37.5	66.7
<i>H. graueri</i>	85.7	84.0	39.4	64.9	58.6	59.3	42.9	75.0
<i>H. olivaceus</i>	100.0	71.4	18.9	7.7	66.7	5.7	3.3	100.0

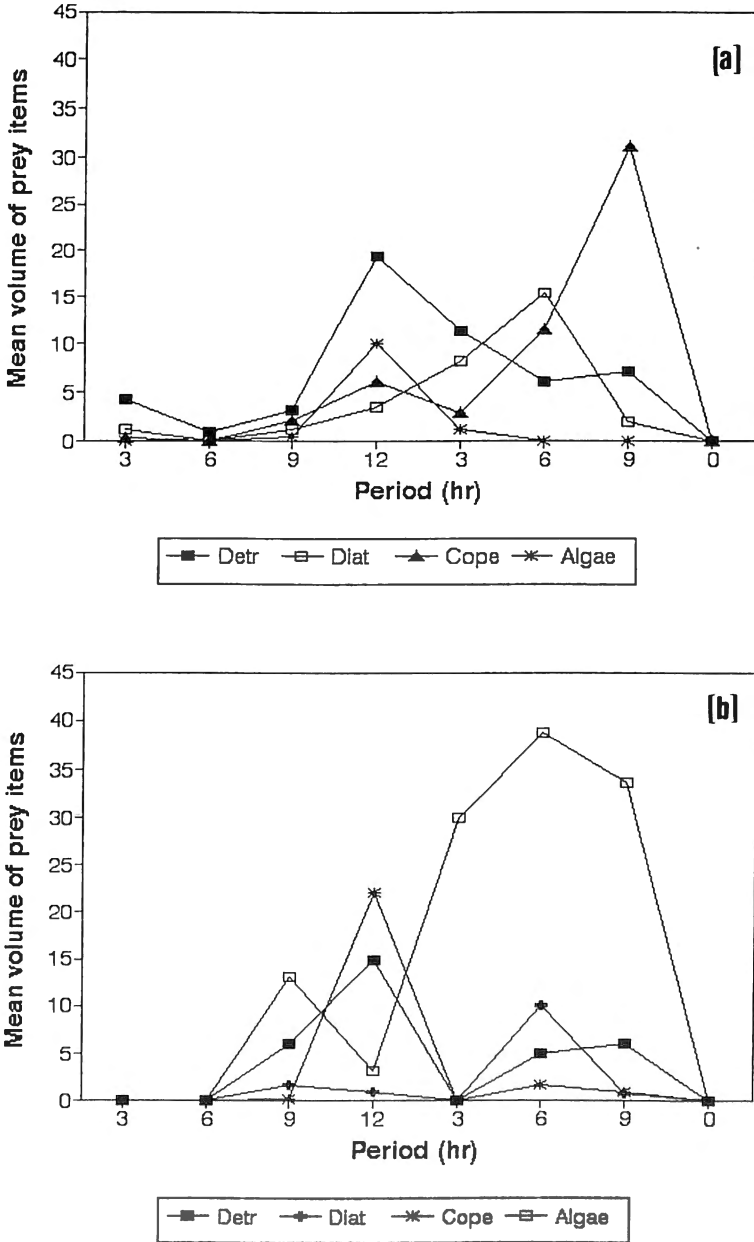


Fig. 6. — Daily dietary changes of food ingested by *H. nigroides* (a), *H. olivaceus* (b). Detr = detritus; Diat = diatoms; Cope = copepods; Chir = chironomids larvae; Clad = cladocerans

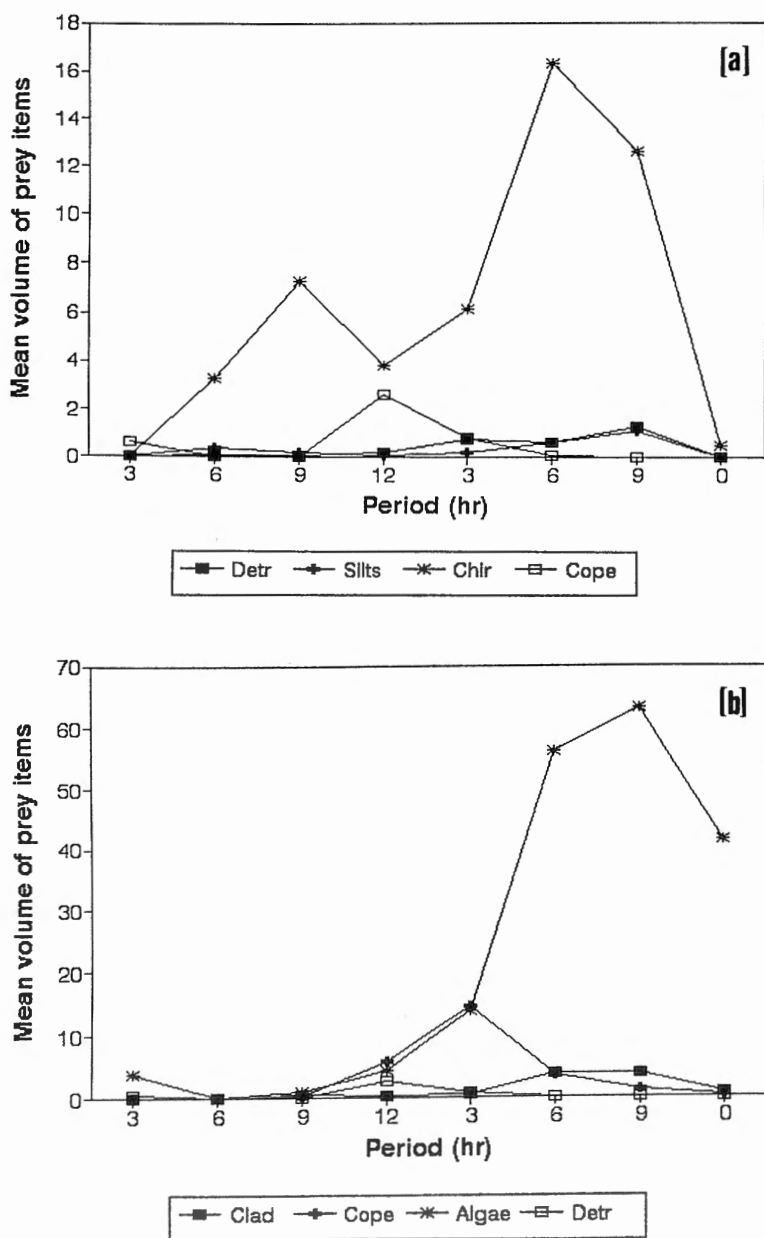


Fig. 7. — Daily dietary changes of food ingested by *H. graueri* (a) and *H. kamiranzovu* (b) (see legends in Fig. 6).

Changes in kinds of food eaten during 24-hours period

All *Haplochromis* species studied presently showed changes in the prey items taken according to feeding periods. Prey items eaten during the day are significantly different from prey items recorded in the stomachs of fish captured during the night ($P \leq 0.001$). This is detected in most of the cases by a high number of empty stomachs and low mean volume of prey eaten during the night and in some cases, by a total absence of feeding activity throughout the night (Table IV ; Fig. 6 (a) and (b) ; Fig. 7 (a) and (b)).

H. nigroides presents a pretrophic feeding activity before sunrise. Three prey categories are apparently present in the stomach at 3.00 a.m. ; they consist of algae, copepods and detritus (Fig. 6 (a)). But the ingestion of these preys decreases significantly in the first half of the day (6.00 a.m.), and then increases significantly at 12.00 a.m. until 3.00 to 9.00 p.m.. On the other side, predation on copepods and algae, mainly benthic algae *Cladophora* sp., goes on increasingly from 9.00 a.m. to 6.00 and 9.00 p.m. respectively (Fig. 6 (a)).

In contrast, for *H. olivaceus* (which has the same microphytophagous diet as *H. kamiranzovu*), the regime is composed of various kind of prey items in the morning till 12.00 a.m. (copepods, organic matter or detritus, algae). In the second half of the day, *H. olivaceus* feeds almost exclusively on multicellular algae *Cladophora* sp. Diatoms and detritus occurred also in the stomach, but in lower proportion than algae (Fig. 6 (b)). *H. graueri* does not show a major variation in the nature of food ingested during whole the day. Chironomid larvae, especially *Chironomus* type *plumosus* and *Tanipus* sp. are the most frequently ingested species. The mean points-volume of other prey items captured by this species presents less variation (Fig. 7 (a)). Despite the evidence for the regular intake of chironomid larvae throughout the day, a decrease in mean volume of chironomid larvae is observed at about 12.00 a.m. Copepods are apparently an important prey item captured at that time (Fig. 7 (a)).

For *H. kamiranzovu*, which feeds almost throughout the day, the main prey eaten remains colonial unicellular algae *Microcystis flos aquae* and copepods. A small quantity of organic matter was found frequently between 12.00 a.m. to 6.00 p.m. indicating that this species feeds near or at the bottom during this period. While copepods show the highest peak at 3.00 p.m., a small proportion of cladocerans in the stomach of *H. kamiranzovu* is observed between 6.00 and 9.00 p.m.. (Fig. 7 (b)).

DISCUSSION AND CONCLUSION

The present study shows that these four *Haplochromis* species from lake Kivu feed during the daytime. The peak of the stomach fullness index appears almost invariably 3 hours after the start of active foraging, detected by a rapid rise in number of fish captured. This is most clearly represented in fishes showing two distinct feeding peaks such as *H. graueri* and *H. olivaceus* (Fig 4 (a) and (b)).

However, in the case of *H. kamiranzovu* and *H. nigroides*, fresh food was almost always present in the stomach at all times of the day, which would suggest continuous and active feeding (ALBERTINI-BERHAUT, 1974 ; ROBB, 1981). (Fig. 5 (a) and (b)).

Catch rates in *Haplochromis* may well be a measure of pre-feeding activity which is reflected by a rapid increase of the average number of fish captured and the fullness index data in this study support such interpretation (Fig. 2). Low catch rates observed in *Haplochromis* from lake Kivu during daylight (between 9.00 a.m. and 3.00 p.m. on February 17, 1987) may be explained by either a low locomotory activity or a possible avoidance behaviour due to the visibility of the fishing nets (RYAN, 1984). It is known that most *Haplochromis* in lake Kivu do not swim over long distances, especially territorial adult males do not migrate. It can be assumed that the main reason for swimming is the search for food (THYS VAN DEN AUDENAERDE, 1986), for the reproduction or the attraction of females. According to THYS VAN DEN AUDENAERDE (1986), *Haplochromis* species are more or less asleep at night. During the night they remain almost immobile on/or near the bottom (THYS VAN DEN AUDENAERDE, 1986, DE VOS *et al.*, 1987). This assertion corresponds to our findings reflected by very low catch rates overnight (Fig. 2) and high percentages of empty stomachs (Table IV). *Haplochromis* species become active at sunrise or shortly after the first daylight (THYS VAN DEN AUDENAERDE, 1986).

This situation is clearly reflected by higher percentages of full stomachs ranging from 50 to 100 in most species between 6.00 and 9.00 a.m. But *H. kamiranzovu* which shows a single peak of diurnal feeding activity, seems also to be active overnight : a part of or the whole population seems to migrate vertically toward the surface before dawn (DE VOS *et al.*, 1987). This situation is clearly demonstrated in this study by the stomach fullness index recorded at 9.00 a.m. till 9.00 p.m., and a relatively high number of fish captured between 3.00, 6.00 and 9.00 p.m. as represented in fig. 2 b.

It can also be suggested that the *Haplochromis* species which were studied prey on various kinds of food items according to the accessibility of preys and the preference and feeding habits of the predators themselves (KEAST and WELSH, 1968 ; NEVEU, 1981a ; SCRIMGEOUR, 1986). Studying feeding periodicity in *Cheimarrichthys forsteri* and *Gobiomorphus hubsi* in New-Zealand River, SCRIMGEOUR and WINTERBOURN (1987) reached the conclusion that by feeding predominantly at different times of the night, the competition between the two species for food, should it be in short supply, was reduced. The different feeding periods of the various fish species of lake Kivu probably influence the selection of the food obtained.

Differences in feeding strategy ensure that all potential food organisms are cropped by at least one fish species during a determined period. According to MACPHERSON (1985), differences in feeding activity may also be due to internal rhythms independent of food availability. Many factors, internal as well as external, which have negative or positive effects on food and feeding habits can be evoked. Feeding activities are influenced by physical (temperature, light intensity, turbidity, eutrophication...) and chemical factors (CO₂, pH, O₂ ...) as well as by biological and

physiological aspects (migration of plankton, digestion, evacuation rates, etc.) and many others (NEVEU, 1981a). DE VOS *et al.*, 1987 studied the vertical migration of some *Haplochromis* in lake Kivu and suggested that the nocturnal vertical migration in *Haplochromis* can be considered as a feeding migration. A similar phenomenon has been observed in many other *Haplochromis* species from lake Victoria (WITTE, 1984; GOLDSCHMIDT *et al.*, 1990). In crater lakes in West Cameroon, it was also observed that *Haplochromis* species migrate according to vertical movements of larvae and nymphs of *Chaoborus* (GREEN *et al.*, 1973). DE VOS *et al.* (1987) concluded that the migration of some *Haplochromis* species from lake Kivu should be explained by the migration and movement of nematoceraans. It has also been observed that chironomid and trichopteran pupae generally move vertically through the water column prior to emerging as adults mostly at night although some of them do so in the forenoon and afternoon. This migration explains, at least partially, the importance and a proportional value of chironomids and trichopterans in the stomach of insect larvae eaters, such as *Haplochromis graueri*, throughout the day and sometimes also later at night.

The variation of the average vacuity coefficient registered in the different *Haplochromis* species studied here seems to be related with the diel feeding rhythm pattern and with the categories of prey items ingested. The high percentage of empty stomachs, the low degree of capture and the low index of stomach fullness during the night indicate that feeding activity declines significantly throughout the night.

We observed that the coefficient of vacuity is higher in carnivorous *Haplochromis* species such as *H. graueri* than in omnivorous fish like *H. gracilior* (in preparation), in detritivorous (*H. nigroides*,) and in algae eaters (*H. olivaceus* and *H. kamiranzovu*). This may also indicate that carnivorous fishes have a relatively high digestion rate and feed less actively than detritus and algae eaters. An experimental study in the laboratory with *Haplochromis* spp. from lake Kivu, fed with dry food, coloured with chromoxide, showed that the evacuation time necessary can be estimated to range from 2 to 3 hours (pers. observ.).

Dietary changes over a 24-hour cycle show that some prey items are more accessible at specific hours of the day (Fig. 6 (a),(b); Fig. 7 (a) and (b)). The relation between the uptake of different prey types and feeding time over the 24-hour periods reflects that each *Haplochromis* species in lake Kivu has developed an appropriate strategy which enables it to crop potential food items at these periods of the day. This leads probably to a further reduction or in some cases even to a complete absence of interspecific food competition (KEAST and WELSH, 1968; NEVEU, 1981b; LECOMPTE-FININGER, 1983; SCRIMGEOUR and WINTERBOURN, 1987; DELBEEK and WILLIAMS, 1988).

Differences in feeding time can serve to reduce interspecific contact and competition, at least in the cases of versatile and generalized feeders (KEAST and WELSH, 1968), such as *Haplochromis nigroides*, *H. olivaceus* and *H. graueri*. Recent findings (ULYEL *et al.*, 1990) showed that *Haplochromis* species from lake Kivu do not compete for major food items of their regimes. Each species occupies in the lake a well defined ecological habitat, sufficiently distinct from others so that competition for

important prey is avoided (ULYEL *et al.* 1990). In conclusion, it can be considered that spatial and temporal exploitation and the use of different resources are an important factor in organizing fish communities. Because fishes, in the presence of potential competitors under natural conditions, alter their behaviour in order to reduce the utilisation of similar resources (WERNER, 1984).

Sometimes, modifications of anatomical structures may occur, virtually independent of size or age (WITTE *et al.*, 1990). The configurations of such anatomical structures may depend also on the ontogenetic stage (such as age and size) at which the environmental switch occurs (HOOGERHOUD, 1987; WITTE *et al.*, 1990). Morphologically, most of the trophic groups are recognizable by a particular facies (BAREL, 1983). A facies and its constituent structures are related to the way food is processed rather than to the food type itself. In *Haplochromis* species from lake Kivu, this assertion may be illustrated in some trophic groups, such as in carnivorous species *H. vittatus* and *H. graueri* (LT \geq 75 mm), by several characteristics like canine-like teeth on the outer-rows on both upper and lower jaws and by relatively protrusible and strong jaws. According to our preliminary studies on dentition structures of *Haplochromis adolphifrederici*, the relationships between ecology and morphology with regard to diet composition can be illustrated by submolariform teeth covering the entero-central part of the lower pharyngeal bones in juveniles and subadult specimens, while they are molariform in adults. Such a degree of development of molariform teeth, as demonstrated in *Astatoreochromis alluadi* from lake Victoria (WITTE *et al.*, 1990), is probably correlated with the relative abundance of molluscs in the diet of the adult of *H. adolphifrederici*. On the other hand, we can hypothesize in the present study that the efficiency of *H. olivaceus* to scrape epilithic algae increases with the numerous rows (4 to 9) of internal tricuspid teeth on both upper and lower jaws.

Since *Haplochromis* from lake Kivu feed on different prey types, different sizes of prey (in preparation) and at different times of the day, the present observations support the view that these species are ecologically isolated. For example, in the presence of a variety of organisms, differences in diet would result from predators following the strategy to which they are best adapted and, in this way, if food was a limiting factor, interspecific competition could be avoided or reduced (ROBB, 1981), and most of the species would become versatile. Further, species apparently specialized for certain food sources, such as *H. kamiranzovu* in lake Kivu, may switch food preferences when other foods become superabundant (WITTE, *thèse de doctorat*, 1983).

ULYEL *et al.*, (1990) suggested that rare cases in which competition for food occurs among *Haplochromis* species of lake Kivu concerns very few prey items of minor importance. This suggestion supports the hypothesis of a partial overlap of some *Haplochromis* species in the use of relatively abundant prey items and the absence of marked food competition which can be considered as a consequence of adaptive radiation resulting in distinct feeding habits of the different species and/or the consequence of fixed adaptations due to a competition which occurred in the past (ULYEL *et al.*, 1990). As claimed by GOLDSCHMIDT *et al.* (1990), the presence of distinct segregation patterns in the absence of interactive competition does not

prove that competition never existed. Another possibility, as suggested by ROBB (1981), is that differences in diet may result from differences in feeding behaviour itself. Analysing ecological segregation in zooplanktivorous *Haplochromis* spp. from lake Victoria, GOLDSCHMIDT *et al.* (1990), stated that these species are ecologically segregated and therefore possibly sufficiently isolated to coexist.

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