Feeding habits of the clupeid *Limnothrissa miodon* (Boulenger), in Lake Kivu

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Abstract

A limnological sampling programme implemented during 1980 in Lake Kivu, Rwanda, confirmed a seasonal increase of the pelagic plankton biomass at the end of the dry season during the windy period of August/September. From plankton samples taken in the littoral and pelagic zones of the Lake it was concluded that a successful introduction of the freshwater clupeid *Limnothrissa miodon* Boulenger, during 1958–1960, had not obviously influenced the species composition of the Copepoda in the Lake.

Examination of stomach contents of different length classes of *Limnothrissa* proved that the Kivu clupeid is not a strict planktonphagic species. Its diet is adapted to its life cycle and inshore/offshore migration patterns. In pelagic waters of the lake it is an exclusive plankton feeder, while in littoral waters it has more littoral bound feeding habits. Cannibalism was observed among individuals larger than 100 mm, near the margins of the lake.

Echosoundings and periodic observations on stomach contents support the hypothesis that *Limnothrissa* feeds in the late afternoon and digests its food during the night, while a second feeding/digestion cycle starts in the early morning, at sunrise.

Introduction

To the biologist the interesting aspects of Lake Kivu are its ecological immaturity and the relative poverty of its fauna. The fish fauna is practically unrelated to that of Lake Tanganyika and there are but few similarities to that of Lake Edward. There are only sixteen species in the lake itself. These belong to the families Cyprinidae, Clariidae, Cichlidae and as a result of recent introductions, Clupeidae. As an ecosystem the lake is poorly developed and several niches are unfilled (Verbeke 1957b). Until the 1960's there was no effective predator on the pelagic zooplankton, much of which was lost in the sediments below. This niche is filled in Lake Tanganyika by the sardines *Stolothrissa tanganicae* and *Limnothrissa miodon*. Suggestions were made by Verbeke (1957b) for the introduction of a suitable species to fill this niche in Lake Kivu, in the hope that more organic matter would thereby be converted to edible fish and less lost in the mud.

In the period 1958–1960 thousands of *Limnothrissa* and *Stolothrissa* fry were transported from Lake Tanganyika to Lake Kivu (Collart 1960). In July 1974 the presence of *Limnothrissa* in the southern part of the lake was proved by Collart and in 1976 an expedition recorded it all over the lake (Frank *et al.* 1977). *Stolothrissa tanganicae* was never encountered in the experimental catches, so it was assumed that this species had not adapted to the specific conditions of the lake. From January 1980 a study was undertaken on the food preferences and feeding habits of the newly introduced Kivu clupeid in relation to the limnological conditions of the lake. This was an activity of the UNDP-FAO project RWA/77/010, a cooperative pro-

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gramme with the Government of Rwanda, for the development of an artisanal fishery for *Limnothrissa*. Research was restricted to the fishing zones of the project in the Bay of Gisenyi and some adjacent bays. This article summarises the results of the limnological programme and our findings concerning the food preferences and feeding habits of different length classes of *L. miodon* in the lake.

Characteristics of Lake Kivu

Geographical characteristics

Situated in the Western Rift Valley, between the south latitude 1°40′(North Basin) and 2°30′(Bukavu Bay), Lake Kivu forms a natural border of more than 100 km between Zaïre to the west and Rwanda to the east (Fig. 1).

Since the Pleistocene volcanic eruptions and after the formation of a new volcanic range (20 000 years ago), the waters of Lake Kivu that used to flow north towards Lake Edward have flowed towards the south and into Lake Tanganyika. The water surface is at an altitude of 1463 m and the lake covers a surface of 2 699 km^2 (Welcomme 1972). Maximum depth are recorded in the northern part of the lake (485 m) which has a mean depth of 285 m (Verbeke 1957a).

The littoral zone is very narrow because the slopes of the lake side are very steep. On the other hand, this same zone has a length of 1 200 km, as a consequence of the very sinuous shore-line. The pelagic zone is the most important and almost touches the lake sides (Beadle 1974).

Limnological characteristics

Water temperatures reach a minimum of 22.1 °C at a depth of 70 m. Surface waters vary between 23.1 °C and 24.1 °C.

Below 100 m the water is rich in salts and because of its density maintains a stable and permanent thermal stratification (Verbeke 1957a).

Due to this, the upward recycling of nutrients from the lower water into the euphotic zone only occurs to a certain degree at the beginning of the wet season. The transparency of the water varies

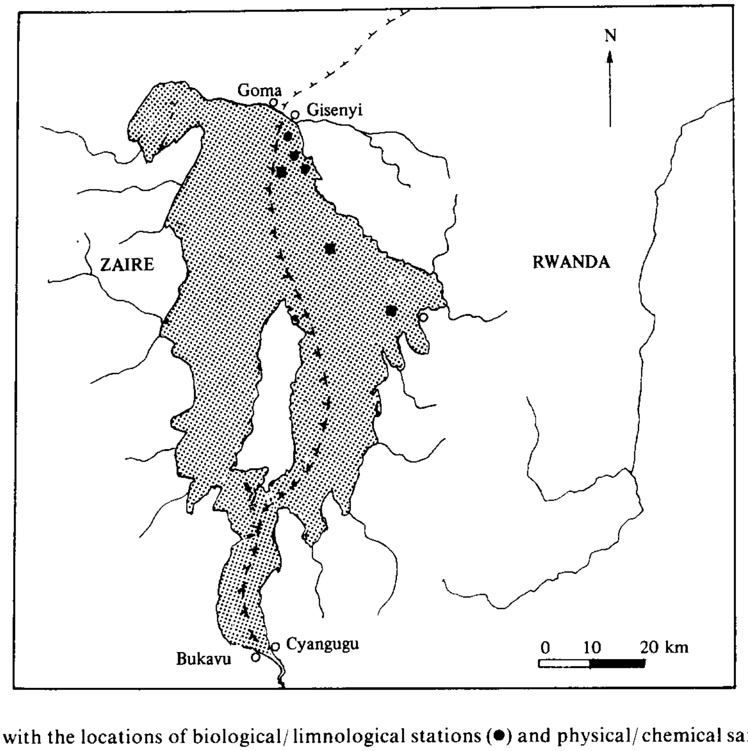

Fig. 1. Map of lake Kivu with the locations of biological/limnological stations (●) and physical/chemical sampling stations, including transects of echosounding (■).

from 2.5 m to 9.35 m. These figures are lower than those of Lake Tanganyika (maximum of 22 m; Chapman 1975) and may affect the efficiency of night fishing with lamps (less penetration of the light in the water and less attraction of the fishes).

The salinity of the water is high (about 1‰) and has a correspondingly high concentration of bicarbonate, which is continously precipitated as carbonate. As a result, a calcareous deposit is formed all along the shore line (Beadle 1974).

Most of the shores are rocky and submerged rocks are covered with the calcareous precipitate and dense mats of filamentous Cladophora. Most members of the invertebrate fauna, such as Nematoda, Turbellaria, Cladocera, Ostracoda, Insecta and Hydracharina, are limited to this zone (Verbeke 1957a).

The pH varies from 8.2 to 9.2, which is relatively high when compared with that of the inflowing rivers (±7.5).

The quantities of dissolved oxygen in the upper layers (20 m) of the lake water vary little (from 6 to 7.5 mg/l or 85 to 110% saturation) throughout the year (Verbeke 1957a). At 50 m there is only 3 mg/l of oxygen and the anaerobic zone starts at 70 m (Damas 1937).

Biological characteristics

The fauna of Lake Kivu is rather poor in species. Until now fewer than 20 species of fishes have been recorded. By comparison Lake Tanganyika has more than 200 species. This poverty is explained by the relatively recent formation of the lake in its present form, and as a result of the violent volcanic activities which occurred in this area. Another explanation for this poverty is the presence of waterfalls on the outflowing Ruzizi River, which prevents most fishes from coming up from Lake Tanganyika. Only one fish from this lake has succeeded in colonising Lake Kivu: *Barilius moorii* BOULENGER.

From an ecological point of view, the lake is characterised by a certain lack of maturity. Verbeke (1957a) noted that certain niches were not used. At the time, he also wrote that there was no real plankton feeding fish in the lake. He added that when the great quantities of zooplankton living in the pelagic waters die, they fall in the deep layers where they enrich the waters in mineral salts and in gas. This niche is occupied by the small sardines *Limnothrissa miodon* and *Stolothrissa tanganyikae*, and the cyprinid *Engraulicypris minutus*, by *Aplocheilichthys* spp. and *Engraulicypris* spp. in the Lakes Mobutu Sese Seko (Albert) and Victoria, and finally by *Alestes baremose* JOANNIS in most of the soudanian waters (Beadle 1974).

In Lake Kivu none of these species was present. Echosoundings made during the exploration mission of 1952–1953 and fishing done by means of explosives did not give and positive results in the pelagic waters.

According to the studies of Degens *et al.* (ex Beadle 1974) and Janash (quoted by Frank *et al.* 1977), it appears that the primary production (240 g $C/m^2/y$ to 540 g $C/m^2/y$ of gross photosynthesis) is similar in magnitude to that of other African lakes of the rift.

For zooplankton, the volume collected per unit of surface is only slightly inferior to Lake Edward (Verbeke 1957a). The same author also writes that the 'living' layer of water does not exceed 75 m of depth. The abundance of pelagic plankton and the absence of predators are the main factors explaining the success of the introduction of *L. miodon* into Lake Kivu.

Materials and methods

The limnological and biological sampling programme was limited to the Bay of Gisenyi in the northern part of the lake, and some adjacent bays. Two open water zones were distinguished: the littoral zone, defined as all water overlying depths of 0–60 m, and the pelagic zone, for all waters deeper than 60 m. Clupeid samples were taken from the artisanal catches at the Fishing Centre and their stomachs were dissected out in 70% alcohol for later analysis.

Bimonthly water samples were taken in 1 l glass bottles from littoral and pelagic sampling stations. Oxygen was measured on the site with a Digital Oxygen meter Oxi Digi 550. Temperature (in °C) and Secchi disk transparency (in m) were also recorded. The same day, the water samples were analysed with a HACH Environmental Laboratory DR-EL/1 for $N\text{-}NO_3$, $P\text{-}PO_4$ and pH. Plankton samples were regularly taken during October and November with a 40 μm plankton net from both

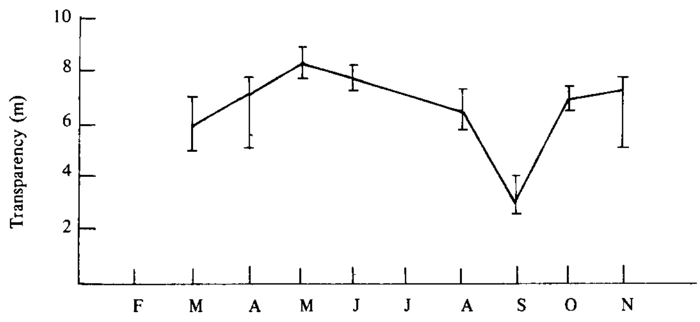

Fig. 2. Average transparency figures measured by Secchi disk in pelagic waters during 1980 (vertical lines represent minima and maxima).

littoral and pelagic sampling stations, and the movements of clupeid shoals were registered with a FURUNO echosounder FE-400. A beam with a transducer was attached to a wooden frame on an inflatable ZODIAC inflatable craft. The speed of the ZODIAC was standardised for all soundings on a throttle opening at 'slow' and for all echosoundings the Power Range Selector of the echo sounder was put on 1, Gain on 3 and Paper Speed on 3.

Results

Secchi disk readings were used as a measure for plankton density in the pelagic sampling stations. It is realised that, especially in the littoral stations, some bias could occur due to the presence of organic particles. The transparency figures during 1980 at pelagic sampling stations are presented in Fig. 2. An absolute minimum was reached during September, which indicated a plankton bloom during this period.

Verbeke (1957a) also reported a similar increase of the biomass of plankton during the windy period of August–September. This increase presumably followed an intensification of photosynthetic production, caused by the stirring up of the lower, nutrient rich water at the end of the dry season (Fig. 3).

During October and November plankton samples were taken from littoral and pelagic sample stations in the Bay of Gisenyi. These were analysed and cumulative counts were made per station up to 1000 specimens. Colonies, such as *Microcystis* sp. were treated in terms of their percentage occurrence. Although this gives only an indication of their relative importance in terms of biomass, it illustrates their relative abundance. Table 1 summarises the relative abundance of different groups of organisms in the samples.

In both littoral and pelagic samples, Copepoda and Cyanophyta combined, accounted for more than 50% of the abundance. In the littoral samples Copepoda were relatively less abundant, Rotatoria

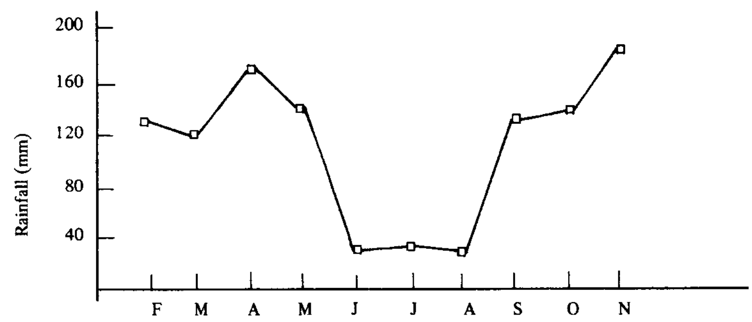

Fig. 3. Monthly rainfall figures in the Gisenyi region during 1980 (data from Meteorological Station, Gisenyi Airport).

Table 1. Relative abundance of different groups of organisms in littoral and pelagic samples (%).

Date (1980)	Littoral			Pelagic			
	23/10	04/11	25/11	09/10	23/10	05/11	25/11
Cladocera	–	1	0.5	3	8	4	–
Copepoda	15	32	10	43	64	74	17
Rotatoria	50	16	12	9	9	4	10
Ciliata	–	–	–	–	–	–	5
Cyanophyta	35	41	68	44	15	17	67
Chlorophyta	–	10	5	1	4	1	1
Chrysophyta	–	–	4.5	–	–	–	–

more abundant than in pelagic samples. The predominant Copepod species was *Tropocyclops confinis* (Kiefer). Less abundant were *Thermocyclops consimilis* (Kiefer) and *Mesocyclops* (non *leuckarti* (Claus)) (determined by Dr. I. van de Velde, Laboratory for Morphology and Taxonomy, University of Ghent, Belgium).

Cyanophyta were almost exclusively represented by *Microcystis viridis;* only on 25/11 was a bloom of *Anabaena flos aquae* observed in a littoral sample. Cladocera, like *Diaphanosoma excisum* and *Moina micrura* were encountered in low numbers, mainly in pelagic samples.

The species composition of the Copepoda is similar to that observed during a Belgian expedition of 1952–54 (Verbeke 1957a). During this period *Tropocyclops confinis* was always very abundant in samples originating from the northern part of the lake, while *Thermocyclops consimilis* and *Mesocyclops* (non *leuckarti*) were less abundant. By comparing these findings with the results of the present sampling programme it can be concluded that the introduction of *Limnothrissa* has not significantly changed the species composition of the Copepoda biomass in the northern part of the lake. No conclusion can be drawn so far concerning possible changes in the relative abundance and species composition of other groups of organisms.

The vertical distribution of plankton in the pelagic zones of the Bay of Gisenyi was measured on different occasions by sampling at 10, 20, 40 and 60 m depth. The spectrometric turbidity test of the HACH DR-EL/1 indicated that more than 80% of the plankton biomass was concentrated in the 5–20 m layer, between 8.00 and 11.00 hours. These findings are similar to those of Hecky *et al.* (1977) in Lake Tanganyika, who found that below 20 m the phytoplankton biomass was negligible throughout the day. This situation persisted throughout the year; only at the end of the dry season was plankton dispersed over deeper layers by strong winds.

Analyses of the results of chemical/physical sampling support previous findings concerning the seasonality of plankton abundance in the lake. NO_3-N and PO_4-P especially showed peaks of 3.5 and 3.0 ppm respectively at the pelagic sampling stations during September/October. pH varied between 8.2 and 8.7, which corresponds with the high concentrations of calcium bicarbonate observed by several authors (quoted by Beadle 1974). Oxygen values ranged between 6.5 and 7.7 mg/l (92–109% saturation when corrected for altitude); no peak values were observed. A maximum temperature of 25.5 °C was registered during the dry season, in July, while a mimimum of 24.0 °C occurred during the monsoon period in November.

The diet of the different length classes of *Limnothrissa* was studied by analysing stomach contents under stereo and high power microscopes. Clupeid samples were grouped by length classes and according to the location of the catch. In the shallow marginal parts of the lake, juveniles of 10–35 mm could be sampled with a dipnet. Two length classes, 85–110 mm and 30–70 mm were always encountered in the littoral and inshore catches, while true pelagic catches throughout the year contained length classes of 65–90 mm and 85–110 mm. Large clupeids of 100–150 mm were mainly caught by gillnets near the lake margins.

The stomachs of 269 clupeids from different length classes were dissected out and examined. The results are summarised in Table 2.

The main food item of the larger clupeids (>100 mm), were juvenile clupeids of 10–30 mm.

Table 2. The food of different length classes of *Limnothrissa* in Lake Kivu.

Date of sampling	Length class	Total number investigated	Stomach contents[a,b]	
6/3, 24/3, 21/5, 22/5, 9/6, 8/7	>100 mm (inshore)	51	Juvenile clupeids	41
			Other	10
12/6, 13/6, 17/6, 19/6, 8/7	85–110 mm (inshore)	106	Chronomids	53
			Juvenile clupeids	30
			Copepoda/Microc.	12
			Terrestrial ins.	10
			Trichoptera	6
			Brewery waste	6
			Indeterminable	13
14/8, 6/10, 17/10	85–110 mm 65– 90 mm (pelagic)	51	Copepoda	47
			Microcystis	34
			Nauplli	3
			Indeterminable	4
15/7, 4/9, 18/9, 18/10	30– 70 mm (inshore)	31	Copepoda	21
			Microcystis sp.	8
			Rotatoria	4
			Chrysophyta	15
			Nauplli	2
			Small insect larvae	4
			Indeterminable	1
10/9, 4/11	10– 35 mm (littoral)	30	Copepoda	17
			Chyrsophyta	55
			Rotatoria	7
			Ciliata	1

[a] Figures following food items for length classes >30 mm represent the number of stomachs in which such food was recorded. Because in some cases several food items were encountered in a stomach, total numbers of food items do not exactly correspond with the number of stomachs investigated.

[b] For the length class of 10–35 mm, per sample stomach contents were mixed (10 individuals) because stomachs are too small for individual analyses. Figures following food items here represent the percentage of the food comprised by the specified item in the pooled samples.

The main food items of clupeids from the length classes 85–110 mm and 65–90 mm, obtained from the pelagic catches, were Copepoda and Cyanophyta. The fractions and species composition were similar to those observed in the pelagic samples. Cochrane (1978) and Begg (1974) also concluded that pelagic *Limnothrissa* in Lake Kariba had copepods and cladocerans as their main food item. Copepods, however, were not as abundant as in Lake Kivu. One of the previous length classes (85–110 mm) also occurred in the littoral catches, and the stomach examinations revealed, besides copepods and *Microcystis*, a relative large fraction of chironomid pupae and juvenile clupeids.

The chironomids had been devoured in the final stage of pupation, as they rose to the surface. *Microchironomus* sp. was the most frequently observed but also *Procladius* sp., *Cladotanytarsus* sp., *Kiefferulus* sp. and some Tanypodinae were identified (determined by ir. A. Klink, Agricultural University, Wageningen, Netherlands). These findings correspond with those of Lays (1979) who studied *Limnothrissa* in Lake Kivu. In their stomachs he encountered mainly insect larvae, but also juvenile clupeids. Also in Lake Tanganyika littoral bound food habits of *Limnothrissa* were observed. Chêné (1975) reported *Limnothrissa* from Kanyosha, with stomachs filled with atyid prawns which, he concluded, were an important food source. According to Matthes (1968) and Roest (1978) the diet of *Limnothrissa* in Lake Tanganyika is more diversified than that of *Stolothrissa*. *Stolothrissa* mainly ate cyclopoid and calanoid copepods, while *Limnothrissa* also consumed atyid prawns, insect larvae and juvenile clupeids.

Stomach analyses of the smaller length class (30–70 mm), which comprises the majority of the artisanal catches of the littoral region, showed besides Copepoda and Cyanophyta a significant fraction of Rotatoria, which corresponded to the species composition of littoral plankton samples. Some incidental change in diet could be observed. A sample in July contained a large number of epiphytic Chrysophyta such as *Navicula* sp., *Synedra* sp. In other samples from September and October almost no Chrysophyta were encountered. There seemed to be a correlation between the presence of Chrysophyta and the occurrence of strong winds. Finally the length class of 10–35 mm (young juveniles), observed only in the very shallow margins of the lake, always had in their stomachs, besides small Copepoda, large amounts of Chrysophyta like *Surirella* sp. and *Navicula* sp., while Rotatoria and Dinoflagellates, like *Gymnodinium* sp., were also present. Also, Chêné (1975) reported juvenile clupeids in Lake Tanganyika with stomachs containing Diatoms like *Cymbella, Navicula, Synedra, Surirella* and *Nitzchia,* and Dinophycees like *Gymnodinium.*

The results of an experiment to gather information about the periodicity of feeding of pelagic *Limnothrissa* and the digestion rate are summarised in Table 3. *Limnothrissa* was sampled throughout the night with regular intervals and the stomachs were examined. Those stomachs which still had a determinable amount of food were classified as 'full', while all others were 'not full'.

The percentage of 'full' stomachs was highest after sunset and decreased gradually during the night. Obviously no feeding took place during the night and shortly before sunrise all food was digested.

Continuous diurnal and nocturnal echosoundings, following a transect in the Bay of Gisenyi, contributed to a better picture of the feeding habits of *Limnothrissa* in Lake Kivu.

In the early morning and late afternoon the clupeids rise and concentrate in a layer of 0–10 m depth (Fig. 4). Especially during the late afternoon, from 17.00 hours they are seen in the littoral zone, making short jumps at the water surface. In the pelagic waters the rising movement of clupeids in the late afternoon corresponds with their feeding on pelagic plankton which is present in the layer of 0–20 m. At 18.30 hours feeding probably diminishes and they 'sink' to an average depth of 20 m at 20.00 hours. This 'sinking' continues and at 21.00 hours they are dispersed over a broad zone at an average depth of 25 m where they remain throughout the night (Fig. 5). After 05.00 hours, at sunrise, they move again to the upper layer. Given the high percentage of empty stomachs, feeding probably starts again. Later in the morning they spread over a wide vertical depth range and form shoals (Fig. 7).

The shoals remain spread over this wide depth range until approximately 14.00 hours, after which they always rise and show a tendency to concentrate in one layer (Fig. 8). From 17.00 hours they concentrate again in the upper layer and feeding starts again. On several occasions (30/7 and 1/7) it was observed that the nocturnal distribution differs somewhat during the full moon. Whilst outside the full moon period the clupeids stay at an average

Table 3. Percentages of *Limnothrissa* with full stomachs, encountered during different hours of the night in pelagic samples of 13/8–14/8.

Sample no.	Hour	Size of sample	% with full stomach
1	22.10	50	64
2	21.30	35	63
3	22.40	36	35
4	24.30	38	13
5	03.00	41	12
6	06.00	54	4

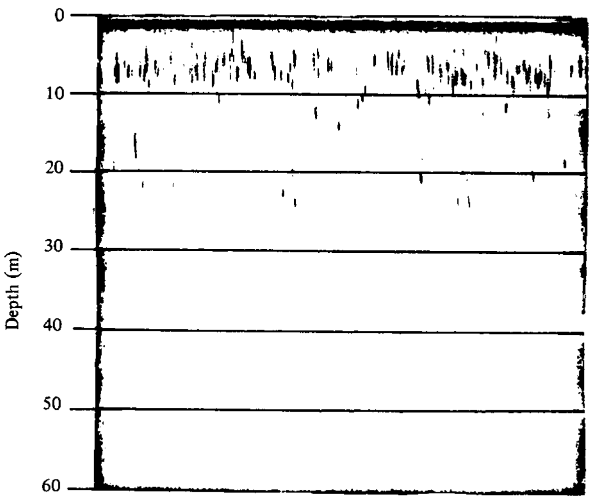

Fig. 4. Typical distribution of *Limnothrissa* in the early morning and the late afternoon; they concentrate in a layer between 0 and 10 m. (echogram 14/8, 6.30–7.00 hours)

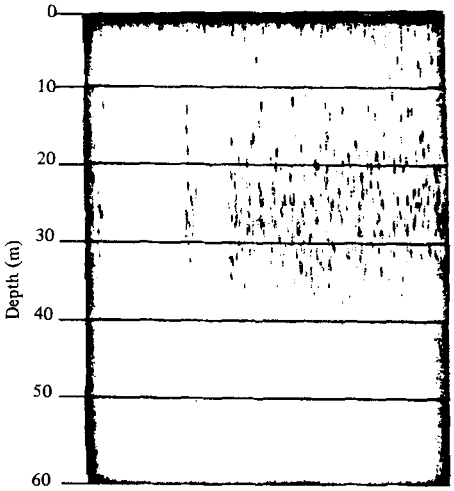

Fig. 5. Typical distribution pattern of *Limnothrissa* outside full moon period; they remain dispersed over a layer with an average depth range of 25 m. (echogram 13/8–14/8, 23.00–23.30 hours)

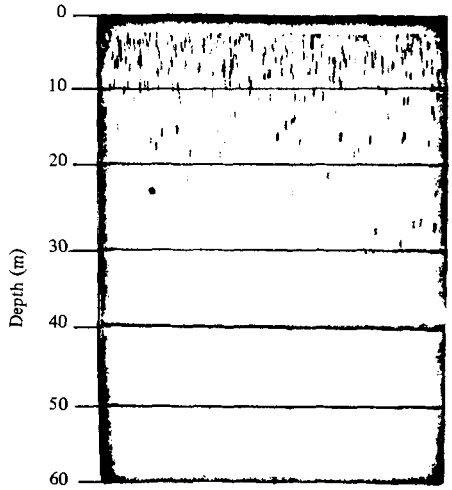

Fig. 6. Typical distribution pattern of *Limnothrissa* during full moon period; they remain dispersed over a layer with an average depth range of 10 m. (echogram 30/6–1/7, 23.00–23.30 hours)

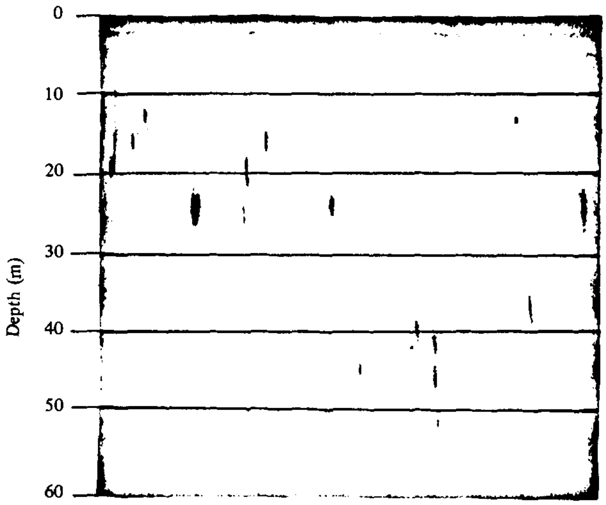

Fig. 7. Distribution pattern of *Limnothrissa* before noon; shoals of *Limnothrissa* are spread over a wide layer with an average depth range of 30 m. (echogram 17/9, 11.30–12.00 hours).

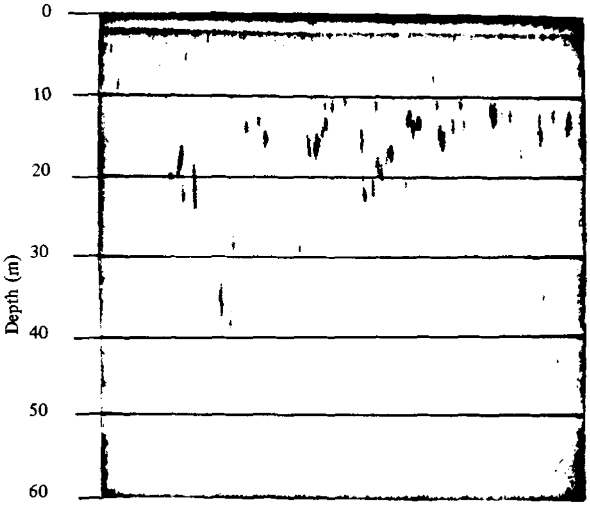

Fig. 8. Distribution pattern of *Limnothrissa* aftrer noon; shoals of *Limnothrissa* concentrate in a narrow layer with an average depth range of 22 m. (echogram 17/9, 14.30–15.00 hours)

depth of 20 m, during full moon they were observed at an average depth of 10 m (Figs. 5, 6). This is similar to findings in Lake Kariba, where clupeids were spread over a continuous layer between 7 and 20 m during the night (Balon 1974). Mann *et al.* (1973) found an average nocturnal depth of 26 m in Lake Tanganyika. During daytime in Lake Tanganyika compact shoals of clupeids were observed at an average depth of 17.6 m. In Lake Kariba the depth of shoals during daytime was 10–18 m.

Summary and conclusions

Measurement of transparency in Lake Kivu, by Secchi disk, confirmed the presence of a major plankton bloom during August–September. This increase in plankton density was presumably caused by rising winds at the end of the dry season, stirring up the lower nutrient rich water layers of the lake. The relative abundance of different groups of planktonic organisms differed in the littoral and pelagic regions. In the littoral plankton samples Copepoda were less, Rotatoria more abundant than in pelagic regions. The dominating copepod in all samples was *Tropocyclops confinis* (Kiefer). Comparison of the present results with those obtained during a Belgian expedition in 1954 shows that the successful introduction of the freshwater clupeid *Limnothrissa miodon* in Lake Kivu during 1958–1960 has not influenced the species composition of Copepoda in the northern part of the lake.

These Copepoda, together with the blue green algae *Microcystis virides,* form the major part of the pelagic planktonic biomass. The position of these Copepoda in the trophic system is not yet known for Lake Kivu.

Limnothrissa is not a strict planktonophagic species in Lake Kivu. Its diet is adapted to its life cycle and inshore/offshore migration patterns.

As well as plankton, chironomid pupae and terrestrial insects are important food items for clupeids in the littoral region. The species composition of the plankton in the stomachs of pelagic clupeids was always identical to that of pelagic plankton samples. The same is true of juvenile clupeids, living at the shallow margins of the lake.

Nocturnal and diurnal echosoundings and periodic observations of stomach contents supported the hypothesis that *Limnothrissa* feeds in the late afternoon and digests its food during the night, while a second feeding/digestion cycle starts in the early morning at sunrise.

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