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SUMMARY

Zooplankton spatial and temporal distribution and productivity have been studied in two small meromictic Western Uganda Crater Lakes, Lake Nkuruba and Lake Nyahirya (fig. 1-5, tab. 1). Water chemistry is characterized by the volcanic quality of the ground, and by fertilization through wash-out from the crater walls which frequently are burned and partially cultivated with bananas and cassava (tab. 2).

The phytoplankton of both lakes is mainly composed of small blue-green and green algae like *Anabaenopsis* spp. and *Cosmarium* spp. Diatoms (*Nitzschia* spp.) play a role only in Lake Nyahirya where *Aphanizomenon* gracile is also common. Chlorophyll a in the epilimnion varies between 4 and 12 µg/l in Lake Nkuruba and between less than 1 and 17 µg/l in Lake Nyahyria (fig. 6).

The zooplankton consists mainly of cyclopoids. Rotifers were numerous and at times abundant. Differences between the lakes were mainly quantitative. Most common cyclopoids of both lakes are *Thermocylops* spp., especially *Thermocyclops macracanthus*. *Mesocyclops aequatorialis* was found only in Lake Nkuruba. The cladoceran *Ceriodaphnia cornuta* appeared in minor numbers in both lakes, the cladoceran *Moina micrura* only in Lake Nyahirya.

Temporal and vertical distribution of the zooplankton was studied during a period of 16 months. Crustacean horizontal distribution (fig. 8,9) and daily vertical migration (fig. 10-12) were studied occasionally. Spatio-temporal development of the cyclopoid populations was found to be very irregular (fig. 13-21, 24-28). Average numbers of *Thermocyclops* were about 80 ind/l in Lake Nkuruba and about 220 ind/l in Lake Nyahirya, nauplii not included. Females were slightly more than males. Clutch sizes (fig. 14, 25) were significantly different in the *Thermocyclops* of the two lakes. *Mesocyclops*, as well as the cladocerans *Ceriodaphnia* and *Moina* (fig. 22, 29) were around 4 ind/l each. The living space of the cyclopoids was generally limited to the upper 10 m in Lake Nyahirya while copepodites spread deeper into the deoxygenated layers in Lake Nkuruba. Experimentally, it could be shown that *Mesocyclops* is able to survive hypoxic and anoxic conditions considerably longer than does *Tropocyclops tenellus* (tab. 5).

Mesocyclops aequatorialis and *Tropocyclops tenellus* could be cultivated in the laboratory. *Mesocyclops*, in culture, could produce up to 7 egg clutches, and *Tropocyclops* up to 6. Embryonic and post-embryonic development times were also determined experimentally (fig. 38-41). Under given temperature conditions in the lakes, about 17 generations per year could be theoretically possible.

The dry weight of *Thermocyclops* increased from less than 1 µg in the nauplii to a mean weight of 3.9 µg in adult females. Adult *Mesocyclops* females

reached a mean weight of 6.2 µg (tab. 6). Calculated population birth rates, instantaneous growth rates, and death rates (fig. 33, 35, 37) show small fluctuations throughout the investigation period in both lakes. Average *Thermocyclops* biomass (fig. 47, 49) was three times higher in Lake Nyahirya than in Lake Nkuruba, but daily P/B ratios of 0.13 were practically identical. *Mesocyclops'* biomass was about 10 % of *Thermocyclops* biomass (fig. 48) in Lake Nkuruba, but daily P/B ratio 0.4 was considerably higher. Comparable values of *Thermocyclops hyalinus* from Lake George are 0.08. Annual averages of crustacean P/B values from temperate and from cold lakes are much lower. However, cyclopoid development times and P/B ratios at similar temperatures are not really different from species of temperate lakes. Thus, adaptation to high temperatures is not evident in the tropical species, which rather seem to be unable to reproduce successfully at low temperatures.

The zooplankton as well as the phytoplankton of the Crater lakes are characterized by very small species. This may partly be caused by short turnover times and nutrient/food limitation, but also points to high grazing and predation pressure at different trophic levels. It seems that the bacterial loop plays an important role in the food web of these lakes.

Changes of dry and rainy periods appear as main determining factors for plankton development as they do in large tropical lakes. However, interannual patterns can show large variations. Also small changes of temperature and turbulence can initiate cascading events in the plankton. Such changes are frequent and unpredictable. This explains irregularities, and lack of similarity even between closely neighbouring lakes.

1. Introduction

Ecological information on Western Uganda Crater Lakes is still limited to a few studies. BEADLE (1963, 1981) described the meromictic stratification patterns and the inhabitation of zooplankton in the virtually oxygen free hypolimnion of Lake Nkugute. MELACK (1978) emphasized the striking limnological diversity of 16 of the lakes he surveyed. A recent limnological survey of some of the lakes of the region including Nkuruba and Nyahirya was given by KIZITO *et al.* (1993). Short-time studies of other African tropical crater lakes were reported by GREEN (1972, 1973, 1986). Succession patterns in phytoplankton are well known from numerous African lakes, though mainly large lakes (TALLING 1986). Succession in planktonic rotifer species has recently been correlated with rapid changes in physical environments and rainfall (KIZITO & NAUWERCK 1995, 1996). The lakes seem to follow patterns known from large tropical lakes.

Information on fluctuations and production of crustacean zooplankton in tropical Africa is still limited to a few studies. Examples are Lake George (BURGIS 1971, 1973, BURGIS *et al.* 1973), Lake Naivasha (MAVUTI 1983, 1994), Lake Chad (GRAS & SAINT-JEAN 1983) and Lake Awasa (MENGESTOU & FERNANDO 1991). These studies point to qualitative continuity and weak quantitative fluctuations of zooplankton populations.

Studies of whole lake plankton horizontal distribution are still restricted (BURGIS *et al.* 1973) and those of zooplankton temporal and vertical distributions are lacking. Comparison can here be made only with temperate lakes (MODER 1986, EINSLE 1987, NAUWERCK 1993a, b) which relate the zooplankton distribution patterns to physical environments like temperature and dissolved oxygen concentrations. The framework of the investigation covers these two aspects and also productivity and production of the plankton.

Dissolved oxygen distribution in the lakes appears to direct the vertical distribution patterns of the plankton. Knowledge of the diurnal migration (DVM) patterns of the zooplankters will provide answers to questions relating to adaptations to hypoxic conditions in the lakes. DVM-studies have only been done on large lakes in Central Africa that do not show permanent dissolved oxygen stratification (e.g. Lake Victoria, WORTHINGTON 1931; Lake Naivasha, MAVUTI 1992). Information on African crater lakes' zooplankton migration patterns (DVM) is lacking.

With continuous reproduction of the cyclopoids already reported by BURGIS (1974), cohorts of zooplankton species are difficult to trace in the lake samples. Data of laboratory egg and instar development time must be extrapolated to simulate lake situations. Also experiments had to be designed in the laboratory to determine the cyclopoid tolerance levels of anoxia and hypoxia.

In this paper, the importance of zooplankton as major primary consumers and converters of algal biomass into animal material consumable by fish will be assessed in the two crater lakes.

The study is divided into two parts: the first part deals mainly with plankton population dynamics of the two lakes and factors governing their time and space distributions. The second part deals with the cultivation of cyclopoid species from the Crater Lakes. The main objective of this study therefore, is to attempt to provide answers to questions relating to zooplankton (mainly cyclopoid copepods) life history, life strategies, survival and adaptations.

2. The lakes

The two crater lakes are located in Western Uganda, Kabarole District (formerly known as Toro District) along the eastern edge of the Western Great Rift Valley about 24 km east of the Ruwenzori Mountains (fig. 1 and 2). The altitude within the Kasenda cluster of crater lakes ranges from 1,300 to 1,400 m where they lie in crater kittles with steep walls. Most of the volcanic crater lakes in Western Uganda occupy maar (OLLIER 1967, cited from MELACK 1978) and are Maar Lakes (type 11, HUTCHINSON 1957). Lakes Nkuruba and Nyahirya' morphometry is shown by figure 3 and table 1.

Fig. 1. — Lake Nkuruba.

The lakes are equatorial in position, Lake Nkuruba 0°32" N and 30°18" and 30°20" E and Lake Nyahirya 0°30" and 30°17" S and 30°20" E. The surroundings of the crater lakes are relatively densely populated. Much of the land is cultivated with crops like banana, cassava, maize, tea, and is used for dairy farming. There exists a mosaic of vegetation types of forest, grassland, woodland, thickets and cultivation. The climate of the area could be described as warm and rainy. Mean annual rainfall recorded at the Makerere University, Biological Field Station Kibale, 15 km from Lake Nkuruba and 19 km from

Fig. 2. — Lake Nyahirya.

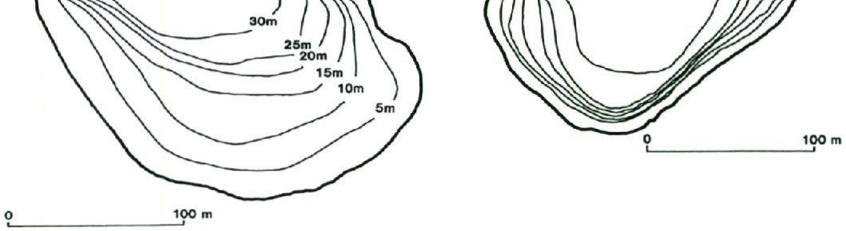


Fig. 3. — Lakes Nkuruba and Nyahirya morphometric maps.

Table 1

Morphometric features of Lake Nkuruba and Lake Nyahirya: surface area (Area), volume, maximum (Zm), mean depth and length of longest straight line on surface of water (l)

Lake	Area (ha)	Volume ($m^3 x 10^3$)	Zm (m)	Mean depth (m)	l (m)
Nkuruba	3.06	481	37	15.7	270
Nyahirya	2.65	996	84	37.52	202

Lake Nyahirya, between 1987 and 1991, has averaged 1,740 mm (range 1,607 - 1,864 mm). There are distinct wet and dry seasons which tend to be bimodal. May through August, and December through February tend to be drier than other months. The first rains of the year (March-April) are less severe than the September-November rains (CHAPMAN & LIEM, in press). The onset and duration of both dry and wet seasons show interannual variation.

The very steep embarkments of the lakes leave very little area for a littoral zone. The drainage area for each lake is not much more than the crater walls. Both lakes are lacking superficial inflow and outflow. Drainage by underground streams has been proposed for the lakes (KIZITO *et al.* 1993). In fact, water levels of the lakes showed little fluctuation during the study period. The air temperatures of this area are moderate and do not fluctuate much over the year. The minimum and maximum temperatures for Fort Portal are 12.7 and 25.5 °C (STRUHSAKER 1975).

Physical-chemical information is given in table 2. The two lakes are classified as freshwater, magnesium and calcium being the dominant cations. They are meromictic and permanently stratified. The depth of the oxycline shows vertical and temporal variations.

Table 2

Crater lakes chemistry March 1992 (after KIZITO *et al.* 1993)

Lake	Depth m	Temp. °C	O_2 mg l^{-1}	Ptot µg l^{-1}	NO_3N µg l^{-1}	Cond. µS cm^{-1}	F^- mg l^{-1}	Cl^- mg l^{-1}	SO_4^- mg l^{-1}	NA^+ mg l^{-1}	K^+ mg l^{-1}	Mg^{2+} mg l^{-1}	Ca^{2+} mg l^{-1}
Nkuruba	2	22.9	7.35	38.4	0	341	1.0	1.88	0.09	3.40	4.90	21.70	39.50
	15	22.1	0	42.6	0	343	1.0	1.92	0.11	3.65	5.00	21.50	38.85
Nyahirya	2	25.3	7.40	49.6	0	463	1.3	2.49	1.58	7.05	6.40	29.40	49.65
	15	21.1	0	162.5	0.3	511	1.6	2.83	2.58	7.10	6.15	30.00	57.50

The simplistic nature of the phytoplankton of the lakes has been pointed out. Dominants are small blue-green algae like *Anabaenopsis* spp. and *Cosmarium* spp. Diatoms (*Nitzschia* spp.) play a role only in Lake Nyahirya where *Aphanizomenon gracile* also was common (KIZITO *et al.* 1993). Further notes on phytoplankton composition are given by KIZITO (1995).

The rotifer plankton of the lakes has been treated by KIZITO *et al.* (1993) and by KIZITO & NAUWERCK (1995, 1996). It consists of species like *Keratella tropica*, several *Brachionus* spp., *Filinia opoliensis* and other common species. A specialty is *Hoarella brehmi*. Among crustaceans, *Thermocyclops macracanthus* KIEFER was most common. Even *Ceriodaphnia cornuta* RICHARD appeared in both lakes. *Moina micrura* KURZ and *Oncocypris* sp. were found only in Lake Nyahirya; *Mesocyclops aequatorialis* KIEFER and *Thermocyclops incisus* KIEFER only in Lake Nkuruba. In addition, along the shoreline *Macrocyclops albidus* JURINE was found in both lakes, and *Mesocyclops ogunus* ONABAMIRO and one *Eucyclops* sp. in Lake Nyahirya only.

The fish fauna of the two crater lakes is rather poor in diversity. It includes mainly introduced tilapine species. Species present in Lake Nkuruba are *Tilapia zillii* (GERVAIS), *Oreochromis leucostictus* (TREWAVAS) (very rare) and *Poecelia reticulata* PETERS. *Oreochromis leucosticus* is the only fish species that had been caught from Lake Nyahirya (CHAPMAN, pers. comm.).

3. Material and methods

3.1. SAMPLING

Sampling of the lakes started in early March 1992. It continued uninterrupted at biweekly intervals for 16 months until June 1993. Sampling was between 9.00 and 10.00 h. One sampling site was fixed at the centre of each lake. A raft and a rubber dinghy were respectively used for sampling. A Schindler-trap (5l) was used to collect water samples for quantitative determination of zooplankton.

3.1.1. Temperature, dissolved oxygen, and Secchi depth

Dissolved oxygen concentrations and temperature were measured with a portable YSI Oxygen Meter (Model 51B). Readings were taken from the lake surface (0 m) at intervals of 1 m down to 30 m deep. Water transparency was estimated with a secchi disc painted with black and white sectors.

3.1.2. Chlorophyll a and primary production

A known water volume (range from 100 milliliters to over a litre) from 2 m deep was filtered through glass fibre filters (0.1 μ) with the help of a portable hand pump. The glass fibre filter was then wrapped in a dry filter paper and marked with a pencil, kept dry and dark in a dessicator until laboratory analysis in Austria.

Primary production was measured on some occasions using the light and dark bottle method (GAARDER & GRAN 1927). The bottles were exposed at 0 m, 1 m, 2 m, 4 m, 6 m and 8 m deep. Incubation time was 6 hours (from 9.30 a.m. to 3.30 p.m.). Winklers Method was used to determine the dissolved oxygen concentrations in the initial, light and dark bottles.

3.1.3. Zooplankton temporal development

Water samples were obtained from surface to 24 m deep at 2 m intervals. Quantitative zooplankton samples were obtained by filtering 5 l water samples through a 63 μm sieve. Samples were preserved with 4 % formalin glycerine solution.

3.1.4. Zooplankton horizontal distribution

The lakes were sampled for horizontal zooplankton distribution from a fixed depth (3 m) around midday (11.00 - 15.30 h) on 12.02.1993 and 15.02.1993 for Nkuruba (29 sites) and Nyahirya (37 sites) respectively.

3.1.5. Zooplankton diel vertical migration (DVM)

The 24-hour diel vertical zooplankton migration sampling of the two lakes was conducted on 17/18.01.1993 (Nyahirya) and on 18/19.01.1993, 7/8.03.1994 (Nkuruba). The sampling times were fixed around 12.00, 18.00, 20.00, 0.00, 6.00, 8.00 and 12.00 h. A Schindler-trap 5 l was used to collect zooplankton samples. Measurements for dissolved oxygen and temperature were taken alongside.

3.2. ANALYSES

All analyses were carried out at the Institute of Limnology, Austrian Academy of Sciences, Mondsee.

3.2.1. Chlorophyll

The Ethanol (90 %) Extraction Method and ultrasonification were used to extract chlorophyll a. The extract was clarified by filtration through glass fibres. Extinction of the extract was measured spectrophotometrically (Beckman Model 34) at the maximum peak of chlorophyll a 665 nm and 750 nm which serves as a background measurement of turbidity.

3.2.2. Zooplankton counting

This was done with an inverted microscope on sedimented whole samples. During counting a distinction was made on the instar stages. The classification for cyclopoid-copepod was nauplii, copepodide I-III, copepodide IV-V, adult females and males. Copepodide instar stages and adults were identified following EINSLE (1971, 1989). In addition, the total number of eggs was counted. Clutch size was calculated as the mean number of eggs per female with intact egg sacs. The cladocerans *Moina micrura* and *Ceriodaphnia cornuta* were grouped into size classes, small, medium and large, and the total number of eggs for the species was counted. *Chaoborus* larvae were also counted. For Lake Nyahirya, the planktonic ostracod *Oncocypris* sp. was also quantified.

3.2.3. Dry weight

Two methods were used: a) length and weight measurements and use of length weight regressions; b) direct dry weight determination according to DUMONT *et al.* (1975).

Zooplankton preserved in 4 % formalin solution was used for dry weight estimations. After sorting out the species and size classes from the samples, they were measured (total length) with an eye-piece micrometer under an inverted microscope. The cyclopoids were measured from the anterior tip of the cephalothorax to the base of the furca rami and the cladocerans from the anterior tip to the base of the posterior spine. Numbers of animals were chosen so that each weighting would produce a minimum of 5 µg. Numbers of weighted specimens ranged between 1 and 15. The size classes were then transferred into small glass vials, washed with distilled water (1-2 hours) and put into preweighted (Mettler ME 22) small aluminium cups that had been oven-dried (2 hours at 110 °C). The cups containing anima were put in a dessicator in covered petridishes (BURGIS 1974).

The length/weight regression equation is

$$\ln W = \ln \alpha + B. \ln L$$

where W = individual weight, L = individual length and α and β are constants that vary from species to species. This equation was previously used by PERSSON & EKBOHM (1980).

The mass of eggs for cyclopoids (dry weight) was estimated from a mass/volume relationship 0.0037 µg/104 μm^3 (according to DUMONT *et al.* 1975), also used by MAIER (1994).

3.3. LABORATORY EXPERIMENTS

3.3.1. Zooplankton cultivation

Three cyclopoids were cultivated: *Mesocyclops aequatorialis*, *Tropocyclops tenellus*, and *Thermocyclops macracanthus*. *Mesocyclops aequatorialis* was collected from Lake Nkuruba, *Thermocyclops macracanthus* from Lake Nyahirya and *Tropocyclops tenellus* from another crater lake in the region, Nyantonde. The live zooplankters were transported in plastic bottles (1 litre) and thermos flasks (1 litre) to Austria. The three species were sorted out with the help of a wide-mouthed plastic pipette and were put in separate glass bottles containing filtered Lake Mondsee water. The animals were first fed on a chemostat green alga, *Monoraphidium minuta* (Culture Collection Göttingen) cultivated by H. Arndt by use of the modified culture medium CHU (1942). Filtered Lake Mondsee water (0.7 µm) was used as medium for the cultures.

Later, also flagellates *Chlamydomonas reinhardi* and *Cryptomonas* sp. (culture collection Göttingen) and rotifer *Brachionus rubens* (isolated by K.O. Rothaupt, Plön) and ciliate *Paramecium biaurelia* were included in the diet of the cyclopoids. Rotifer and protozoan food was particularly important for advanced copepodides stages of *Mesocyclops aequatorialis* because of its carnivorous feeding habits (BRANDL & FERNANDO 1975). The first month of cultivation was primarily devoted to mass cultivation of the cyclopoids and trial experiments of development times under laboratory temperature and light conditions. After some time, *Thermocyclops tenellus* and *Mesocyclops aequatorialis* became acclimatized to the laboratory rearing conditions, but the *Thermocyclops macracanthus* culture died out.

Thermocyclops tenellus was fed on a mixture of *Monoraphidium minuta* (3.5 x 10 cells/ml), *Chlamydomonas reinhardi, Cryptomonas* sp. and *Paramecium biaurelia.* For *Mesocylops aequatorialis, Brachionus rubens* was added to its diet. Excess feed was added daily. The medium was added daily for temperatures above 25 °C, and every other day for incubation temperatures below 20 °C.

3.3.2. Interclutch time and reproduction biology

The interclutch time, *i.e.* the time between hatching and the extrusion of the next egg sac, was determined in a separate series of experiments but under similar conditions of temperature, illumination and diet. The exercise requires more frequent observations of the egg-carrying females. A knowledge of the expected egg development time enables one to roughly approximate the hatching time. In the case of *Tropocyclops tenellus*, an observation time of 15 minutes to 1 hour was necessary in order to get more accurate results at all temperatures. In the 20 °C cultures a number of males and females were mated and reproduction biology studied. Eggs contained in successive clutches were counted and also the possible number of clutches produced by a breeding female.

3.3.3. Egg development

The two cyclopoid species *M. aequatorialis* and *T. tenellus* already acclimatized to cultivation conditions were used in the experiments. Late copepodide stages were incubated at different temperatures of 15, 20, 25, 30, 33 and 35 °C. The offspring of these that had acclimatized to the temperature conditions were used for the experiments. The Direct Observation Method (Elster 1954) was used to determine the egg development times. The adult female and male of the respective species were paired up in plastic petri dishes containing food medium. Frequent observations (3-17 hours) followed until egg sacs were extruded. The male was then removed leaving behind the female. Daily observations followed and at the expected time of hatching, hourly observations were made. The appearance of nauplii was taken to be the hatching time. The rearing petri dishes were housed in a thermostatistically controlled incubator, and the temperature was monitored daily. The animals were subjected to 12:12 hours light: dark photoperiod with illumination provided by four cooled white 36 W fluorescent tubes. The rearing petri dishes were shaded from direct light with paper. The dishes were gently swirled 3-6 times daily to resuspend particles.

3.3.4. Post-embryonic development

The nauplii that hatched from the egg development time experiments were used to determine the naupliar development times.

5 - 7 nauplii were grouped together in the food suspension. Daily observations of nauplii followed until they moulted to copepodides. The copepodides were singly placed in petri dishes containing media. Thanks to the individual rearing of copepodides it was possible to determine the development times of males and females in retrospect. The light microscope was used to distinguish the adult instars. This was possible by counting both the thoracic and abdominal segments and also by a close inspection of the genital segments (EINSLE 1993).

To describe the relationship between the duration of both embryonic and post-embryonic development times, the following regression equation was used:

$$\ln D = \ln a + b (\ln T)^2$$

where D = development time, T = temperature, a and b are constants. This equation was previously used by BOTTRELL (1975), VIJVERBERG (1980) and MAIER (1989).

3.3.5. Calculation of population dynamic parameters and secondary production

PALOHEIMO'S (1974) instantaneous birth rate formula used by HART (1987) was chosen for the estimation of birth rate b´

$$b' = \ln (E/N + I/D)$$

where b´ is the instantaneous birth rate, E = egg density, N = post-embryo density and D = the embryonic development time at 23 °C, approximate temperature of the epilimnion of the two lakes.

Successive population estimates (N_t, N_o) were used to calculate the instantaneous rate of population change r´ over sampling interval (t) using the familiar exponential equation

$$r' = (\ln Nt - \ln No)/t$$

The instantaneous death rate (d´) was estimated as the difference between instantaneous birth rate and rate of population change

$$d' = b' - r'$$

In computing the production, a population without emigration or immigration and with a continuous reproduction was assumed. The turnover rate method derived from birth rate (BURGIS 1971, HART 1987) was used.

The *per capita* finite birth rate (b) is given by

$$ß = E/N.D$$

where E, N and D have already been defined above.

The production estimate is given by

$$P = ß.B$$

where B is the standing stock biomass. This method allows the estimation of production especially in a situation where it is difficult to trace cohorts in a population.

The egg development time of *Thermocyclops* spp. at 23 °C was estimated by fitting egg development data of *Thermocyclops hyalinus* (BURGIS 1970) to the regression equation [2].

In computation of *Thermocyclops* spp. generation time, naupliar and copepodide development times of *Thermocyclops oblongatus* at 22.0 ± 2.4 °C MAVUTI (1994) were used.

3.3.6. Dissolved oxygen level tolerance

Laboratory reared *T. tenellus* and *M. aequatorialis* were sorted under a stereo microscope (Wild 400). Complete deoxygenation of a medium supplied with abundant food was ensured by having positive pressure of nitrogen in a small aquarium where incubation tubes containing the cyclopoid copepods were put. In case of *M. aequatorialis*, it was necessary to keep only one animal, in order to avoid cannibalism in the incubation tube. For *T. tenellus*, ten of the copepodides were put into each tube. For details of the apparatus set up, see GEIGER (1990). Hypoxic levels of dissolved oxygen (0.1 and 0.5 mg/l) were obtained by the use of a gas mixing pump (DIGMIX, SA 2713, WÖSTHOFF), delivering a constant mixture of nitrogen and room air to the water bath (GNAIGER 1985). The vessels were first incubated for 12 hours at full oxygen saturation before adjustment to the required levels of concentrations (GEIGER 1990). The experiments were conducted in total darkness at 22 ± 0.1 °C. This is a temperature close to that of the crater lakes' epilimnetic waters where the cyclopoids originally were collected. A total of 42 tubes containing cyclopoids were incubated from the start of the experiment. At regular intervals of between 4 and 24 hours, a set of six tubes were drawn and the number of live, dead and missing after allowing a 6 hours' recovery time was recorded. In the control experiments, the animals were incubated similarly but the dissolved oxygen level was maintained at saturation.

4. Results

4.1. TEMPERATURE, DISSOLVED OXYGEN, SECCHI DEPTH AND PRECIPITATION

4.1.1. Lake Nkuruba

Figure 4 shows Lake Nkuruba's temperature and oxygen development together with precipitation and secchi depth. Temporal and spatial variations in temperature are very small. Mean temperature in the upper 10 m fluctuates between 22 °C and 24 °C, and in the hypolimnion between 21 °C and 22 °C. The water tends to be warmer during the rainy season than during the dry season. Sudden changes between mixing and stratification can occur within a range of 1 or 2 degrees in the upper 10 m or even deeper. Apparent mixing with respect to temperature is observed mostly during the dry months, August in the first year and during January and June in the following year. The oxygenated zone is limited to the upper 8 - 10 m. It extends to greater depths in August in the first year and in June of the following year. Maximum values of dissolved oxygen up to 8.5 mg l^{-1} (109 % saturation) are repeatedly found near the surface. Dissolved oxygen increases with decreasing temperature. This tendency is shown in the first year in September, November and in June of the following year. The secchi depths are higher during the rainy season than the dry season. The annual precipitation for 1992/93 shows two marked rainy seasons, March to May, and September to November. The dry season extends from May to August, and from December to early March.

4.1.2. Lake Nyahirya

Figure 5 shows temperature and oxygen development in Lake Nyahirya together with secchi depth and rainfall data. Temperature shows very small temporal and vertical variations. Mean temperature varies between 22 °C and 23 °C in the upper 10 m. The warmest surface temperature is about 24 °C. Hypolimnion temperature varies between 20 °C and 22 °C. Sudden changes between mixing and stratification can take place within a range of one or two degrees in the upper 10 m zone or deeper. The oxygenated zone is mainly limited to 8-10 metres. Beyond a depth of 6 metres, the dissolved oxygen concentration is below 2 mg l^{-1}. Maximum values of 7.8 mg l^{-1} (90 % saturation) are repeatedly found near the surface. These are interrupted by longer or shorter periods with low concentrations, minimum 3.9 mg l^{-1} up to the surface. The regular changes of dissolved oxygen are correlated with temperature. The secchi depths tend to be lower during the dry season than during the rainy season.

The feature common to both lakes is the presence of a persistent thermocline despite the presence in the lakes of very small temperature gradients. There is generally more dissolved oxygen in Lake Nkuruba than in Lake Nyahirya.

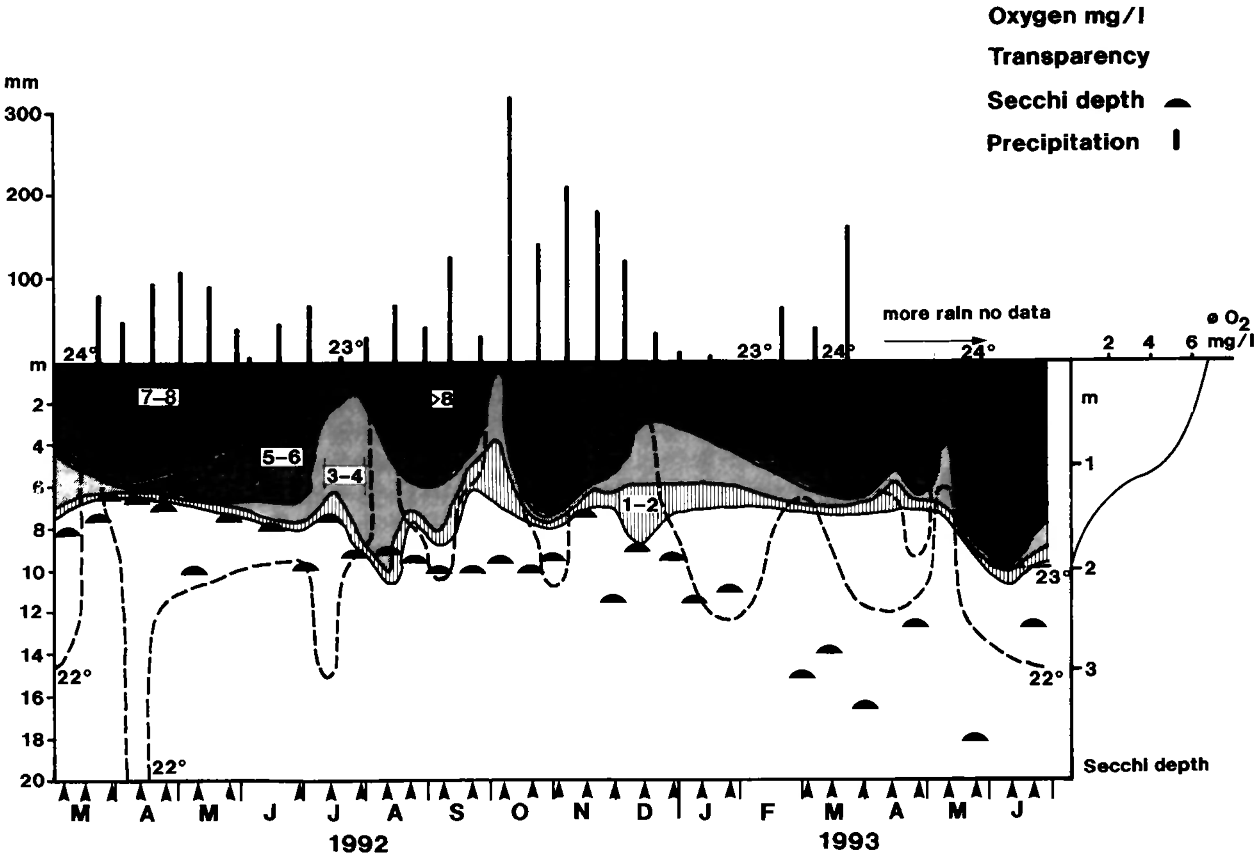


Fig. 4. — Lake Nkuruba 1992/1993, temperature, oxygen, transparence and precipitation.

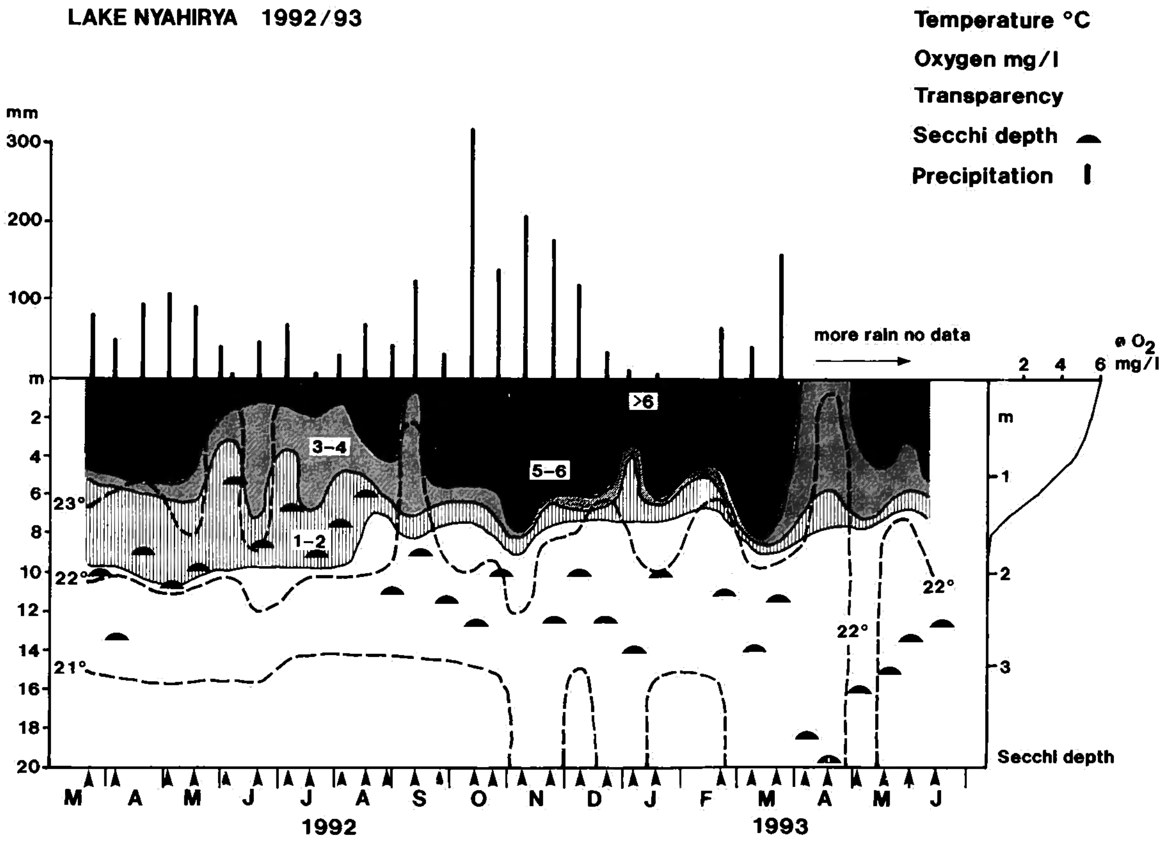


Fig. 5. — Lake Nyahirya 1992/1993, temperature, oxygen, transparence and precipitation.

4.2. CHLOROPHYLL (CHLA) AND PRIMARY PRODUCTION

Figure 6 shows the phytoplankton biomass (Chla) development for the two lakes. A relatively higher phytoplankton biomass occurs in Lake Nkuruba than in Lake Nyahirya. In Lake Nkuruba a first peak, 12.8 μg l^{-1}, occurs in the first year during late March. This is followed by a decrease reaching a minimum value of 3.3 μg l^{-1} in October. Another peak of 13.0 μg l^{-1} appears in November of the same year.

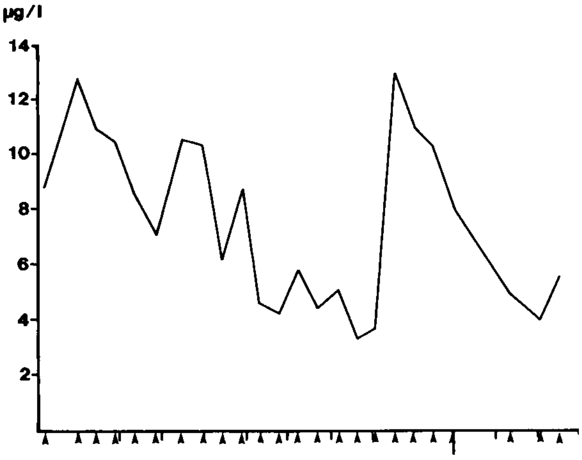


Fig. 6. — a) Lake Nkuruba 1992/1993, 2 m depth, Chlorophyll a.

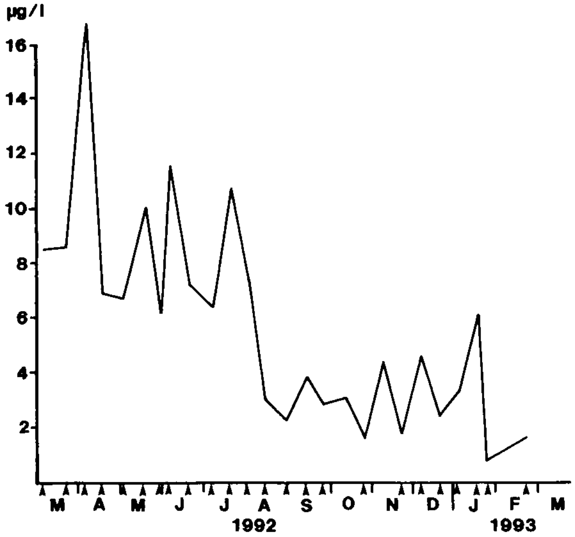


Fig. 6. — b) Lake Nyahirya 1992/1993, 2 m depth, Chlorophyll a.

Lake Nyahirya's maximum peak of 16.8 µg l^{-1} Chla occurs at the beginning of the investigation in April. There is a sharp chlorophyll decrease in July-August from August of the first year to the end of the investigation. The lowest concentration of 0.8 µg l^{-1} is observed during late January the second year.

There is a general decrease in chlorophyll concentrations in both lakes from the beginning of the investigation to the end of October of the same year. A rise in chlorophyll a concentration is observed for both lakes thereafter and is more marked in the case of Lake Nkuruba than Lake Nyahirya.

Figure 7 shows primary production determinations for Lake Nkuruba on three occasions. The production appears to be low when compared to that of shallow Lake George (GANF & VINER 1973). Limitation of light penetration and nitrogenous compounds seem to be the explanation.Very little assimilation occurs beyond 6 m deep. An increase in respiration rate occurs rather sharply below 6 m deep.

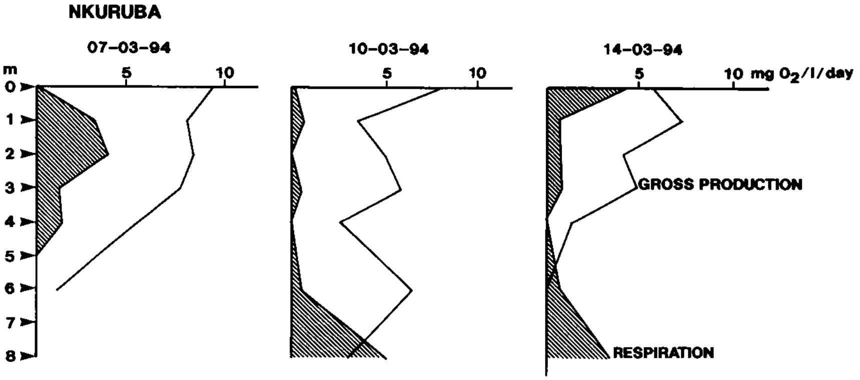


Fig. 7. — Lake Nkuruba primary production determinations on three dates.

4.3. ZOOPLANKTON DISTRIBUTION PATTERNS

4.3.1. Horizontal distribution

Crustacean zooplankton horizontal distribution patterns at a fixed depth (3 m) are shown in figures 8 and 9.

In Lake Nkuruba (fig. 8), the cyclopoids are more to be found in the south and southwest of the lake. They seem to avoid much of the shoreline. A relatively high correlation exists between *Mesocyclops* and *Thermocyclops* distribution (r = 0.66, n = 26). Also the abundances of the nauplii and *Thermocyclops* are positively correlated (r = 0.41, n = 26). *Ceriodaphnia cornuta* is concentrated at a distance from the lake shore in the north western part of the lake. Low densities do not allow conclusions about its distribution pattern, but features from Lake Nyahirya indicate that they may have been transported from preferred nearshore areas towards the open water by a persistently blowing wind which also swept the cyclopoids from the central lake to the southeastern shore.

Lake Nyahirya's crustacean horizontal distribution pattern is shown in figure 9. The adult *Thermocyclops* and copepodide stages show very clearly an avoidance of the shoreline. Their maximum density is found northwest of the middle of the lake. *Ceriodaphnia*, in contrast, is concentrated along the shore, while *Moina* avoids both the lake centre and the shoreline, and shows a ring-shaped distribution between the *Cyclops* and the *Ceriodaphnia* regions.

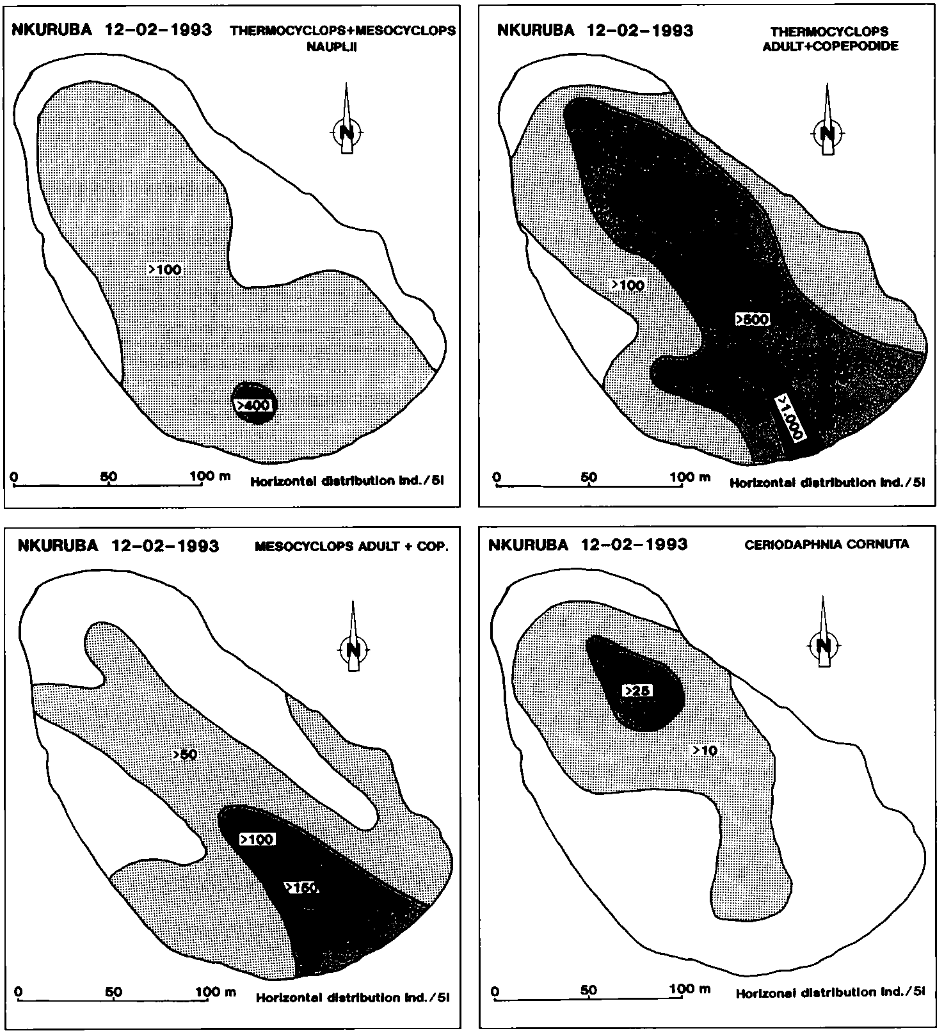


Fig. 8. — Lake Nkuruba 12-02-1993, fixed depth (3 m) crustacean zooplankton horizontal distribution patterns.

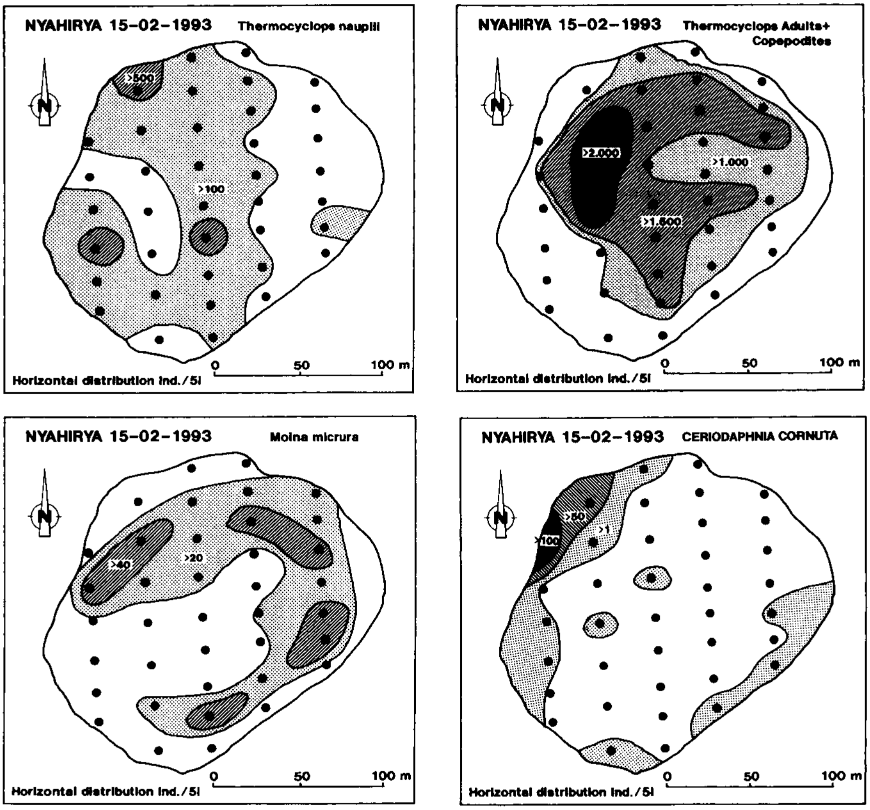


Fig. 9. — Lake Nyahirya 12-02-1993, fixed depth (3 m) crustacean zooplankton horizontal distribution patterns.

4.3.2. Diel vertical migration

Figure 10 shows the diel vertical migration (DVM) patterns of some of the crustaceans of Lake Nkuruba on 18/19.01.1993 and 7/8.03.1994. The adults and copepodide stages of *Thermocyclops* and *Mesocyclops* show a descent of their populations at sunset from 2 m peaks to 6 m depths midnight peaks. The various populations ascend thereafter. To a lesser extent, the same pattern seems to be true for the nauplii of the two.

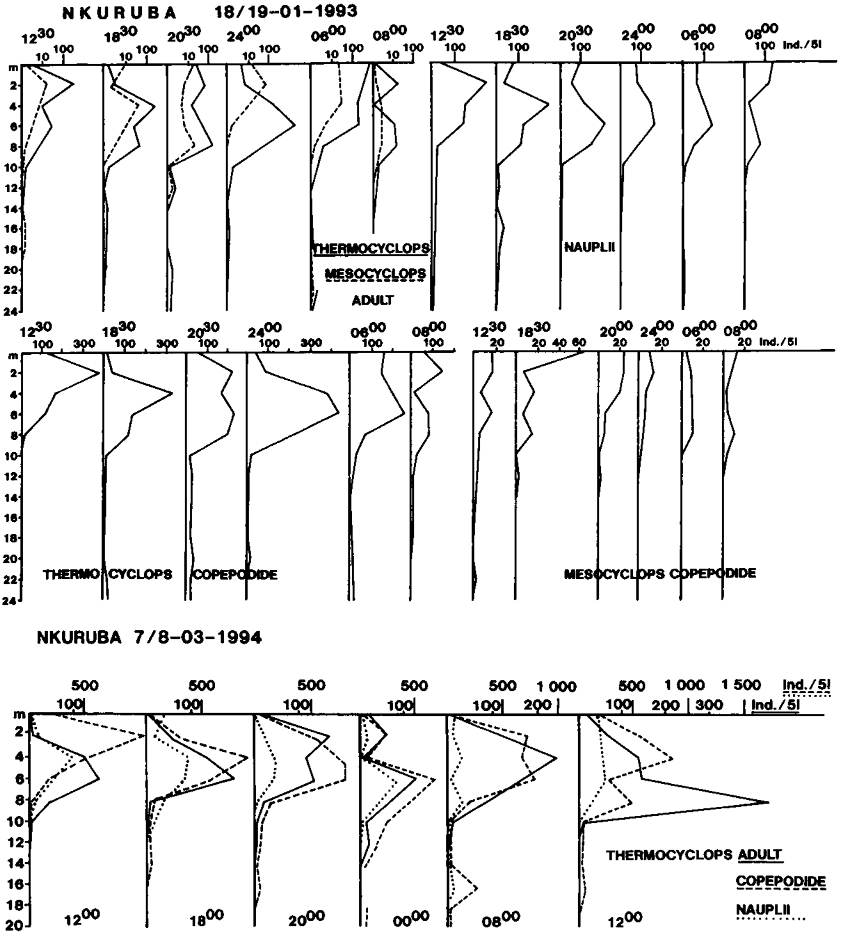


Fig. 10. — Lake Nkuruba 18/19-01-1993 and 7/8-03-1994, crustacean zooplankton diel vertical migration.

Figure 11 shows the diel vertical migration (DVM) patterns of some of Lake Nyahirya zooplankton on 17/18.01.1993. *Thermocyclops macracanthus* nauplii do not appear to migrate significantly, but seem to be mainly bound to depths around 8 m. Cyclopoid nauplii preference of metalimnic depth has also been demonstrated by NAUWERCK (1993a,b). The adults and copepodides behave in the same way as in Lake Nkuruba, descending in the evening and ascending in the morning.

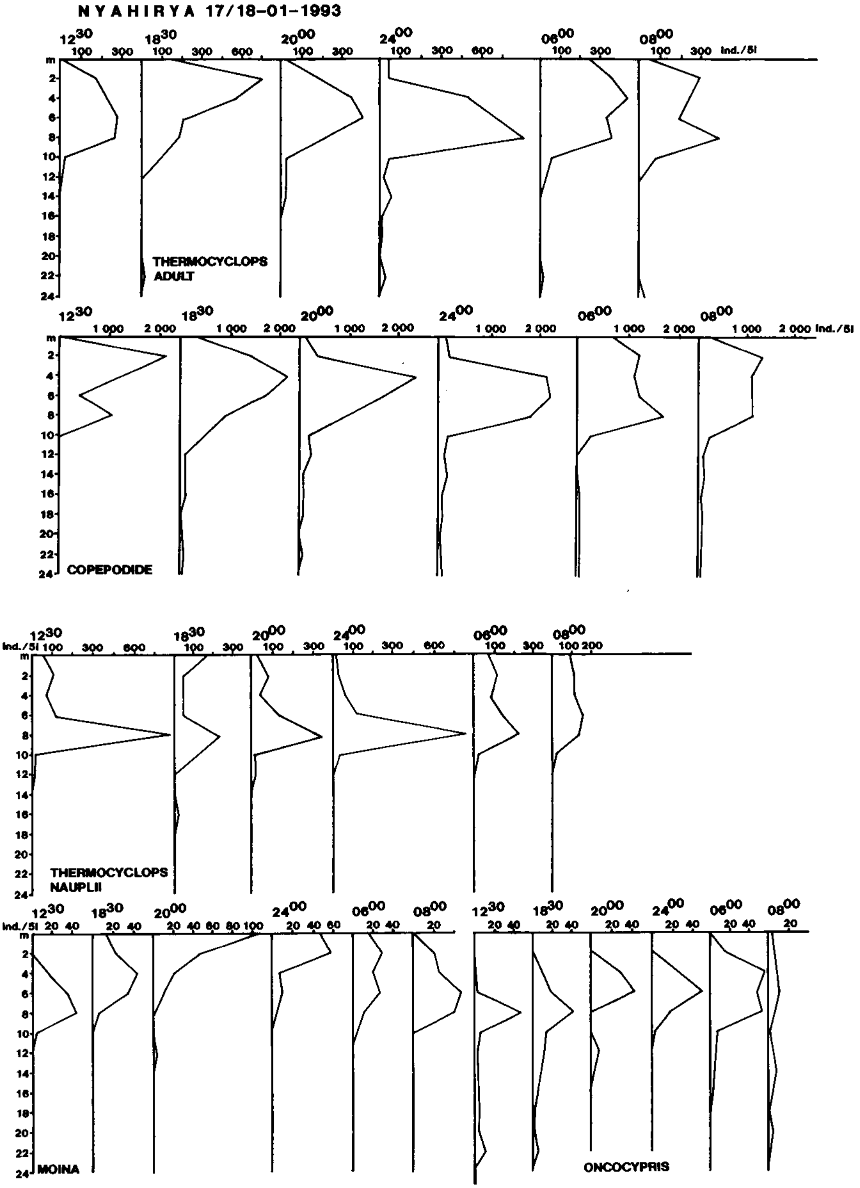


Fig. 11. — Lake Nyahirya 17/18-01-1993, crustacean zooplankton diel vertical migration.

The opposite migration pattern is displayed by *Moina micrura* which shows an ascent of its population after sunset and a descent after midnight. *Oncocypris*, more or less, follows the same pattern.

Chaoborus larvae in both lakes (fig. 12) show the greatest amplitude of migration (from *ca.* 18 m - 24 m deep at midday to near lake surface in the late evening). The population descends again therafter and by 8.00 the following morning, much of its population is below 8 m deep.

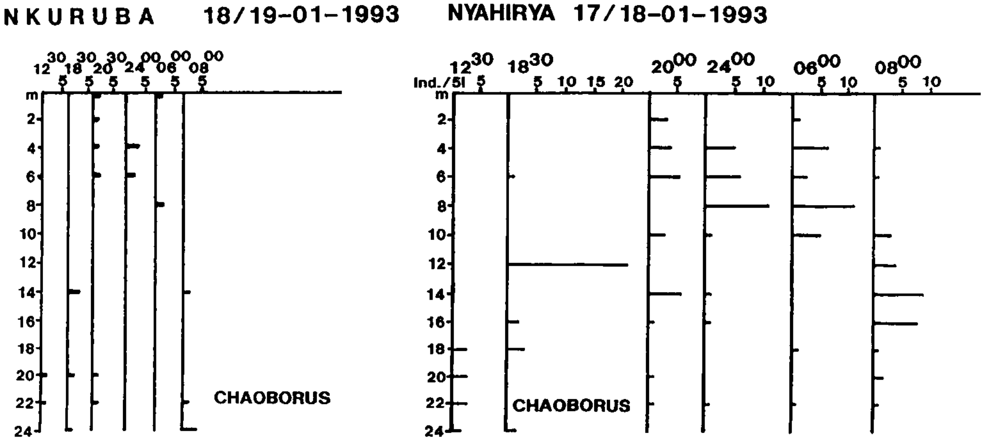


Fig. 12. — a) Lake Nkuruba 18/19-01-1993, *Chaoborus* larva diel vertical migration; b) Lake Nyahirya 17/18-01-1993, *Chaoborus* larva diel vertical migration.

The majority of the zooplankton, apart from *Chaoborus* larvae and *Moina,* do not migrate very significantly. However, reversed migration (downward movement during night) seems to be characteristic of the *Thermocyclops* of the two lakes. Most zooplankters, apart from *Chaoborus* and *Oncocypris,* avoid the anoxic hypolimnion during their diurnal migrations. However, nauplii stay in rather oxygen-limited layers.

4.3.3. Zooplankton temporal and vertical distribution

4.3.3.1. Lake Nkuruba

Figures 13-22 show the temporal and vertical distribution patterns of Lake Nkuruba crustacean zooplankton throughout the investigation period. Most numerous and always present in reasonable numbers is the *Thermocyclops* complex (T. *macracanthus* and T. *incisus*).

At the beginning of the investigation, both adults and younger instars show abundance peaks in the anoxic hypolimnion (Kizito *et al.* 1993). Adult population peaks appear in the first year in March-April, then fluctuate until the end of

September. Low population densities are observed for both sexes from October in the first year to January of the second year. Their populations then build up once more to form peaks in March the following year. The fluctuation pattern for both sexes is very much the same. The highest abundances for both sexes reach some 10 ind.l^{-1} (50 ind.5 l^{-1}) at a depth of 2-8 m. Egg production by females is continuous throughout the investigation period. Pronounced peaks occur in the first year in March, late July and September, and the following year during March and June. The highest egg density of 63 eggs.l^{-1} (314 eggs.5 l^{-1}) occurs in the first year in July (dry season) and the lowest density of 9 eggs.l^{-1} in April (rainy season) in the following year. The clutch size varies between 14.9 in March and 10.0 in August in the first year.

The separation of the three coexisting cyclopoid species nauplii was not possible. However, *M. aequatorialis* makes up to approximately 10 % or slightly less of the total counts. The nauplii are found in rather low densities throughout the period of investigation. This is likely to be an underestimation of their numbers resulting from the filtering efficiency of the mesh size used. Nauplii abundance peaks appear repeatedly in the first year in March, June to beginning of August, September and December, and in the following year in March, May and June. Low population densities are observed in the first year during April-May, August, October, November and February, end of April and end of May the second year. The highest abundances reach some 50 ind.l^{-1} at a depth of 0-10 m. During early September and October in the first year, population abundances greater than 5 ind.l^{-1} are found beyond 14 m deep.

Thermocyclops copepodides stages I-III are present throughout the investigation period. Their abundance peaks appear repeatedly during the larger part of the first year. The lowest population densities are met during the wet months in April and November in the first year and the highest peaks appear at the end of the dry seasons in August and December. The highest abundances reach some 50 ind.l^{-1} at a depth of 2-10 m.

Thermocyclops copepodide stages IV-V are present throughout the investigation period. Population abundance peaks appear in the first year in March and May with a sharp incision between September and October peaks. The population falls to low levels during November and December. It rises again in March and April in the following year. The highest abundances reach some 50 ind.l^{-1} at a depth of 2-6 m.

Mesocyclops aequatorialis occurs sparsely in the lake plankton. Adult females and males are present much of the time except during late November (females) and late November to mid-December. Moderate population peaks occur for females in the first year in March, July-August and February to March in the following year. Male abundance peaks occur in the first year in April-May, August and September, and during February-April in the following year. The highest abundance peaks for both sexes reach about 1 ind.l^{-1} at a depth of

2-12 m. The clutch size varies much from a minimum value of 12.0 in May to a maximum value of 20.7 during September in the first year of investigation.

Egg peaks appear in the first year during late June, late July and late September. Another peak appears during February-March the following year. The highest abundance reaches some 10 ind. l^{-1} at a depth of 2-12 m.

M. *aequatorialis* copepodide stages are present throughout the investigation period showing peaks mostly during the dry season from July to early November in the first year and January to March in the second year. Minimum densities occur during the rainy season from March to June and October to December in the first year and March to the end of the investigation in the second year. The highest abundance peaks reach some 10 ind. l^{-1} at a depth of 2-12 m.

Ceriodaphnia cornuta occurs in very low numbers in the first year with minor peaks in May and September. The highest abundance peaks appear the following year during March-April and May. The highest abundances reach some 50 ind. l^{-1} at a depth of 2-6 m. *C. cornuta* is virtually absent from the lake plankton from the beginning of November in the first year to February of the following year.

Figure 23 shows Lake Nkuruba average relative depths distribution of the zooplankton under investigation. The zooplankton is mainly distributed in the oxygenated epilimnion between the surface and 8 m deep. Part of the population stretches into the hypoxic/anoxic hypolimnion. The cyclopoid nauplii are mainly distributed from the surface to 8 m deep with maximum densities occurring at a depth of 4 m. The most preferred depth is between 2 m and 6 m. The copepodides stages I-III and IV-V live closer to the surface. The median point copepodide stages IV-V is slightly above that of copepodide stages I-III.

Thermocyclops spp. adult males and females show similar depth distribution patterns avoiding the surface and also having their maximum densities distributed at a depth of 6 m which borders the hypoxic waters of the lake. *Mesocyclops aequatorialis* copepodide stages I-V live closer to the surface with a maximum at a depth of 2 m. The adults of *M. aequatorialis* (males and females) have similar depth distribution patterns only that the median point of females is above that of the males.

The *Ceriodaphnia cornuta* distribution is located in the middle of the epilimnetic zone with a maximum density concentration at a depth of 4 m.

Chaoborus larvae show a maximum distribution peak in the hypoxic/anoxic hypolimnion with only little of its population stretching into the epilimnion.

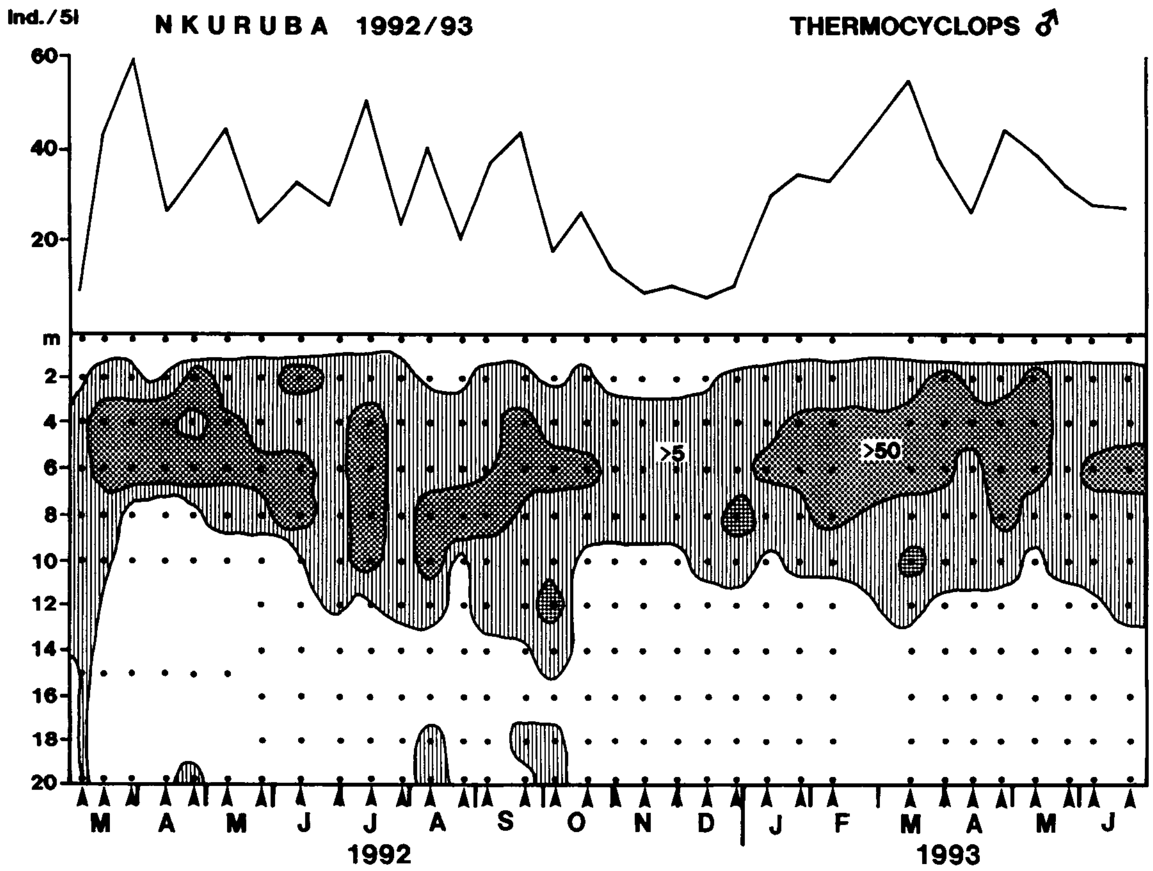


Fig. 13. — Lake Nkuruba 1992/1993, *Thermocyclops spp.* male spatio-temporal distribution and 0 - 10 m average density.

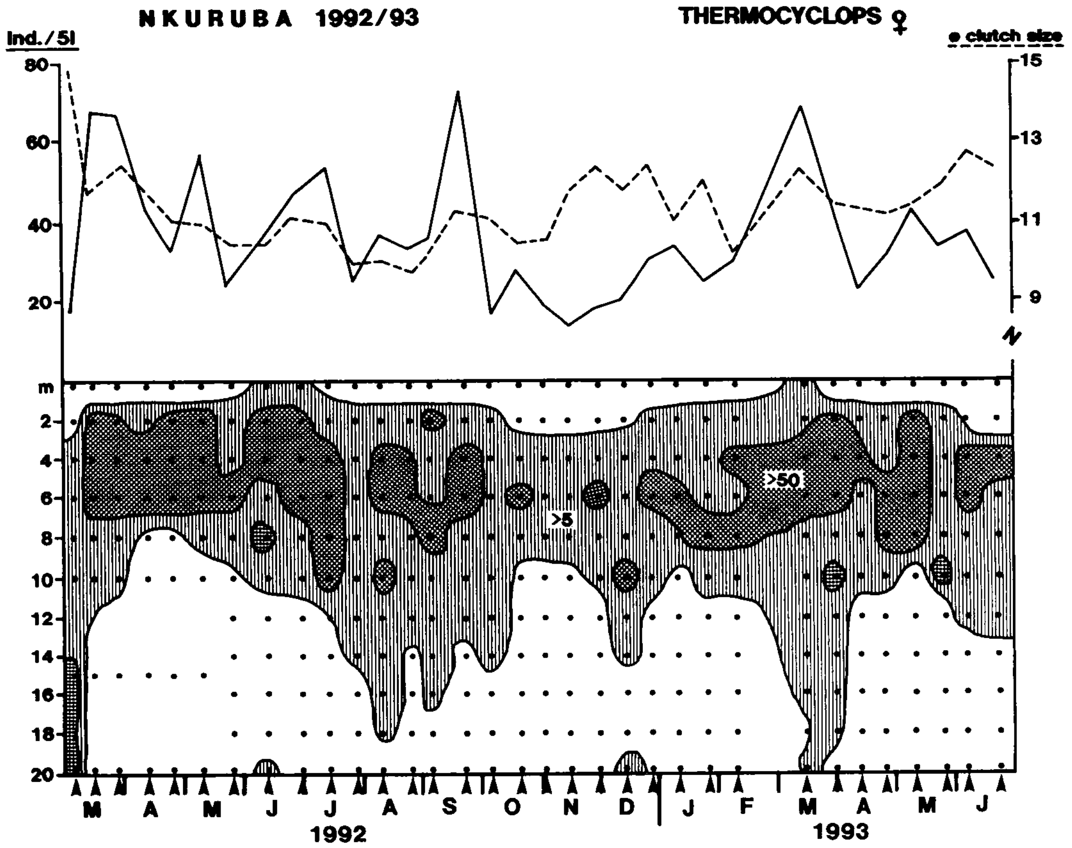


Fig. 14. — Lake Nkuruba 1992/1993, *Thermocyclops spp.* female spatio-temporal distribution, clutch size and 0 - 10 m average density.

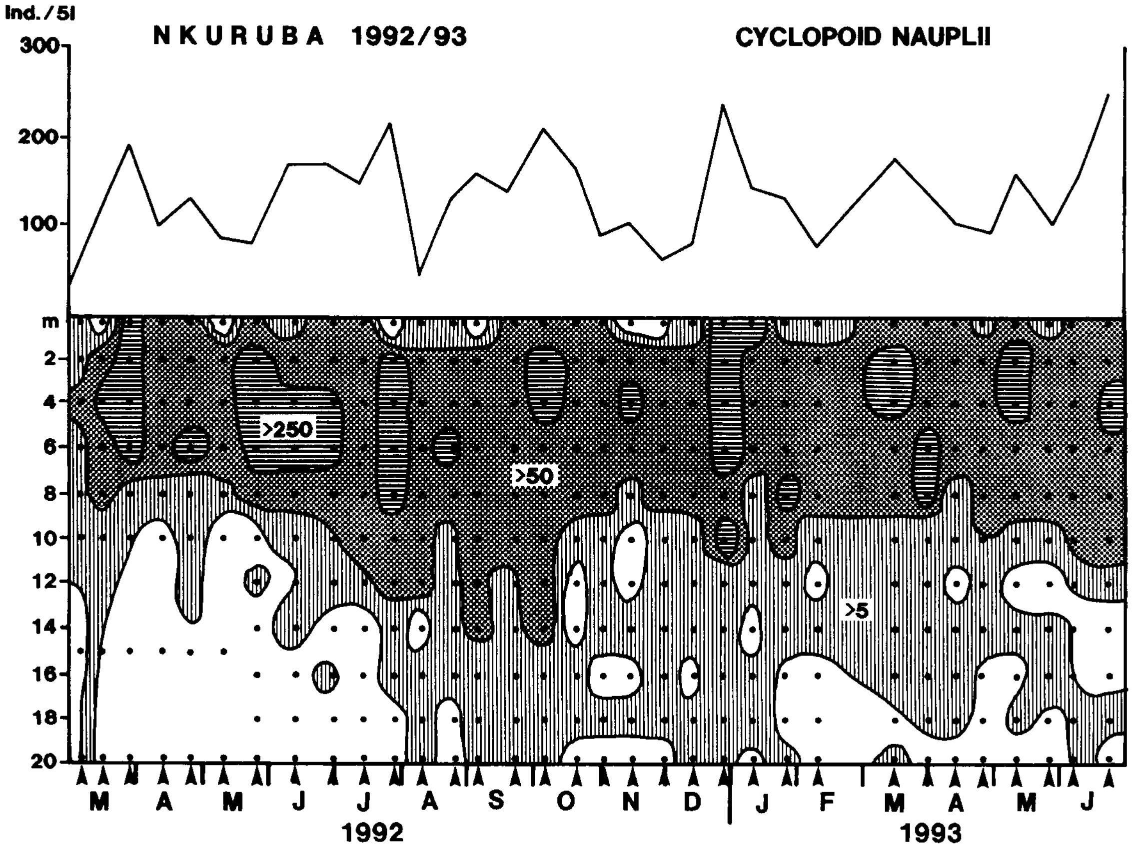


Fig. 15. — Lake Nkuruba 1992/1993, *Thermocyclops spp.* and *Mesocyclops aequatorialis* nauplii spatio-temporal distribution and 0 - 10 m average density.

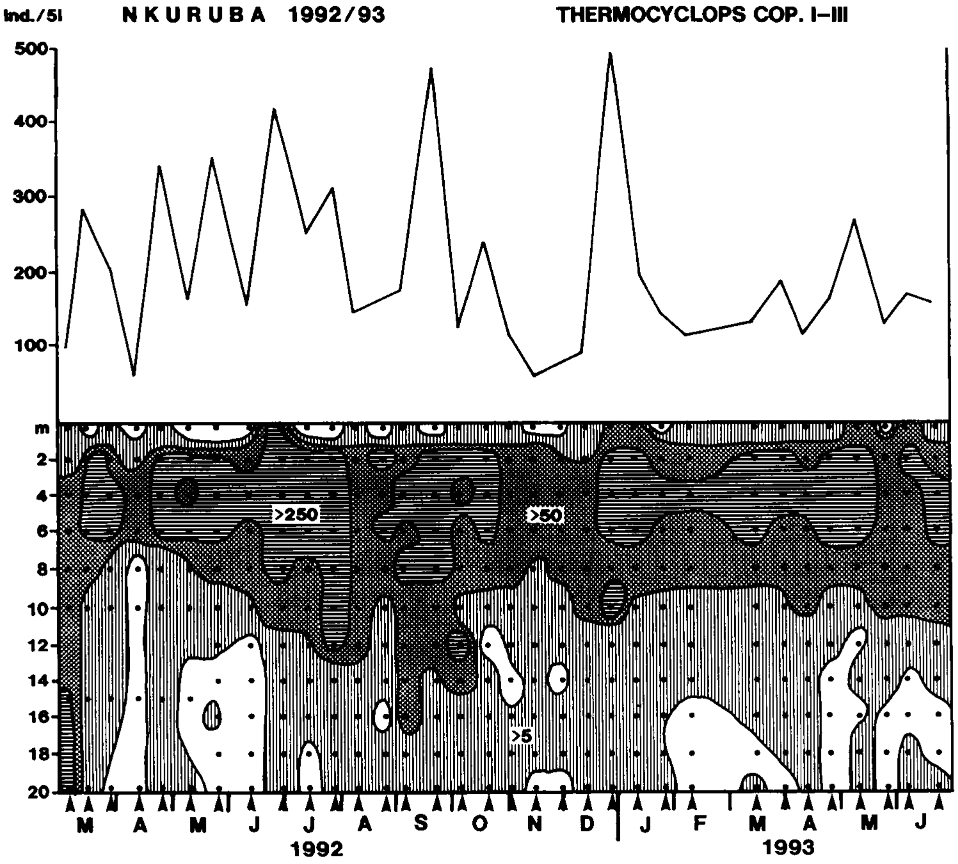


Fig. 16. — Lake Nkuruba 1992/1993, *Thermocylops spp.* copepodite I-III stages spatio-temporal distribution and 0 - 10 m average density.

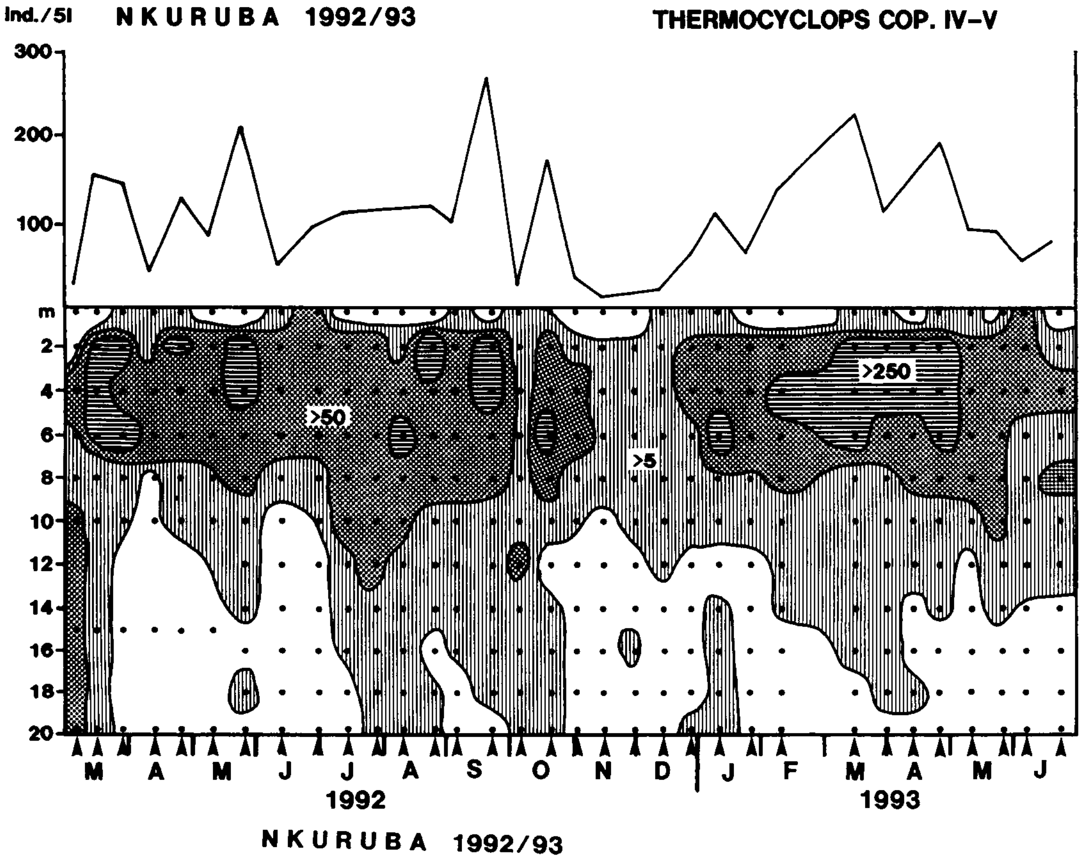


Fig. 17. — Lake Nkuruba 1992/1993, *Thermocyclops spp.* copepodite IV-V stages spatio-temporal distribution and 0 - 10 m average density.

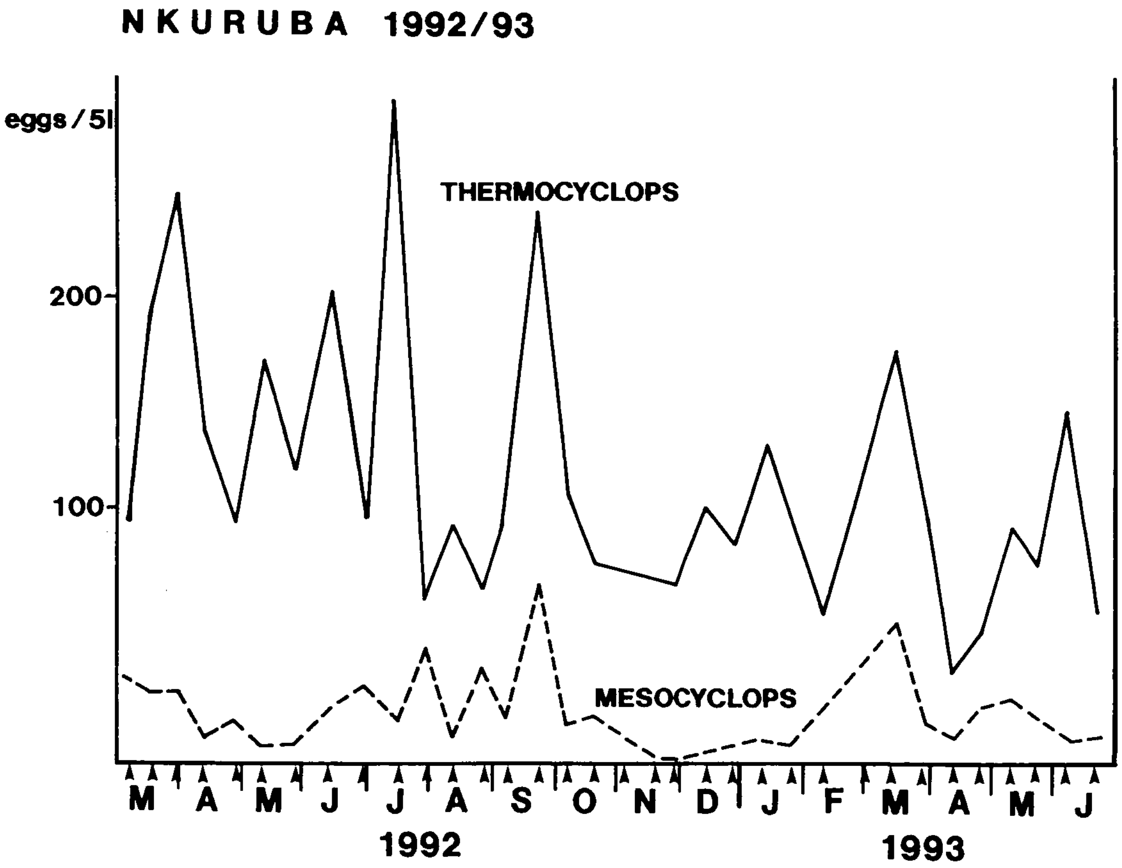


Fig. 18. — Lake Nkuruba *Thermocyclops spp.* and *Mesocyclops aequatorialis* 0 - 10 m eggs average egg density.

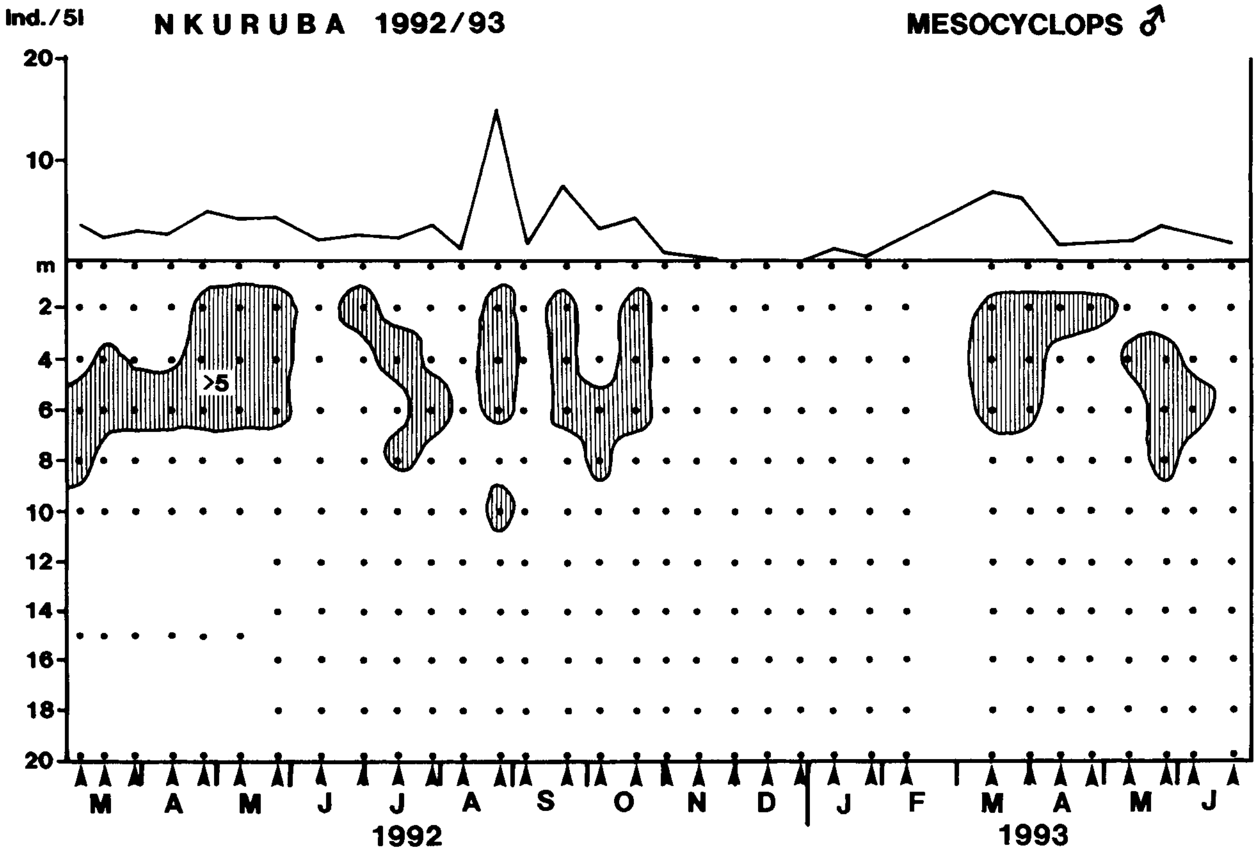


Fig. 19. — Lake Nkuruba 1992/1993, *Mesocyclops aequatorialis* males spatio-temporal distribution and 0 - 10 m average density.

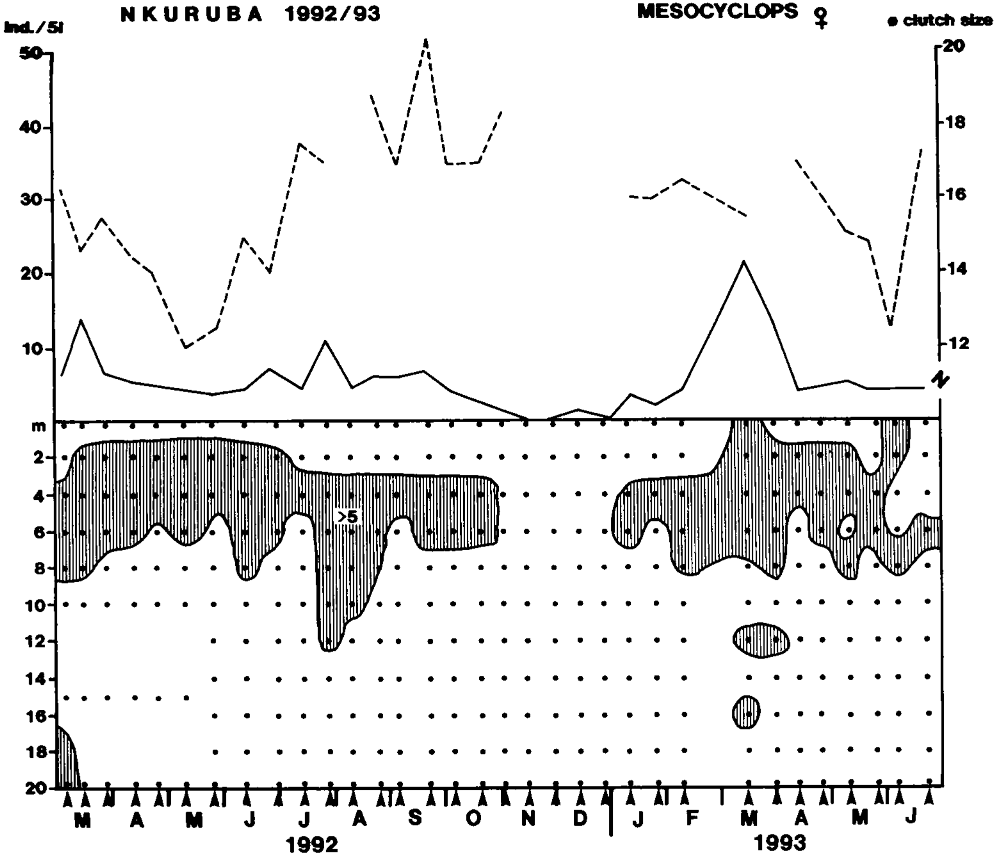


Fig. 20. — Lake Nkuruba 1992/1993, *Mesocyclops aequatorialis* female spatio-temporal distribution, clutch size and 0 - 10 m average density.

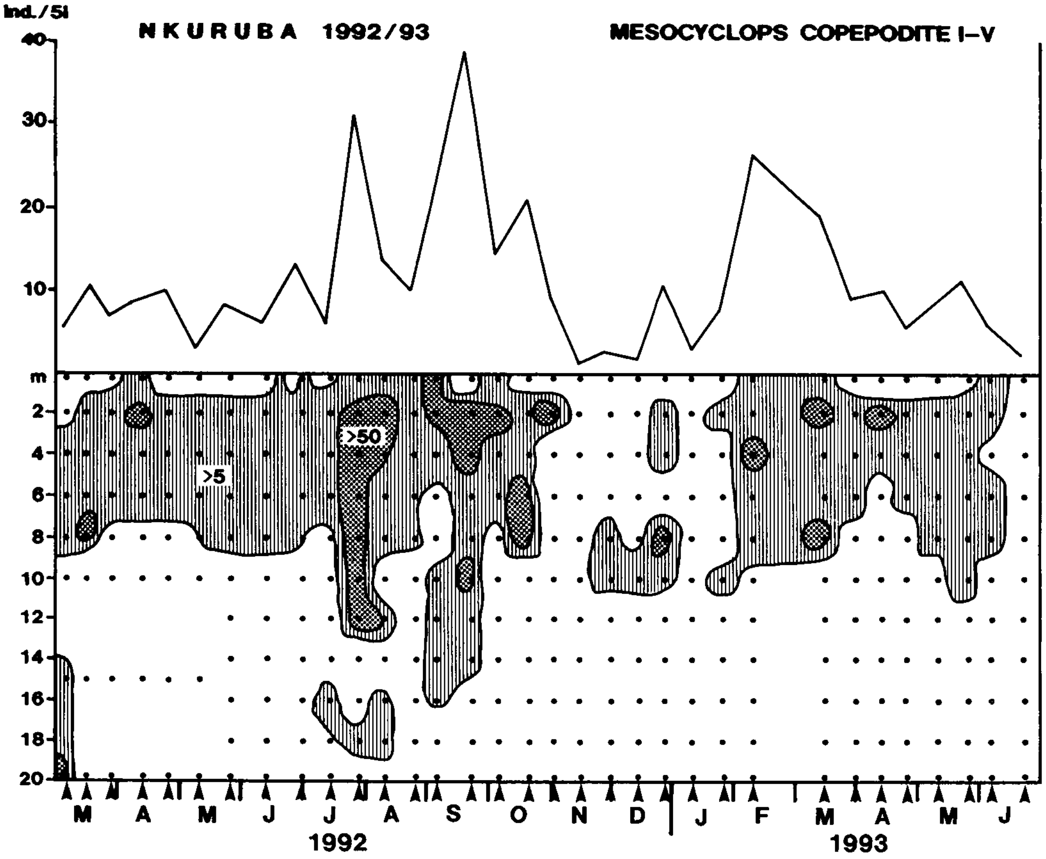


Fig. 21. — Lake Nkuruba 1992/1993, *Mesocyclops aequatorialis* copepodite spatio-temporal distribution and 0 - 10 m average density.

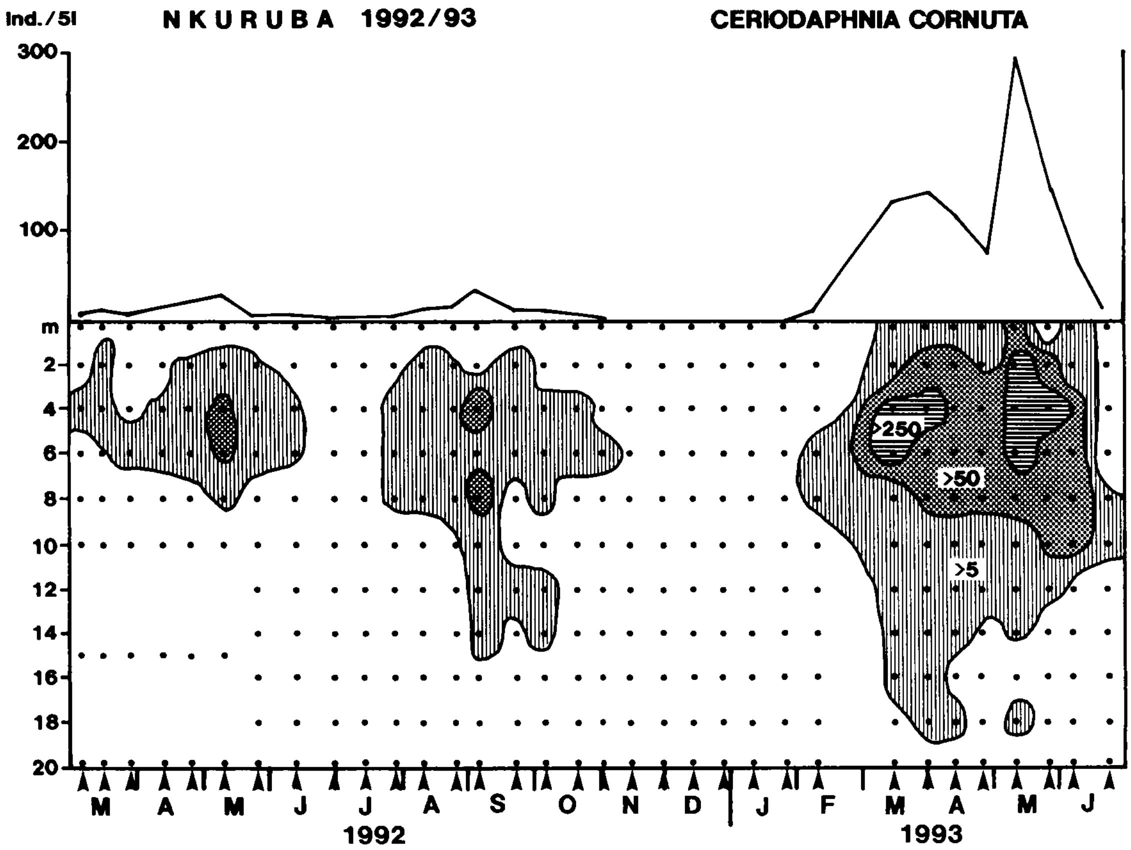


Fig. 22. — Lake Nkuruba 1992/1993, *Ceriodaphnia cornuta* spatio-temporal distribution and 0 - 10 m average density.

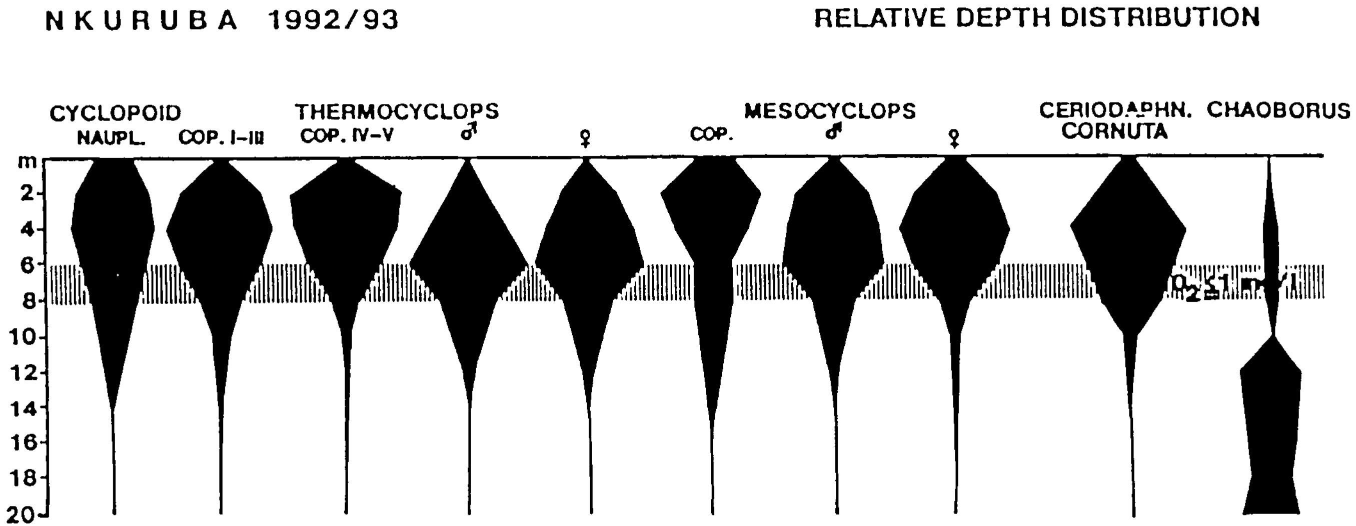


Fig. 23. — Lake Nkuruba 1992/1993, crustacean zooplankton and *Chaoborus* larvae relative depth distributions.

4.3.3.2. Lake Nyahirya

Figures 24-31 show the temporal and vertical distribution patterns of Lake Nyahirya crustacean zooplankton.

Most numerous and always present in the plankton is *Thermocyclops macracanthus*. Population abundance peaks of adult females appear in the first year in March, early May, late May, late June, October and in March and April of the following year.

The lowest population densities occur in January in the second year. The males show abundance peaks in the first year in March, May, July and end of August. Low population densities are observed thereafter. Minor abundance peaks appear in March and May in the second year.

The highest abundances for both sexes reach some 50 ind.l^{-1} between surface and 8 m deep. An exceptional case is at the beginning of the investigation when high population densities are found from surface to 20 m deep. The clutch size (fig. 25b) varies during the investigation period from a minimum size of 6.8 occurring on 22.03.1992 to a maximum size 12.7 occurring on 23.11.1992. The egg standing-stock density (*cf.* fig. 36) fluctuates between 188.3 eggs.l^{-1} at the beginning of the investigation and 11.1 eggs.l^{-1} at the end of October in the first year. The egg stock is comparatively more abundant in the first year of investigation when also the phytoplankton biomass (Chl a) was higher than in the second year (*cf.* fig. 6b).

T. macracanthus nauplii show highest abundance peaks in March and June in the first year. This is likely to be due to the high egg stock density present at the time. The lowest density occurs at the beginning of August in the first year. The nauplii show two preferences: near the surface and between 8 m and 10 m deep. The highest abundances reach some 100 ind.l^{-1} near the surface and in strata, lying between 7 and 10 m deep.

Copepodide stages I-III are present in reasonable numbers throughout the investigation period. Population abundance peaks appear in the first year in April, June, July-August, October and December and January, March, April and June in the following year. The population density development is characterized by increases and decreases. The highest abundances figures reach some 100 ind.l^{-1} at a depth strata of 2-10 m.

Copepodide stages IV-V abundance peaks appear in the first year in April and July and only moderate peaks appear thereafter. The lowest population densities are observed in February of the following year. The highest abundance figures reach some 100 ind.l^{-1} at a depth of mainly 2-8 m.

Moina micrura is only thinly represented in the lake plankton. Moderate population density peaks appear in the first year in May, June, September and November, and in April the following year. During July and August in the first year, *M. micrura* is practically absent. The highest abundance figures reach some 10 ind.l^{-1} at a depth of 2-8 m.

Oncocypris sp. seems to be distributed in two layers, occupying mostly the 4 - 10 m stratum and the 12 - 20 m stratum. Population abundance peaks appear in the two strata. Abundance peaks appear in the first year in May, August-September and in February-March and April in the following year. A minimum population density for the 0-10 m stratum occurs in February the following year. The highest abundances reach some 15 ind.l^{-1}.

Figure 31 shows Lake Nyahirya average relative depths distributions of the zooplankton under investigation. With the exception of *Chaoborus* larvae and of *Oncocypris*, it shows a confinement to the oxygenated epilimnion.

Thermocyclops macracanthus adults and copepodides have similar depth distribution patterns occupying the stratum from 2 - 10 m deep. Female and copepodide maxima are 2 m deep, the male maximum appears at 4 m. The nauplii have a surface peak and another one at 8 m.

Moina micrura has its median point 4 m deep while that of *Ceriodaphnia cornuta* is located in hypoxic waters 8 m deep. This clearly shows different depth preferences. *Oncocypris* has two distribution maxima, one 6 m deep and the second one 12 m deep. The explanation for such a distribution pattern is not clear but could be due to the existence of two species in the population or to niche separation by different development instar stages. *Chaoborus* larvae show their maximum 16 m deep. The majority of its population occupy strata between 12 m and 20 m deep.

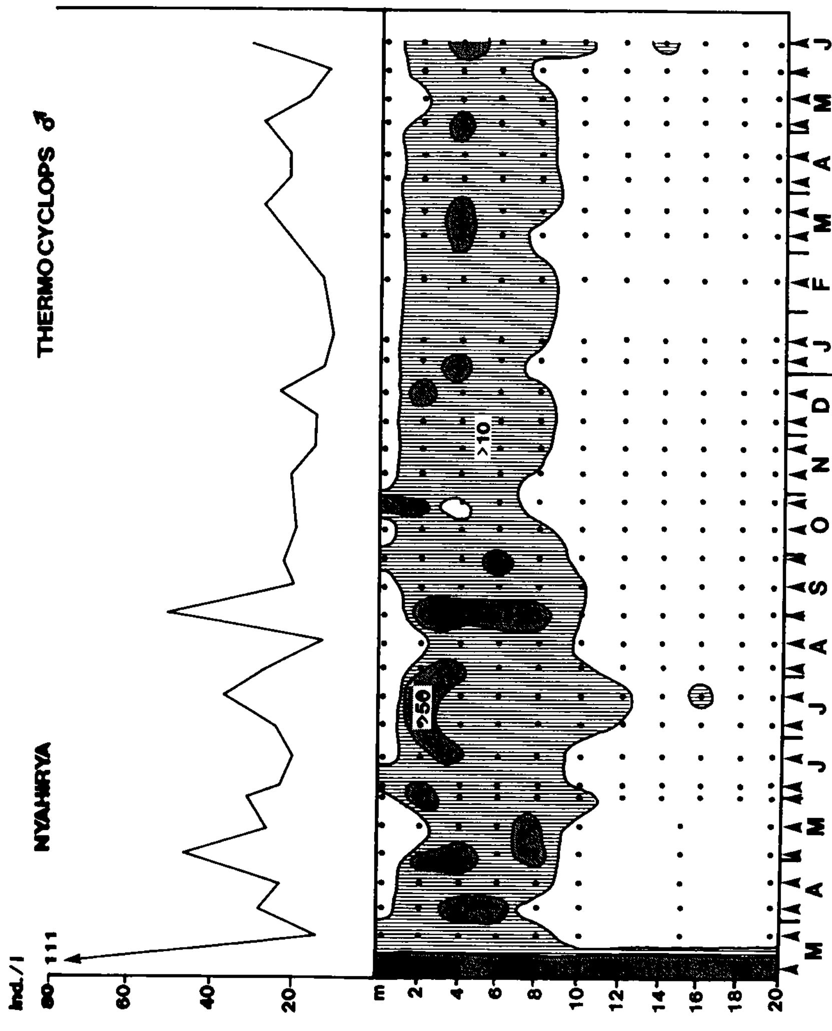


Fig. 24. — Lake Nyahirya 1992/93, *Thermocyclops macracanthus* males spatio-temporal distribution and 0 - 10 m average density.

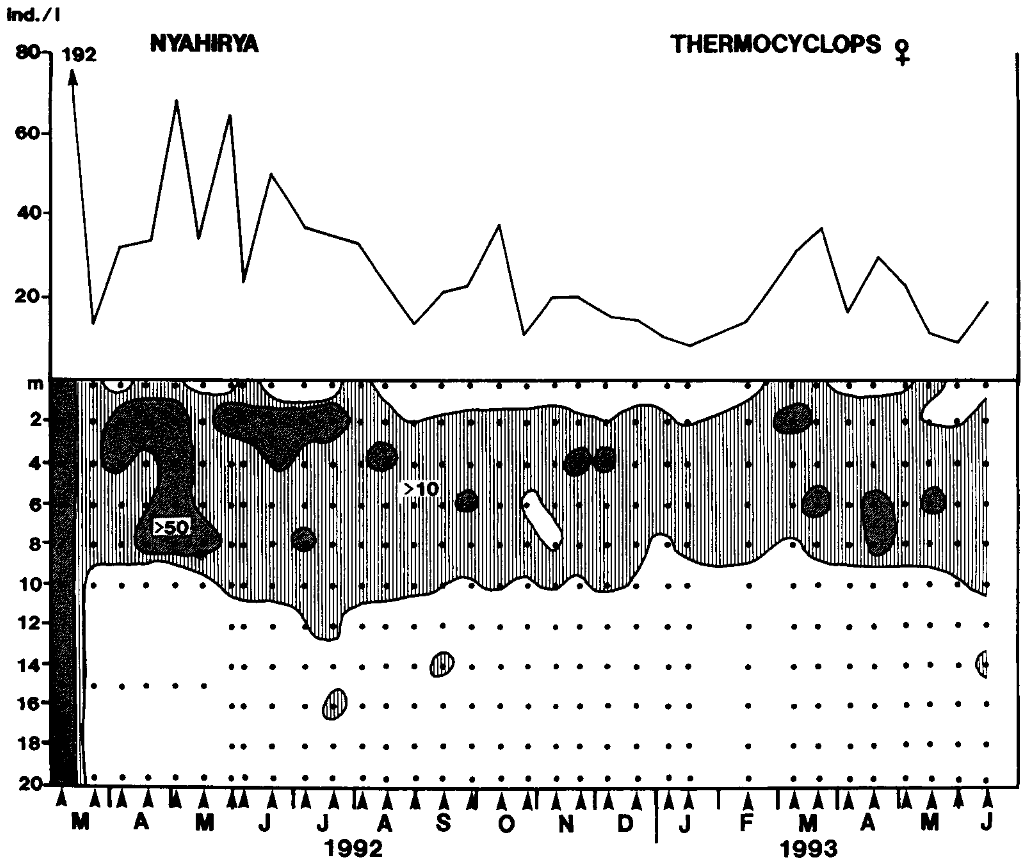


Fig. 25a. — Lake Nyahirya 1992/1993, *Thermocyclops macracanthus* females spatio-temporal distribution and 0 - 10 m average density.

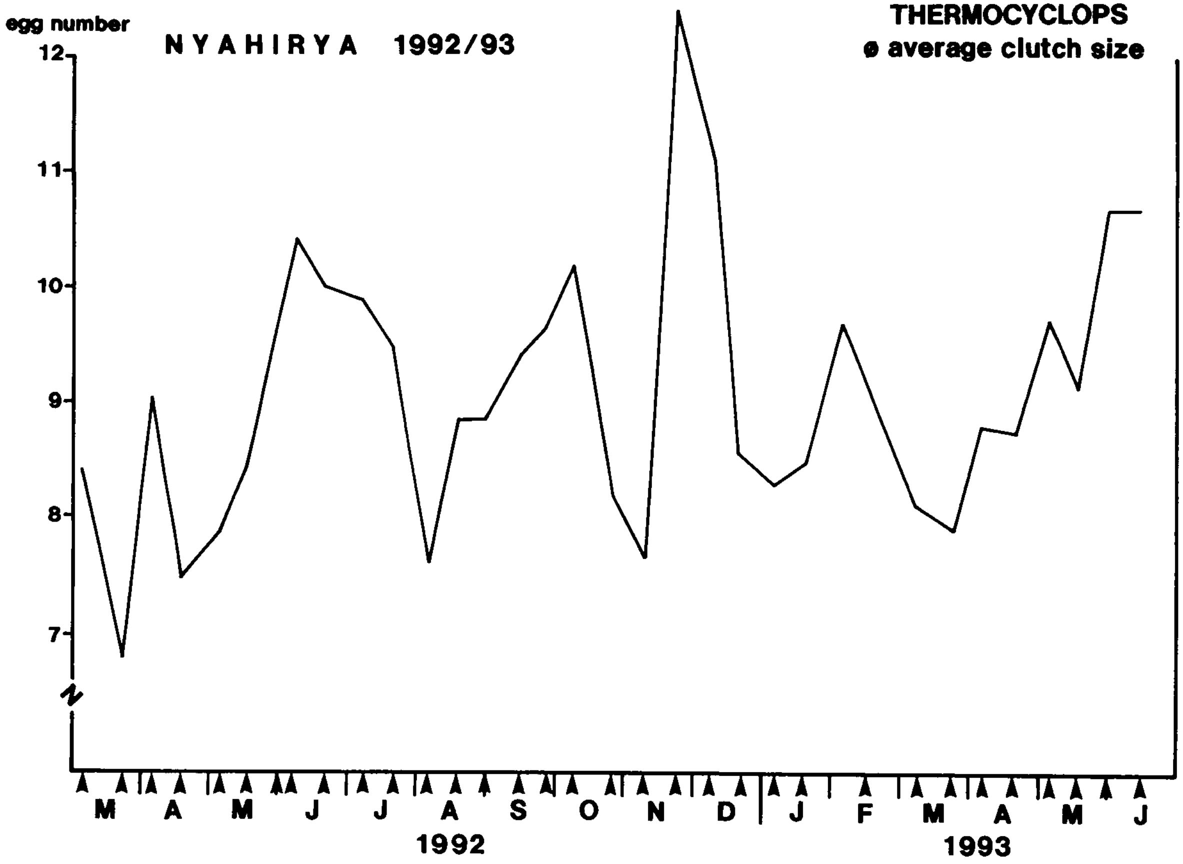


Fig. 25b. — Lake Nyahirya, *Thermocyclops macracanthus* females average clutch-size variation.

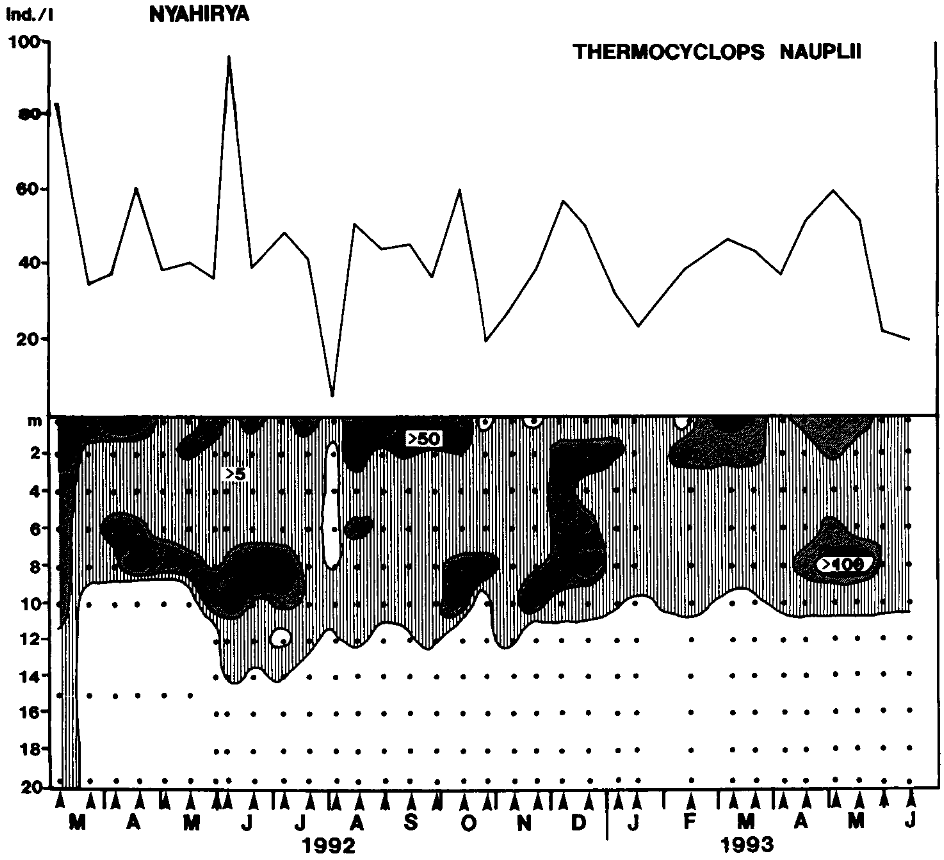


Fig. 26. — Lake Nyahirya 1992/1993, *Thermocyclops macracanthus* nauplii spatio-temporal distribution and 0 - 10 m average density.

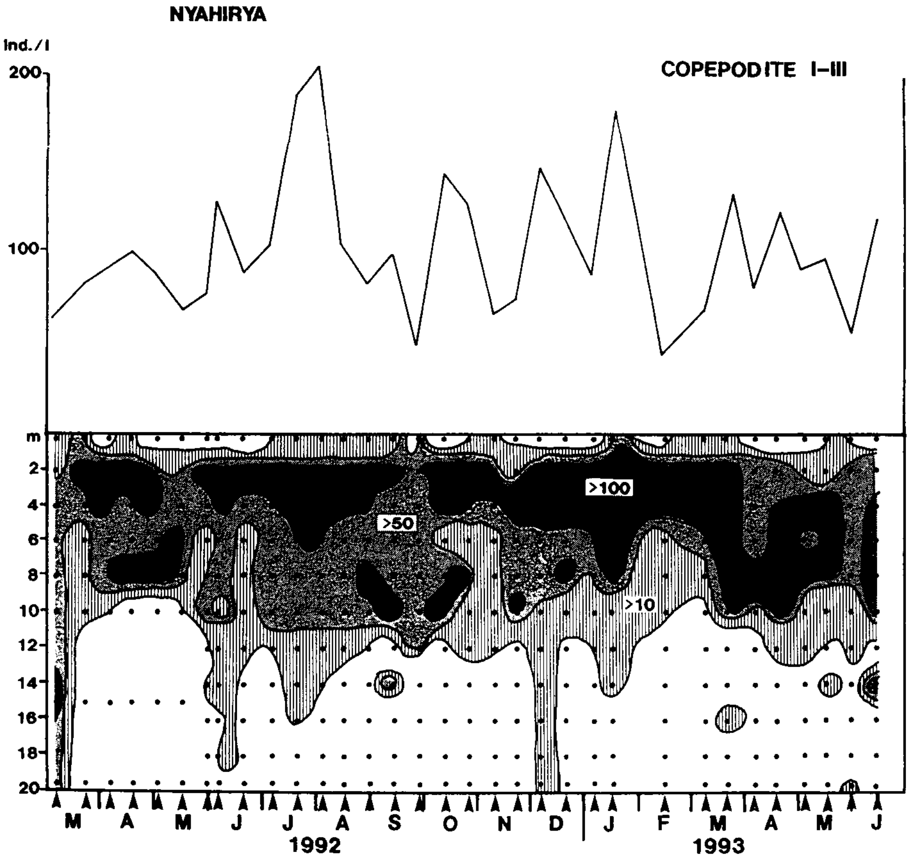


Fig. 27. — Lake Nyahirya 1992/1993, *Thermocyclops macracanthus* copepodite I-III stages spatio-temporal distribution and 0 - 10 m average density.

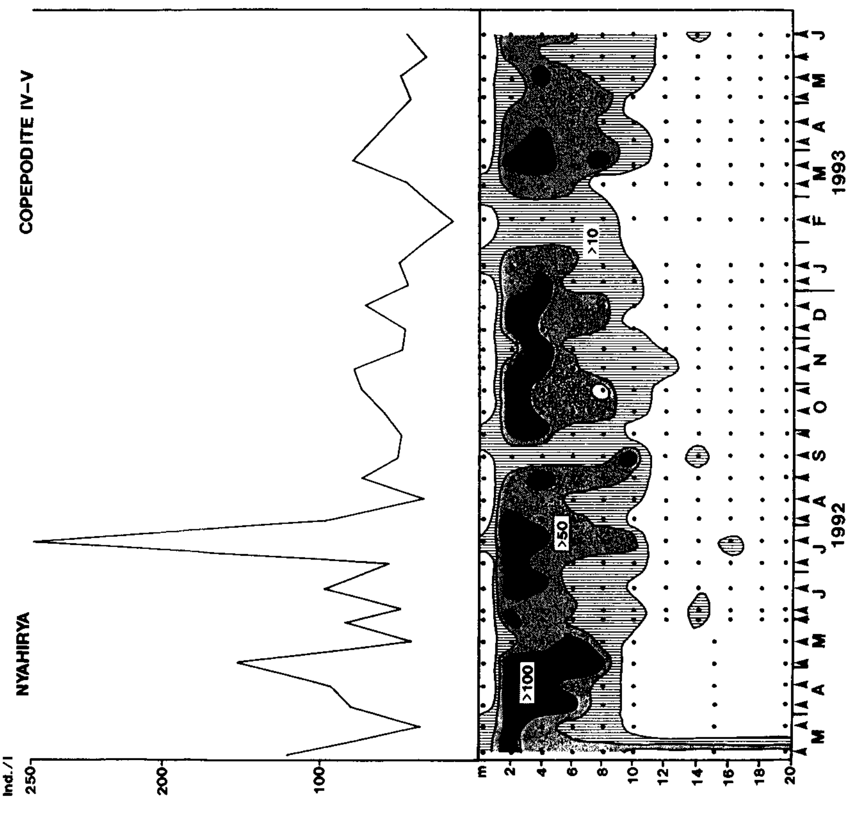


Fig. 28. — Lake Nyahirya 1992/1993, *Thermocyclops macracanthus* copepodite IV-V stages spatio-temporal distribution and 0 - 10 m average density.

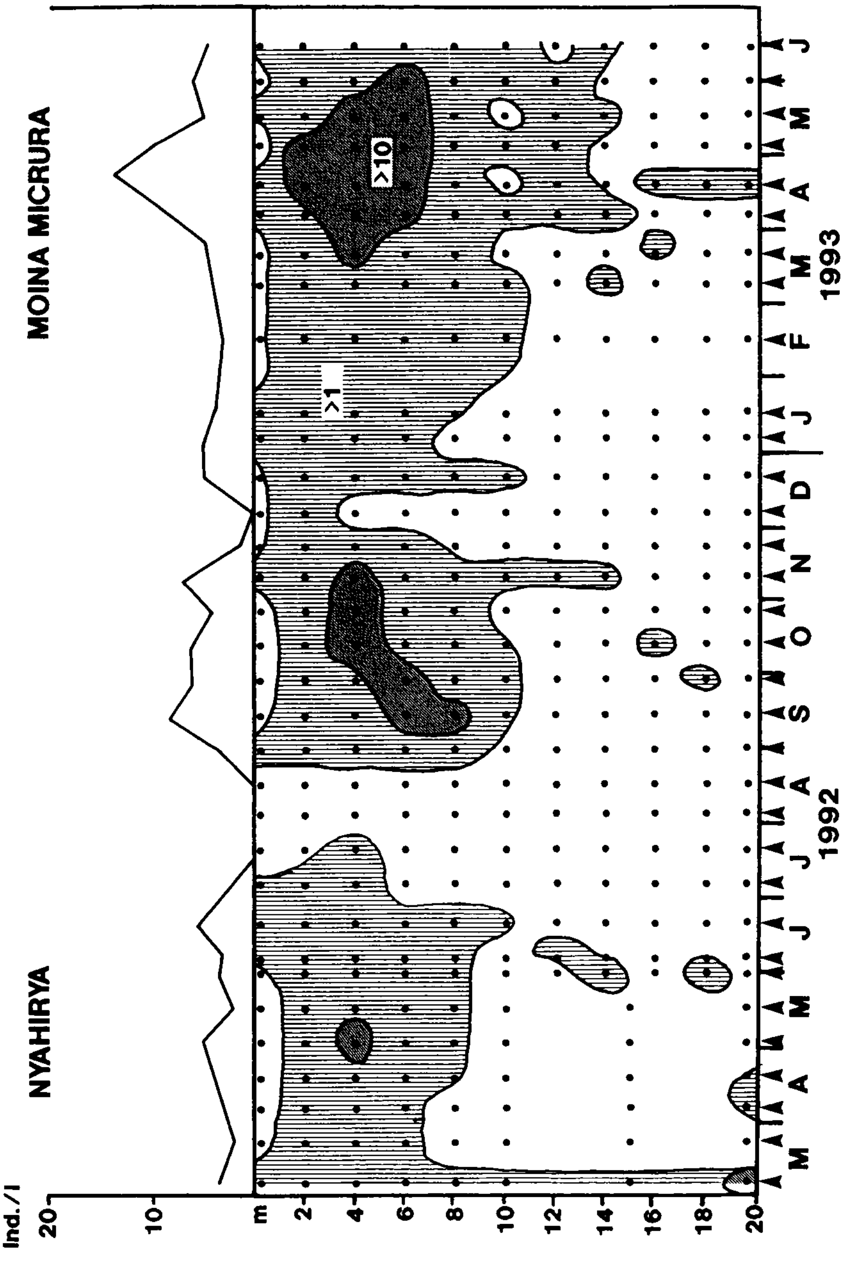


Fig. 29. — Lake Nyahirya 1992/1993, *Moina micrura* spatio-temporal distribution and 0 - 10 m average density.

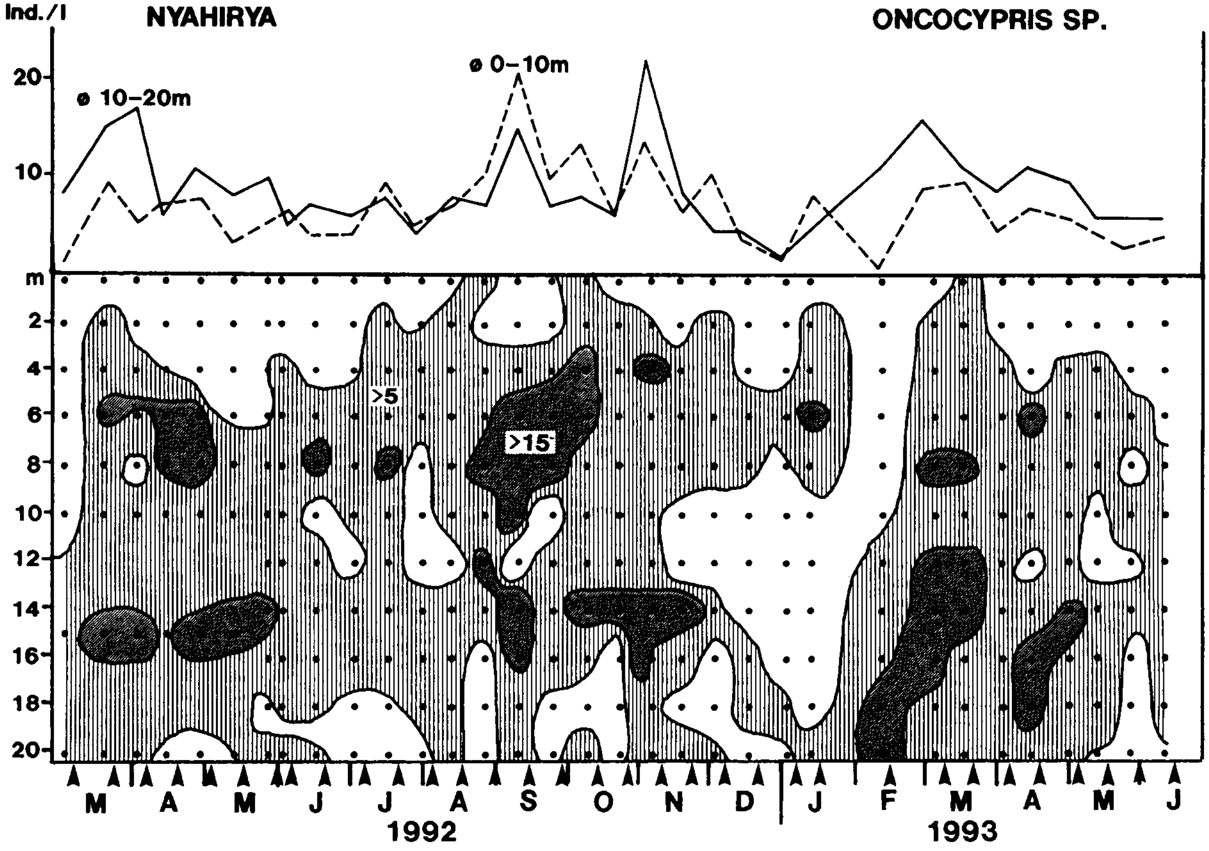


Fig. 30. — Lake Nyahirya 1992/1993, *Oncocypris sp.* spatio-temporal distribution and 0 - 10 m average density.

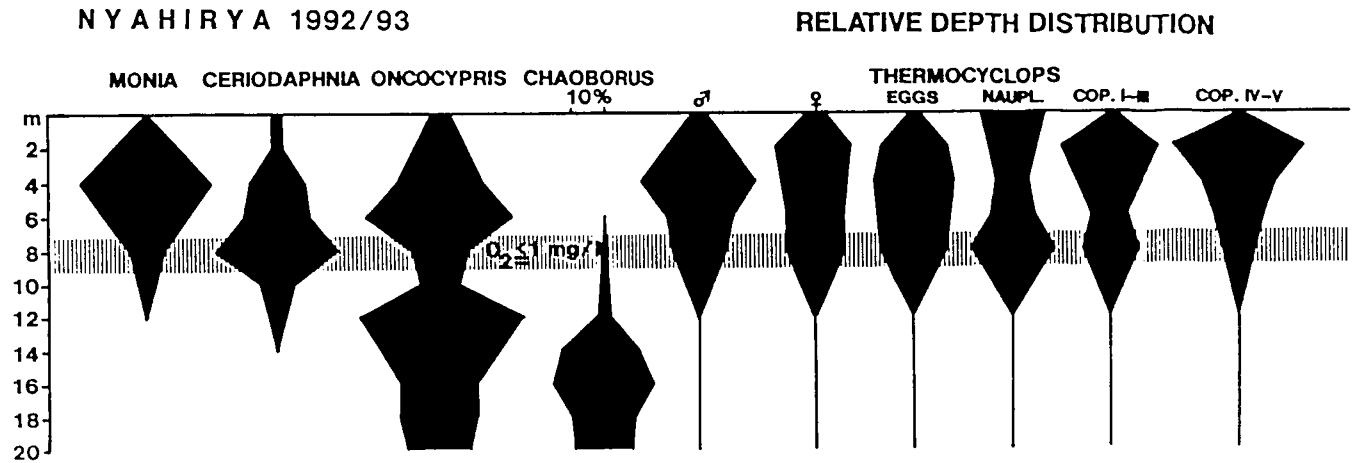


Fig. 31. — Lake Nyahirya 1992/1993, crustacean zooplankton and *Chaoborus* larvae relative depth distribution.

4.4. POPULATION DYNAMICS

Figure 32 shows Lake Nkuruba's epilimnic mean numbers of *Thermocyclops* eggs, copepodides, nauplii, adults as well as total individual counts throughout the period of investigation. As all calculations are based on the zooplankton content of the upper 10 m, the low values at the beginning of the investigation are an underestimate, because a large portion of the zooplankton was dispersed to the anoxic hypolimnion at the time.

Total numbers show repeated increases and decreases. During the first year the maximum occurs in September and the minimum at the end of November. Another peak occurs at the end of December. In the following year, moderate peaks occur in March and in May. The copepodide stages contribution to total numbers is usually higher than that of other stages.

The mean value of the percentage of males of all adults is 44.5 % (SD = 8.50, n = 33). It varies between 25.2 % in November and 56.4 % in October of the first year. After that, it remains relatively constant at 50.7 % from end of January the second year until the end of the investigation.

A dependence of total numbers on egg stock and on algal biomass is recognizable (*cf.* fig. 6). The mean clutch size per egg carrying female throughout the investigation period is 11.4 (SD = 1.01, n = 33). The highest value, 12.5, occurs at the beginning of the investigation from March to the end of April. This is a time of high algal biomass. The mean clutch size then shows some stability with a value of 11.9 from November of the first year to the end of the investigation period.

Assuming continuous egg production during the year at temperature range 22-23 °C, and also assuming that each female is capable of producing at least one egg clutch that hatches successfully, the number of days in a year divided by the species generation time (*i.e.* from egg to egg) allows the calculation of the mean turnover time of *Thermocyclops* during the investigation period. It can be estimated at 8.5 ± 4.4 days, its range being 3.3-18.9 days. The average loss per day, which can be estimated from the turnover time is 11.75 %. *Thermocyclops* is thus capable of making 14 generations in a year. This number is likely to be exceeded because of the production of several clutches by different individuals. Many overlapping cohorts of development instar stages may thus occur in the population.

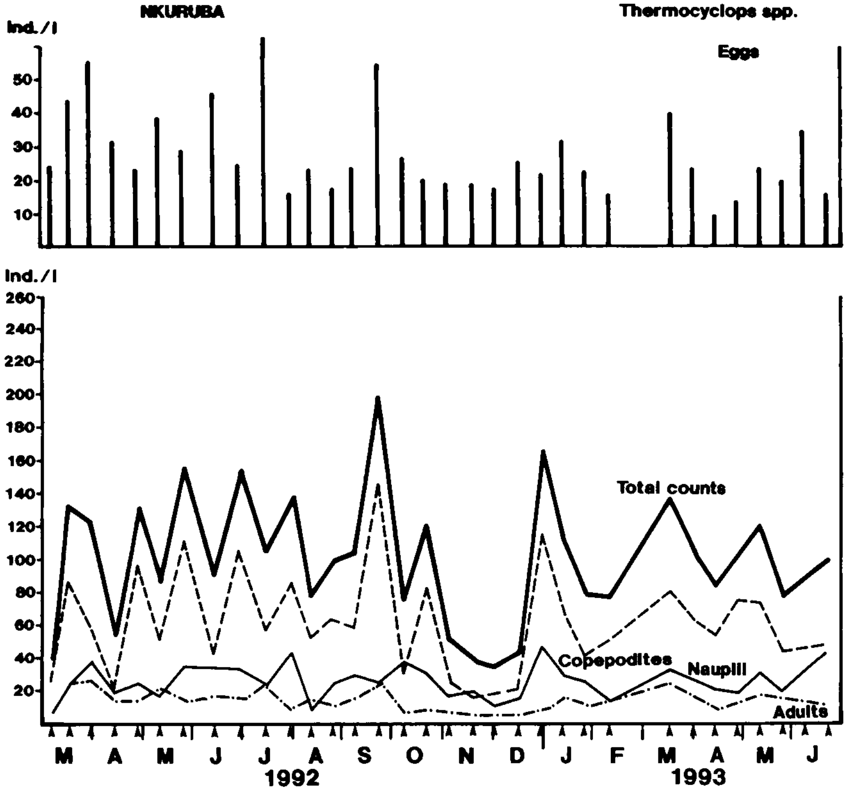


Fig. 32. — Lake Nkuruba 1992/1993, 0 - 10 m, *Thermocyclops spp.*, eggs, developmental instar stages and total count density variations.

Figure 33 shows the fluctuations in the population parameters b′, r′ and d′ for *Thermocyclops spp.* Birth rate peaks are preceded by population maxima. The birth rate varies between 0.051 and 0.226. The minimum rate occurs on 12.04.1993 and the maximum on 13.07.1992. The birth rates are generally lower in the second year than in the first year. The instantaneous growth rate (r′) does not vary much from the horizontal during the investigation period. Its value ranges from - 0.065 on 6.10.1992 to 0.125 on 15.03.1992. The r′ fluctuates relatively more in the first year than in the following year of investigation. Trends of death rates d′ parallel those of birth rates with more fluctuations in the first year followed by stabilization in the following year. The maximum death rate occurs in the first year in April and the minimum at the end of December. The negative death rate in December could be a result of the rapid population increase that occurs in December.

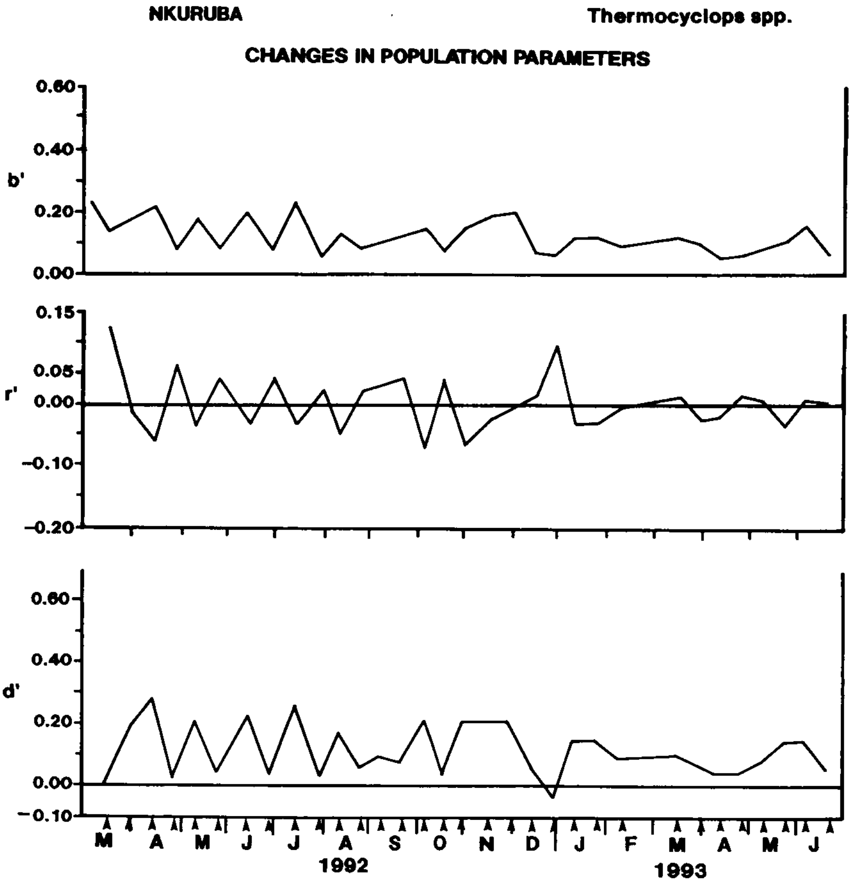


Fig. 33. — Lake Nkuruba 1992/1993, *Thermocyclops spp.* changes in population parameters b′, r′ and d′.

Population density variations of total counts and instars of *Mesocyclops aequatorialis* are shown in figure 34. Pronounced maxima of total counts occur in the first year in July and late September and in March of the following year. A dependence of egg numbers on female numbers and environmental factors (e.g. rainfall) is revealed (*cf.* fig. 4). Total numbers increase during the dry season. The male to female percentages in the population remain low most of the time, mean 35.5 % (SD 13.60, n = 33). The highest percentage of males, 56.0 %, appears during late September and October in the first year, and minimum of 14.9 % during mid-March in the first year.

The mean clutch size of 15.82 (SD 2.06, n = 29) of the whole investigation period is larger than that of *Thermocyclops spp.* The relationship between the clutch size and algal biomass in contrast to *Thermocyclops* is not apparent. This could be a reflection of the feeding habits of *M. aequatorialis* whose later copepodide stages of development become partly carnivorous.

The mean turnover time of *M. aequatorialis* for the investigation period can be estimated at 2.85 ± 2.48 days. The range of the turnover time is 1.06-15.15 day. The average loss per day is estimated at 35.09 %. The possible number of generations in the year is 14.8. But because *M. aequatorialis* breeding females are capable of producing many clutches, there appears in the population overlapping cohorts. High daily losses for the species could be attributed to fish (*Poecelia reticulata*) selective predation.

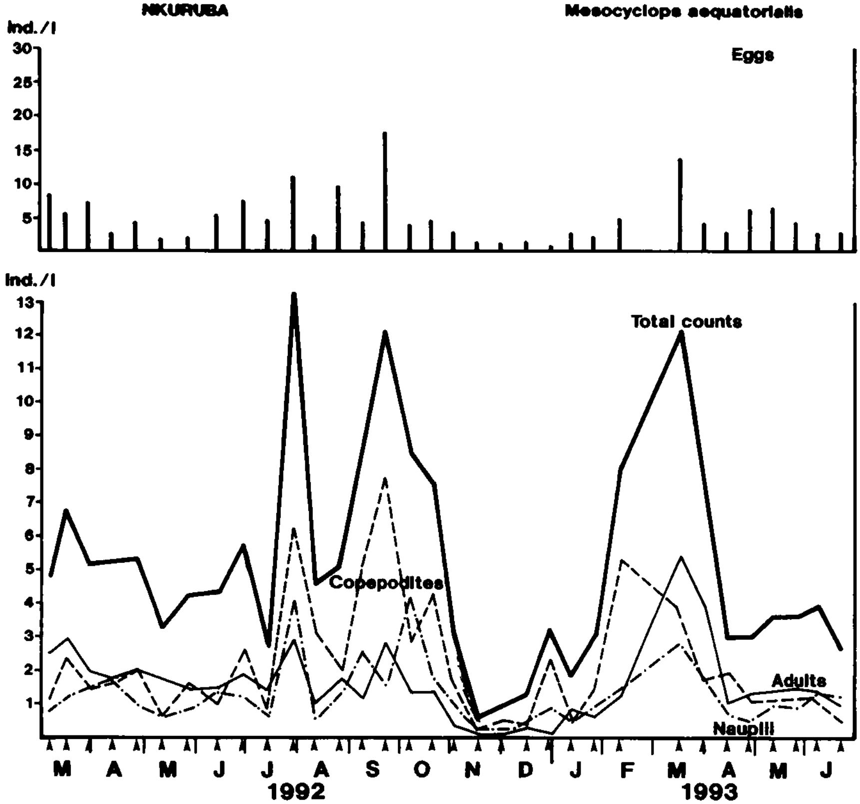


Fig. 34. — Lake Nkuruba 1992/1993, 0 - 10 m, *Mesocyclops aequatorialis* eggs, developmental instar stages and total counts density variations.

Figure 35 shows the fluctuations of the population parameters (r´, b´ and d´) for the *Mesocyclops*. The birth rates vary considerably (range 0.061-0.572). The lowest birth rate occurs in the first year during late December when population densities (fig. 34) are also low, and maximum in the following year in January.

The instantaneous rate of change (r´) shows minor fluctuations in the first four months of investigation. From the end of June in the first year to April in the second year, fluctuations are bigger and thereafter show some stability. A minimum value (r´) in November is a result of sharp population decline that occurs from October to November. The death rate d´ parallels the birth rate (b´); d´ fluctuates between - 0.008 and 0.631. The highest death rate (d´) occurs in the first year in November and the lowest at the end of December.

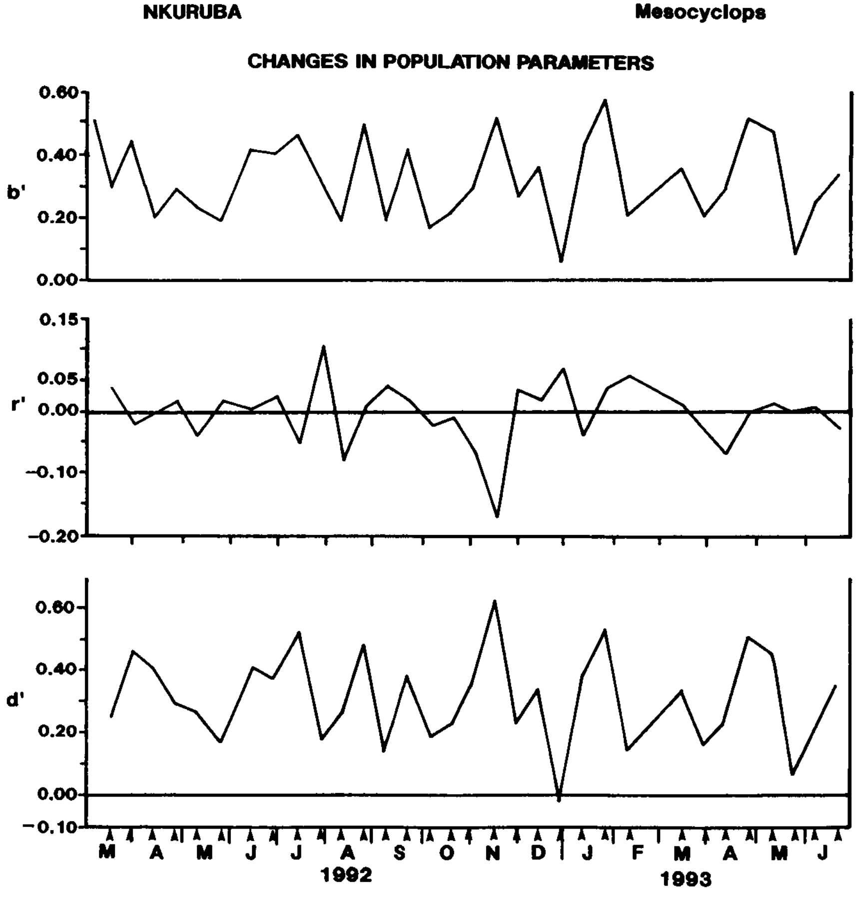


Fig. 35. — Lake Nkuruba 1992/1993, *Mesocyclops aquatorialis*, changes in population parameters b´, r´ and d´.

Figure 36 shows variations of total counts, instar stages and egg standing-stock densities of *Thermocyclops macracanthus* in Lake Nyahirya. The highest total count of 576 ind.l^{-1} is found at the beginning of the investigation. The adults contribute significantly to this number. Other abundance peaks appear in May and July in the first year. Copepodide instars contribute most toward the second and third peaks. Total counts' densities fluctuate with increases and decreases up to the end of the investigation period. The lowest total count appears in February of the second year. A dependence of total counts on egg standing stock and phytoplankton biomass is revealed (*cf.* fig. 6b). The percentage of males in the adults, 48.33 %, remains close to that of the females. The highest percentages are observed in the first year during August-September (53.9 %), late October to mid-January of the following year (57.1 %) and end of March to the end of the investigation period.

The mean clutch size for egg carrying-female is 9.11 (SD 1.21, n = 33) which is again smaller than for the Lake Nkuruba population. This could reflect the prevailing food condition of the two lakes.

T. macracanthus' high total counts in the first year could be due to the comparatively high phytoplankton biomass prevailing in the lake at that time. The egg stock density is correspondingly higher in the first part of the first year.

The mean turnover time of *T. macracanthus* in Lake Nyahirya is 12.45 ± 9.56 days with a range of 4.27-45.45 days. *T. macracanthus* is capable of making 14.05 generations per year. This number is likely to be exceeded because of the possibility of the production of many successive egg clutches by the breeding females. This results in many overlapping cohorts of development instar stages in the population.

The fluctuations of the population parameters r´, b´ and d´ for *T. macracanthus* in Lake Nyahirya are shown in figure 37. The birth rates b´ range from 0.021 to 0.189. The highest rate occurs at the beginning of June in the first year and the lowest during October in the same year. The birth rate fluctuates relatively more in the first year of study than in the following year. The instantaneous population change r´ fluctuates more in the first year than the following year. It stabilizes towards the end of the investigation period. Trends of death rates d´ parallel those of birth rates. High death rates occur in the first year. The death rate stabilizes in the following year from March to May. Two minimum death rates occur during July-early August in the first year and in January the following year.

The most pronounced feature is the dependence of the population parameters b´, r´ and d´ of the tropocyclopoids of the two lakes on the lakes' phytoplankton development (Chl a).

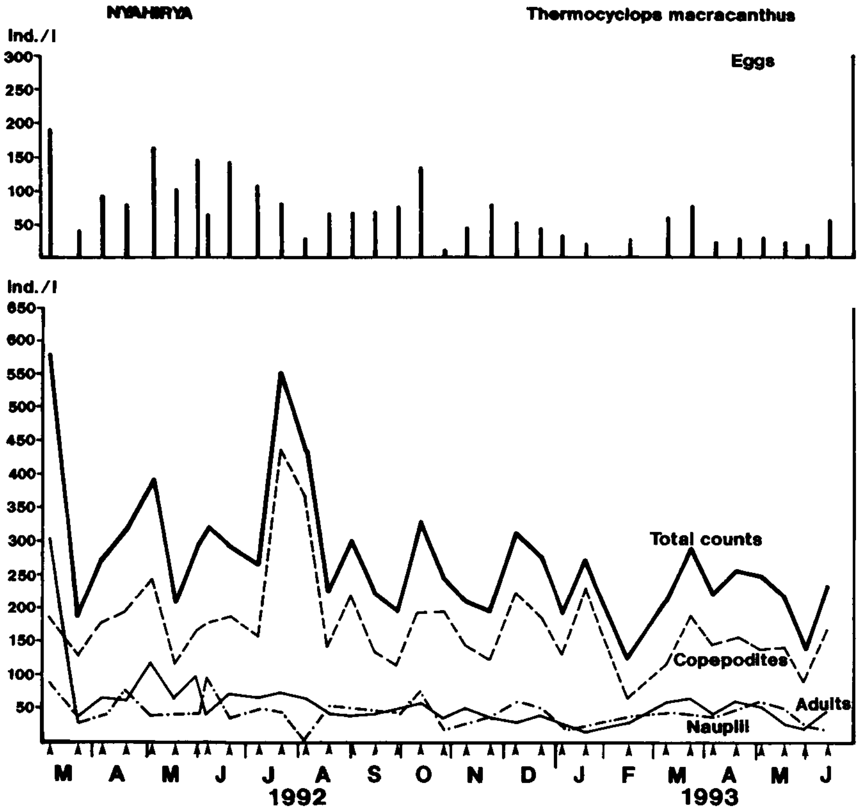


Fig. 36. — Lake Nyahirya 1992/1993, 0 - 10 m, *Thermocyclops macracanthus* eggs, developmental instar stages and total counts density variations.

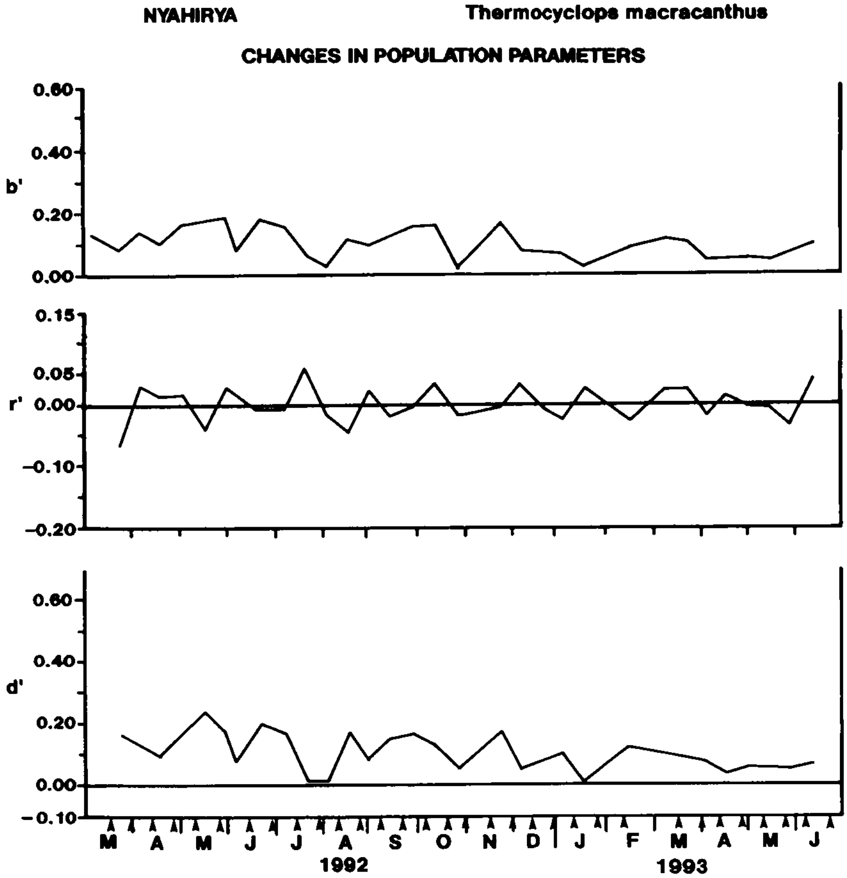


Fig. 37. — Lake Nyahirya 1992/1993, *Thermocyclops macracanthus* changes in population parameters b´, r´ and d´.

4.4.1. Reproduction biology, interclutch times and egg development

In a few cases, it was possible to observe the mating of the cyclopoids directly. During mating, the male of *M. aequatorialis* moves in the direction of the females and after many trials, it attaches to it with the help of its antennae. The male then positions itself rightly and transfers the spermatophore. The mating time lasts about half an hour.

The time of egg extrusion by females of *M. aequatorialis* from the time a male is introduced ranges from 2.0 to 2.7 days at 20 °C.

Most females are able to produce more than one egg clutch. The number varies greatly. Clutch sizes of laboratory cultured *T. tenellus* ranged from 1 to 16 eggs and of *M. equatorialis* from 20 to 76 eggs. *T. tenellus* females can produce up to 7 clutches at 20 °C and *M. aequatorialis* up to 6. Older females generally make small egg clutches. Table 3 shows the diminishing clutch size of *M. aequatorialis* after successive extrusions.

Table 3

Diminution of egg clutch size of *Mesocyclops aequatorialis* after successive extrusions

Egg club	**size**	**N ***	**SD ****
1st	59.58	12	6.29
2nd	63.90	10	2.92
3rd	44.25	8	11.39
4th	30.40	5	10.83

* number
** Standard deviation

The adults of *M. aequatorialis* live for a considerable length of time in cultures at 20 °C. The first egg clutches are generally produced in quick succession followed by others at longer intervals. The fertility of adult females declines with age. Old females are incapable of egg production on the introduction of males.

The interclutch times for the two species generally appear to be inversely related to temperature. *T. tenellus'* mean clutch time varies from 17.0 hours at 15 °C to 1.4 hours at 30 °C and that of *M. aequatorialis* from 47.5 hours (1.98 days) at 15 °C to 11.8 hours at 30 °C. The interclutch range is greater at lower temperatures (15 °C and 20 °C) for *T. tenellus* than at 25 °C and 30 °C. (tab. 4).

M. aequatorialis interclutch intervals are longer than those *of T. tenellus*. At 15 °C they range from 21.1 h (0.88 d) to 106.1 h (4.42 d). The mean interclutch time of *M. aequatorialis* also remains relatively stable from 20 °C to 30 °C. Due to failure of the two species to extrude successive egg sacs, despite the presence of abundant feed, at higher temperatures, it was not possible to determine the interclutch times at 33 °C and 35 °C. The observed variations in interclutch times may be a combined attribute of intrinsic factors like age and the physiological condition of the animal.

The egg development times of *Tropocyclops tenellus* and *Mesocyclops aequatorialis* at different temperatures are shown in figure 38. They range from 4.77 days at 15 °C to 1.18 days at 33 °C for *T. tenellus*, and from 5.19 days at 15 °C to 1.16 days at 33 °C for *M. aquatorialis*. The eggs do no longer develop at 35 °C, and only uncompletely hatch at 15 °C. The eggs of *T. tenellus* develop faster than those of *M. aequatorialis* except at 33 °C where those of *M. aequatorialis* show slightly faster development.

Table 4

Interclutch time between hatching of one brood to the extrusion into sacs of the next of (a) *Tropocyclops tenellus* and of (b) *Mesocyclops aequatorialis* at different temperatures

	Temp. °C	N	Days	(hours)	Range
(a)	*Tropocyclops tenellus*				
	15	12	0.71	(17.04)	0.10-1.81
	20	9	0.22	(5.28)	0.08-0.42
	25	6	0.08	(1.92)	0.07-0.10
	30	6	0.06	(1.44)	0.03-0.10
(b)	*Mesocyclops aequatorialis*				
	15	7	1.98	(47.52)	0.88-4.42
	20	12	0.42	(10.08)	0.21-1.08
	25	10	0.47	(11.28)	0.25-1.66
	30	7	0.47	(11.76)	0.21-0.95

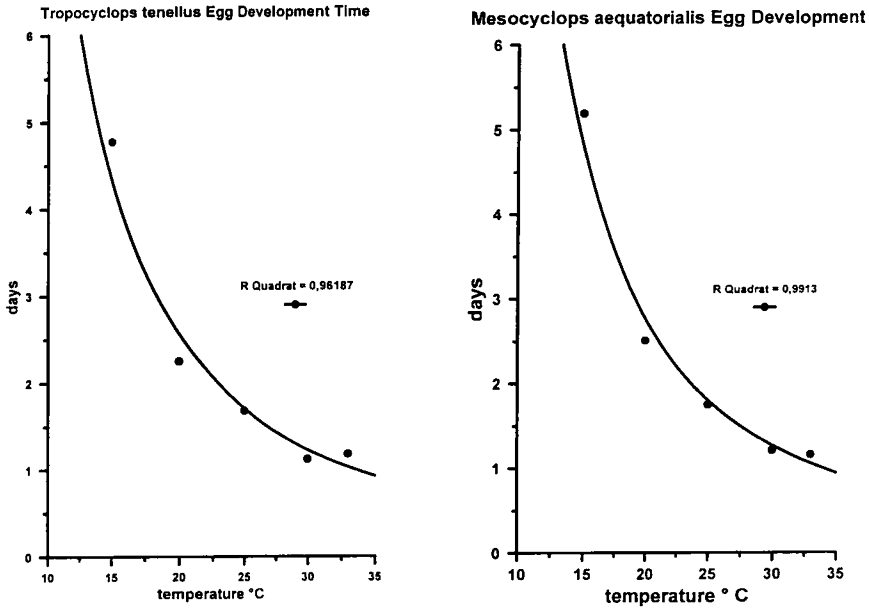
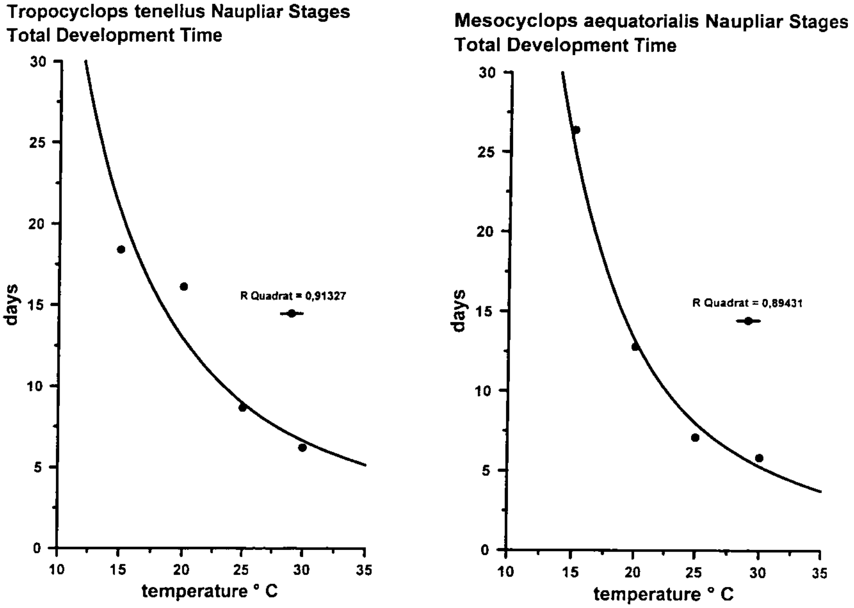


Fig. 38. — *Tropocyclops tenellus* and *Mesocyclops aequatorialis* embryonic development times.

4.4.2. Post-embryonic development

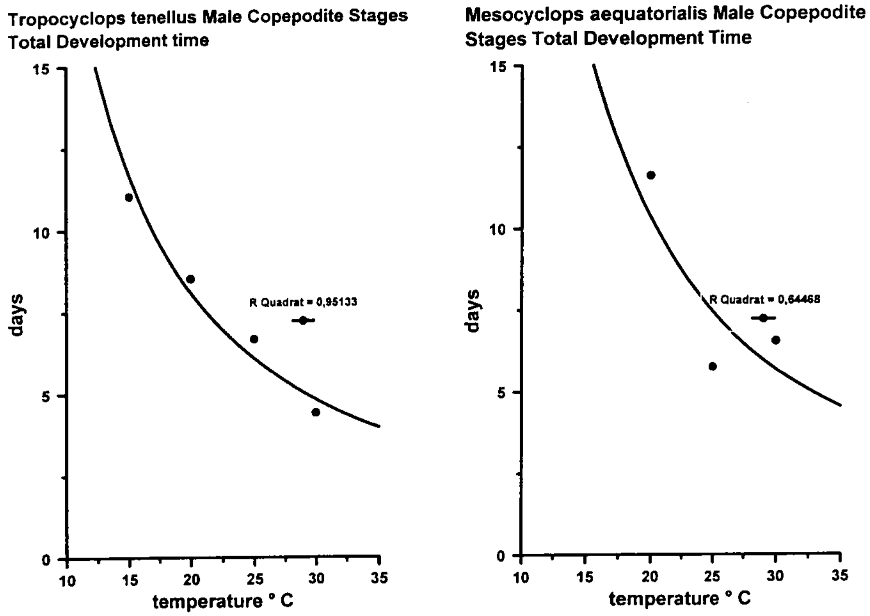
Figure 39 shows the total naupliar development times. It varies for *T. tenellus* from 18.37 days at 15 °C to 5.84 day at 30 °C and for *M. aequatorialis* from 26.36 days at 15 °C to 5.84 days at 30 °C. *M. aequatorialis* shows a faster development at temperatures of 20, 25 and 30 °C than is the case for *T. tenellus*. Higher mortality of *M. aequatorialis* nauplii than of *T. tenellus* occurs at 15 °C.


Tropocyclops tenellus Naupliar Stages Total Development Time

Mesocyclops aequatorialis Naupliar Stages Total Development Time

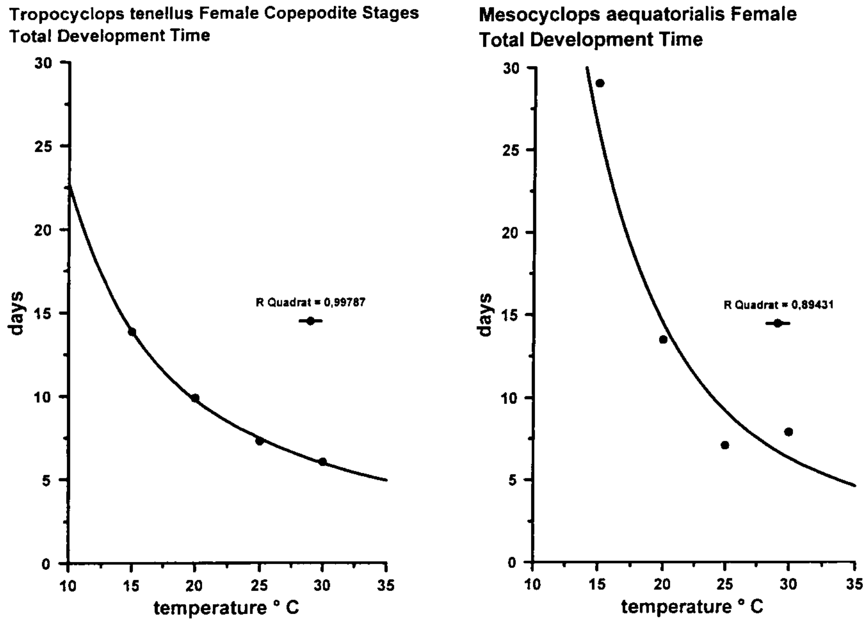
Fig. 39. — *Tropocyclops tenellus* and *Mesocyclops aequatorialis* naupliar stages total development times.

The duration times of development of combined copepodide stages of females and males respectively of *T. tenellus* and *M. aequatorialis* are shown in figure 40. *T. tenellus* males' total copepodide development time varies from 11.04 days at 15 °C to 4.41 days at 30 °C. In *M. aequatorialis* it varies from 11.61 days at 20 °C to 6.55 days at 30 °C. The development of the combined females' copepodide stages ranges for *T. tenellus* from 13.84 days at 15 °C to 6.03 days at 30 °C and for *M. aequatorialis* from 29.04 days at 15 °C to 7.88 days at 30 °C. It seems that the development time for the *M. aequatorialis* copepodides slightly increases again at 30 °C, which may indicate deteriorating living conditions.


Tropocyclops tenellus Male Copepodite Stages Total Development time

Mesocyclops aequatorialis Male Copepodite Stages Total Development Time

Fig. 40a. — *Tropocyclops tenellus* and *Mesocyclops aequatorialis* male copepodite stages total development times.


Tropocyclops tenellus Female Copepodite Stages Total Development Time

Mesocyclops aequatorialis Female Total Development Time

Fig. 40b. — *Tropocyclops tenellus* and *Mesocyclops aequatorialis* female copepodite stages total development times.

The total duration times from egg to adult obtained in laboratory cultures for *T. tenellus* and *M. aequatorialis* are shown in figure 41. *T. tenellus* male duration time ranges from 34.18 days at 15 °C to 11.74 days at 30 °C, and female duration time from 36.98 days at 15 °C to 13.36 days at 30 °C. For *M. aequatorialis* males, it ranges from 26.92 days at 20 °C to 13.6 days at 30 °C and for females from 60.59 days at 15 °C to 14.93 days at 30 °C. The males of both species generally show faster development at all temperatures. No *M. aequatorialis* male copepodides moulted to adult instar stages at 15 °C.

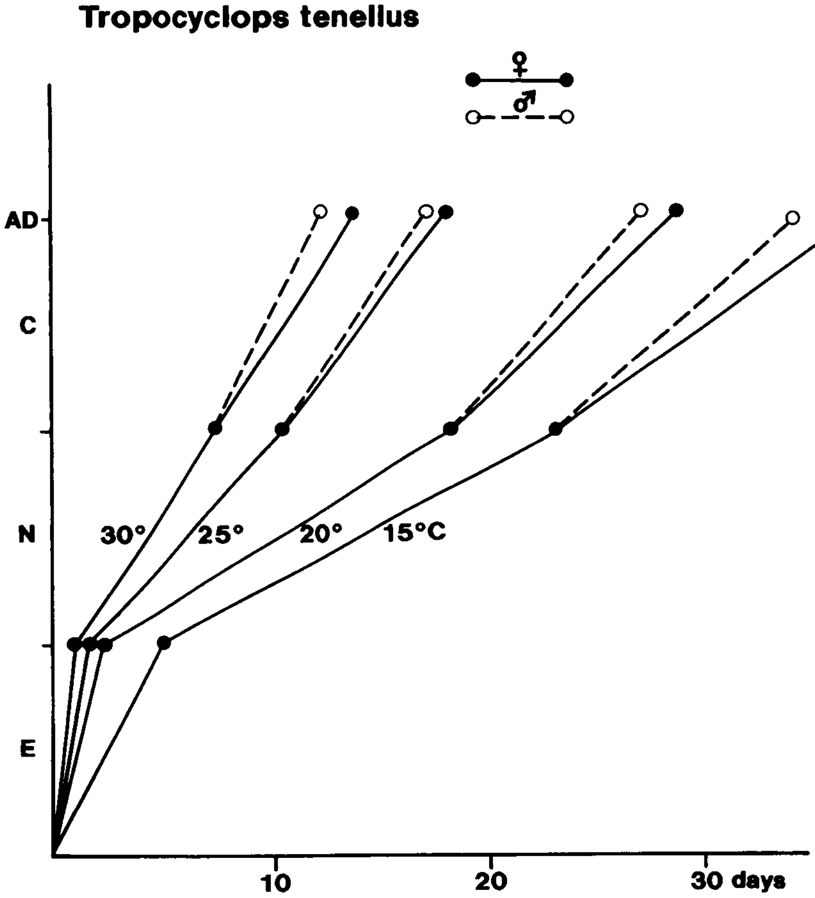


Fig. 41a. — *Tropocyclops tenellus* duration times from eggs to adults at different temperatures.

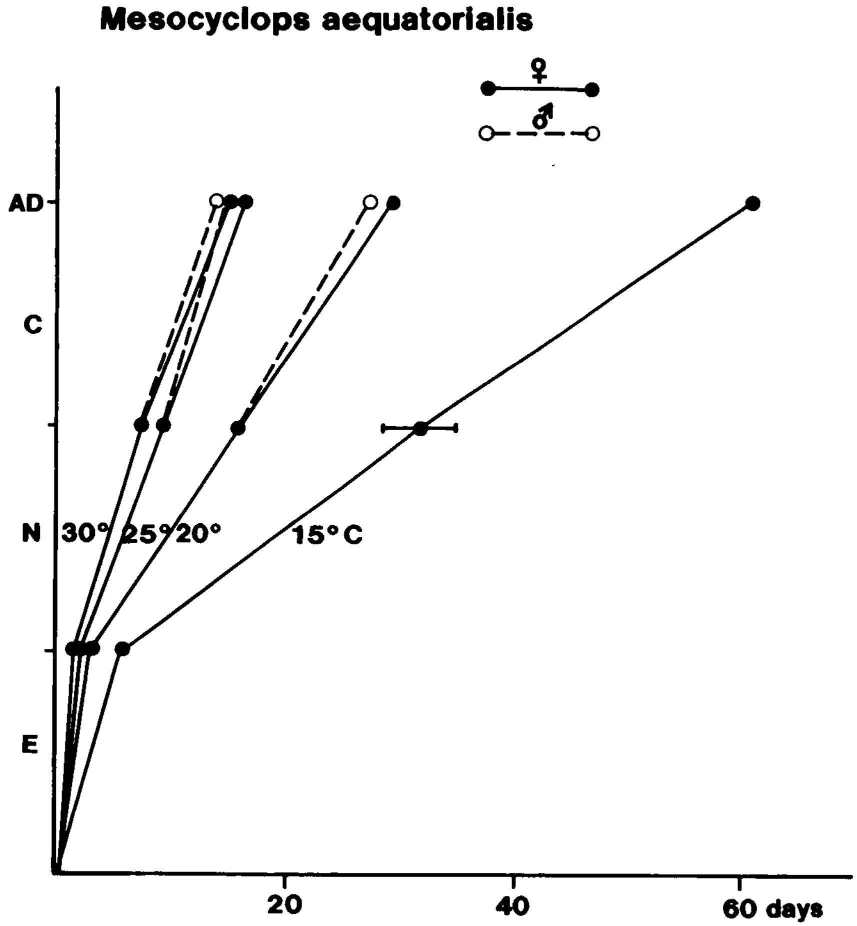


Fig. 41b. — *Mesocyclops aequatorialis* duration times from eggs to adults at different temperatures.

Tropocyclops tenellus development times are generally faster than those of *Mesocyclops aequatorialis*. Males of the two studied species show faster development at temperatures above 20 °C.

4.5. DISSOLVED OXYGEN TOLERANCE LEVELS OF THE CYCLOPOIDS

Table 5 shows the levels of tolerance (LD_{50}) of *T. tenellus* and *M. aequatorialis* to anoxia and hypoxia. The adults and copepodide stages of *M. aequatorialis* survive for a considerably longer time at 0.00 mg l^{-1} dissolved oxygen than those of *T. tenellus*. Copepodides of both species are less tolerant against anoxia than adults. An adaptation to withstand anoxia and hypoxia for some time is revealed.

Table 5

LD_{50} of *Mesocyclops aequatorialis* and *Tropocyclops tenellus* at different oxygen concentrations at 22 °C (42 observations)

mg $O_2.l^{-1}$	0.00	0.10	0.50
M. aequatorialis, Adults	49.0	167.0 (42)	>186.0
M. aequatorialis, Copepodites IV-V	36.0	139.5 (42)	
T. tenellus, Adults	27.5		
T. tenellus, Copepodites IV-V	20.0		

4.6. BIOMASS

4.6.1. Dry weight determinations

The relationship of formalin dry weight to total length (excluding the furcal rami) in three cyclopoids from Lakes Nkuruba and Nyahirya is shown in figure 42. Lengths and biomasses of developmental stages of Lake Nkuruba and Lake Nyahirya crustacean zooplankton are given in tables 6 and 7.

The dry weights of the zooplankton of the two lakes of related species like *Thermocyclops* fall within similar ranges. The adults and copepodide stages of Lake Nkuruba *Thermocyclops spp.* are generally larger than those of Lake Nyahirya.

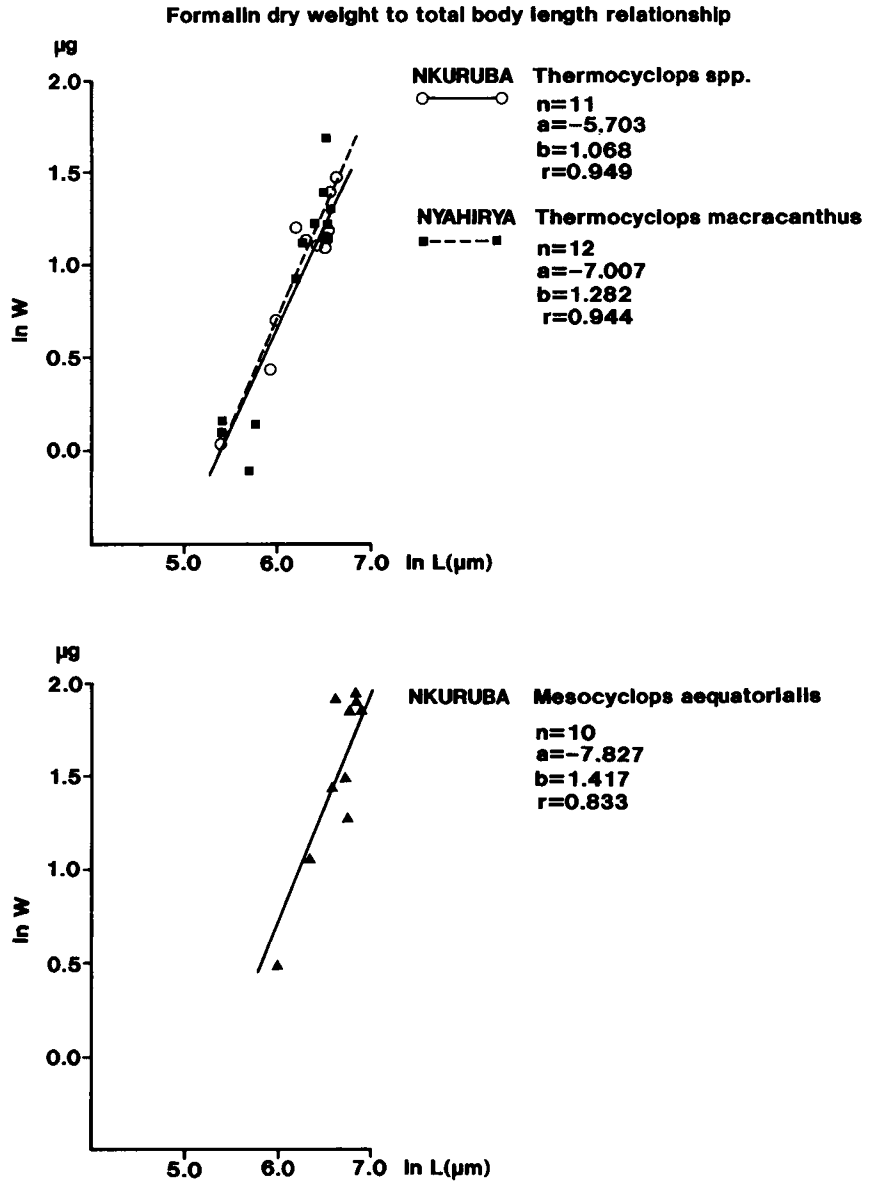


Fig. 42. — Formalin dry weight (µg) to body length (µm) relationship of the planktonic cyclopoid species of the two lakes.

Table 6

Mean values of formalin dry weight and total body length for individuals of various components of crustacean plankton in Lake Nkuruba

	Thermocyclops spp.		*Mesocyclops aequatorialis*	
	Mean length µm	**Mean weight µm**	**Mean length µm**	**Mean weight µm**
Naupli (all stages)	230	1.12	230	1.12
Copepodite I-II	375	1.12	400	1.95
Copepodite III	476	2.43	560	3.14
Copepodite IV	594	3.07	682	4.16
Copepodite V	675.5	3.53	818	5.36
Adult male	623	3.23	702	4.32
Adult female	723	3.80	907.5	6.22
Egg		0.073	230	0.14

	Ceriodaphnia cornuta	
	Mean length µm	**Mean weight µm**
small	436	0.5
medium	570	2.1
big	668	4.2

Table 7

Mean values of formalin dry weight and total body length for individuals of various components of crustacean plankton in Lake Nyahirya

	Thermocyclops macracanthus	
	Mean length µm	**Mean weight µm**
Naupli (all stages)	220	0.91
Copepodite I-II	304	1.38
Copepodite III	478	2.47
Copepodite IV	592	3.25
Copepodite V	641	3.60
Adult male	520	2.76
Adult female	684	3.92
Egg		0.061
	Moina micrura	
	Mean length µm	**Mean weight µm**
small	356	0.6
medium	452	2.07
big	514	3.11

4.6.2. Biomass fluctuations

In the estimation of the standing crop biomasses in the lakes, the individual zooplankters' mean dry weight is multiplied by the zooplankters' mean densities (for a water column from lake surface to 10 m deep).

Figure 43 shows the biomass fluctuations of *Thermocyclops* in the upper 10 m of Lake Nkuruba during the investigation period. Copepodide stages contribute most to the total biomass followed by the adults. Contributions by nauplii and eggs towards the total biomass are rather low. The total biomass (fig. 47) remains mostly above 200 µg l^{-1} except during the rainy season in April and

October-November. Minor biomass fluctuations occur repeatedly in the first half of the year. The highest value (498 μg l^{-1}) occurs in the first year in September at the end of the dry season and the lowest during the rainy season in November of the same year.

The mean annual biomass for *Thermocyclops spp.* in Lake Nkuruba (from 12.4.1992 to 29.3.1993) is estimated to be 232 mg (dw) m^{-3}, and assuming a depth of 10 m, this gives 2 320.9 mg m^{-2}.

Figure 44 shows the seasonal variation of biomasses of *M. aequatorialis* instar developmental stages and adults. The copepodides and adults contribute relatively more to the total biomass standing stock than the nauplii do. Figure 48 also shows the total biomass variations for the same species. The total biomass decreases during the rainy season in April-May and October-November in the first year, and in April-May in the following year, but increases relatively during the dry season of June-July, July-August and September in the first year and from January to March the following year.

The mean annual standing crop biomass of *M. aequatorialis* is 19.80 mg (dw) m^{-3}, and assuming a depth of 10 m, 198.0 mg (dw) m^{-2}.

The variation in *Ceriodaphnia cornuta* biomass is shown in figure 45. Only low biomasses appear in the first year with minor peaks occurring during April-May and September. An increase appears the following year from February to the end of March. The maximum biomass peak is reached in May. The biomass increases during the rainy season of both years.

Lake Nyahirya's *Thermocylops macracanthus* biomass variation is shown in figures 46 and 49. Again, the copepodides contribute most towards the total biomass followed by the adults. Nauplii and egg stock contributions are rather low. The biomass generally is high during the dry season, e.g. July-August in the first year and February to March in the following year. It decreases after the onset of the rains in the first and second year, for example during late March and August-September in the first year and March-April in the following year. Low standing crop biomasses are prevalent in February in the second year.

The mean annual standing crop of *T. macracanthus* (from 5.4.1992 to 22.3.1993) is 688.37 μg (dw)m^{-3}, and assuming a depth of 10 m, this gives 6883.7 mg (dw)m^{-2}.

Figure 45 shows the variation in biomass of *Moina micrura*. The standing crop biomass increases after the onset of the rains in April, September-October in the first year and April in the following year. Low biomasses are observed during the dry months of July and December in the first year.

The biomasses of the studied zooplankton show a strong dependence on environmental conditions like rainfall and mixing rate of the water column. The biomasses of the cyclopoids of the two lakes develop more during the dry season than the rainy season. The cladoceran biomasses in the two lakes develop more during the rainy season than the dry season.

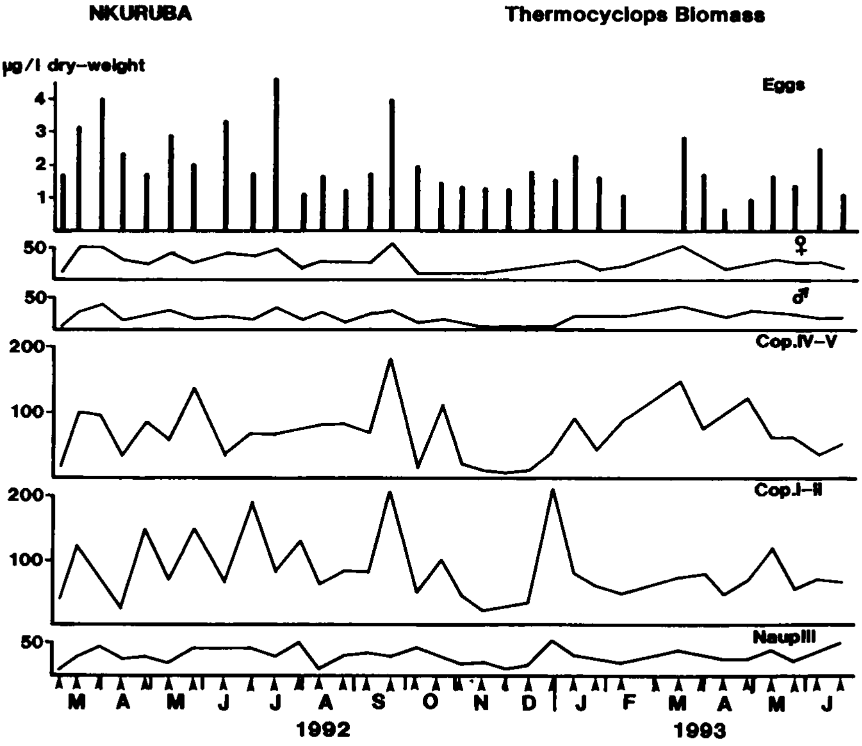


Fig. 43. — Lake Nkuruba 1992/1993, 0 - 10 m *Thermocyclops spp.* eggs and instar stages biomass variations.

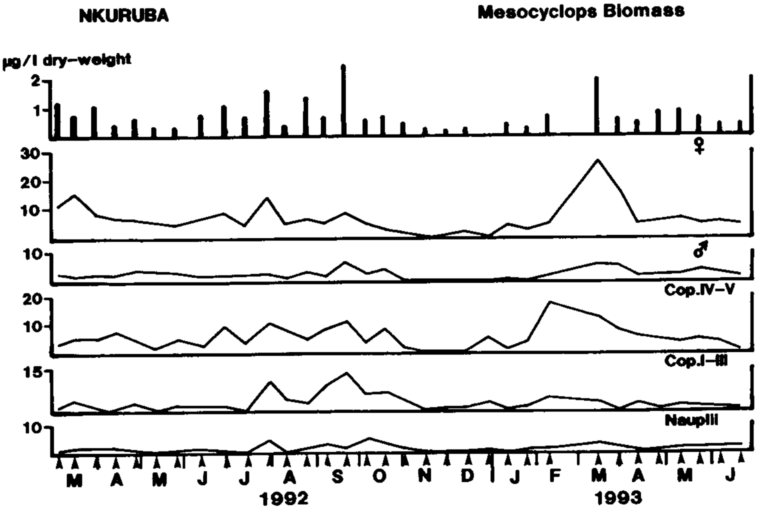


Fig. 44. — Lake Nkuruba 1992/1993, 0 - 10 m, *Mesocyclops aequatorialis* eggs and instar stages biomass variations.

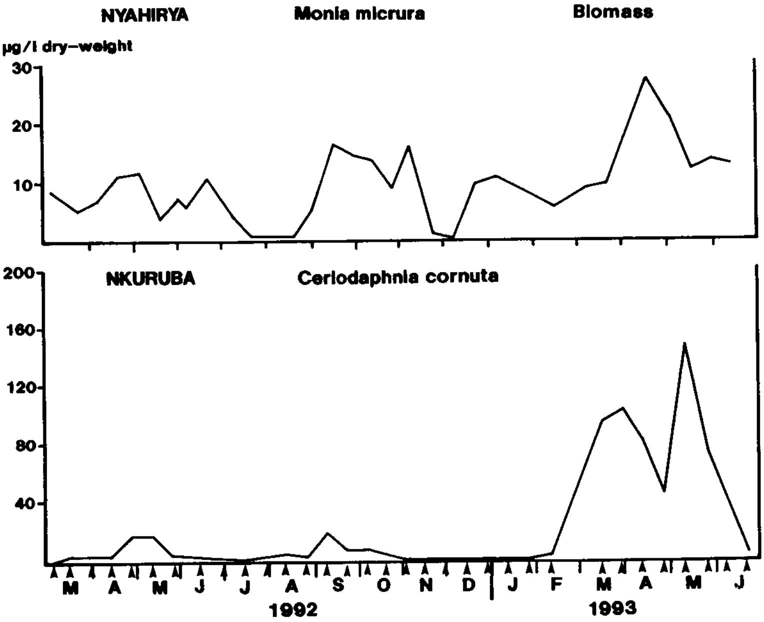


Fig. 45. — Lake Nyahirya *Moina micrura* and Lake Nkuruba *Ceriodaphnia cornuta* 0 - 10 m, 1992/1993, biomass variations.

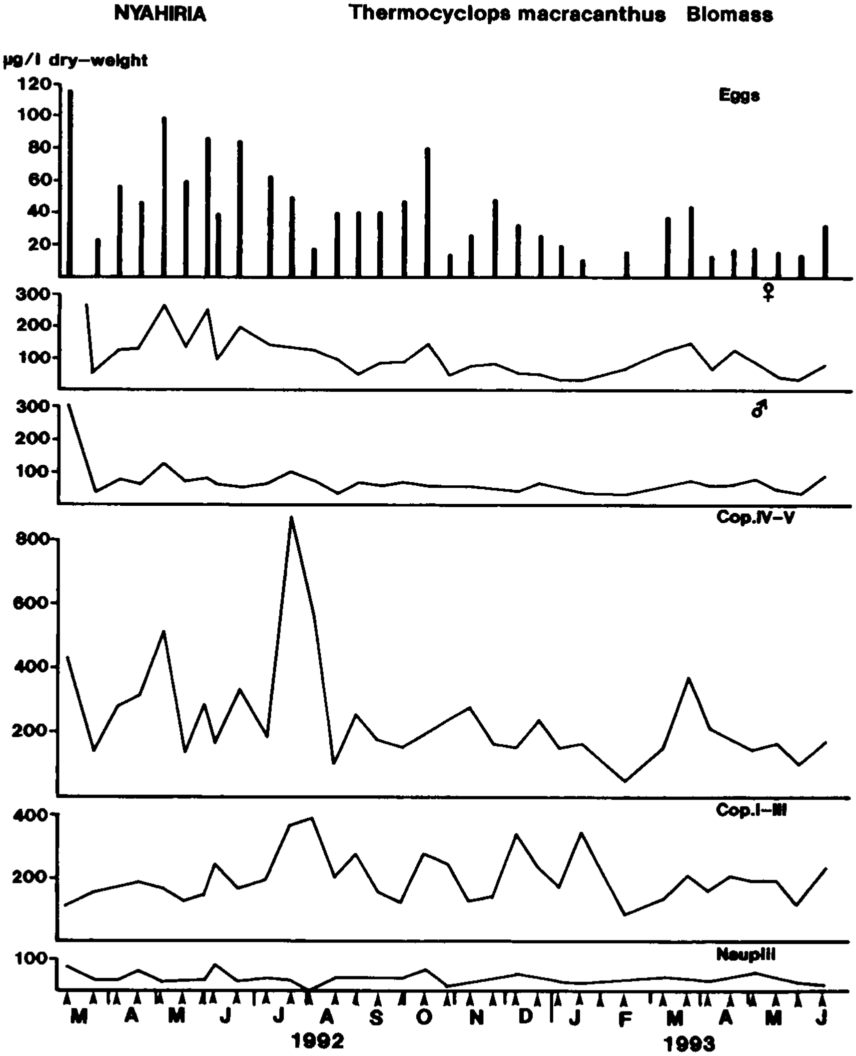


Fig. 46. — Lake Nyahirya 1992/1993, 0 - 10 m, *Thermocyclops macracanthus* and instar stages biomass variations.

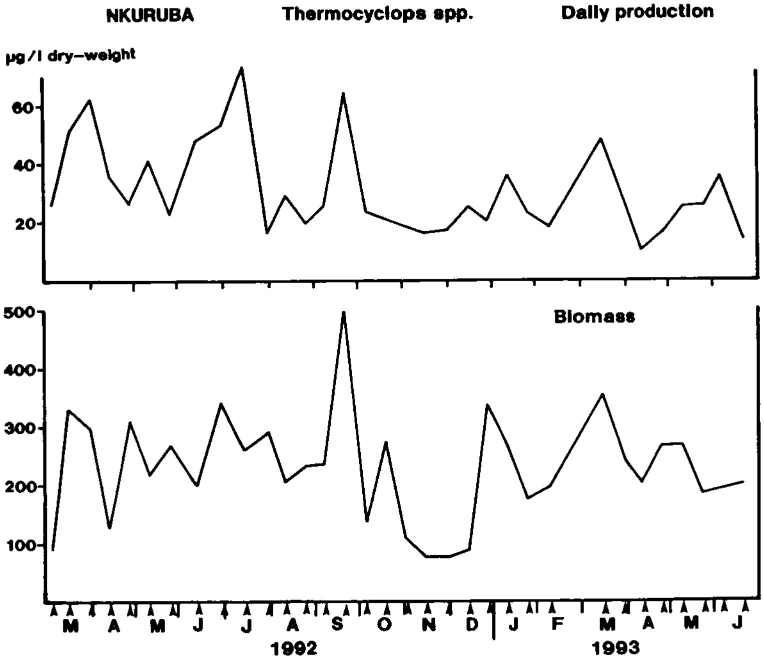


Fig. 47. — Lake Nkuruba 1992/1993, 0 - 10 m, *Thermocyclops spp.* mean biomass μg l^{-1} (dw) and mean daily production μg l^{-1} (dw) d^{-1} variations.

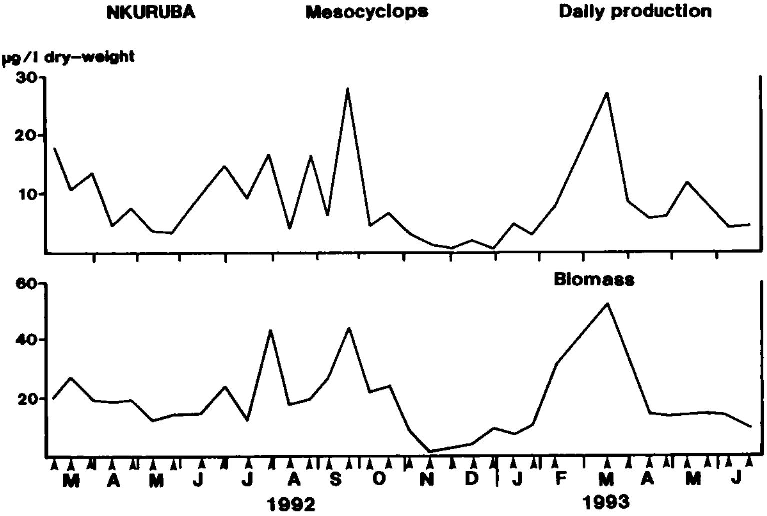


Fig. 48. — Lake Nkuruba 1992/1993, 0 - 10 m, *Mesocyclops aequatorialis* mean biomass μg l^{-1} (dw) and mean daily production μg l^{-1} (dw) d^{-1} variations.

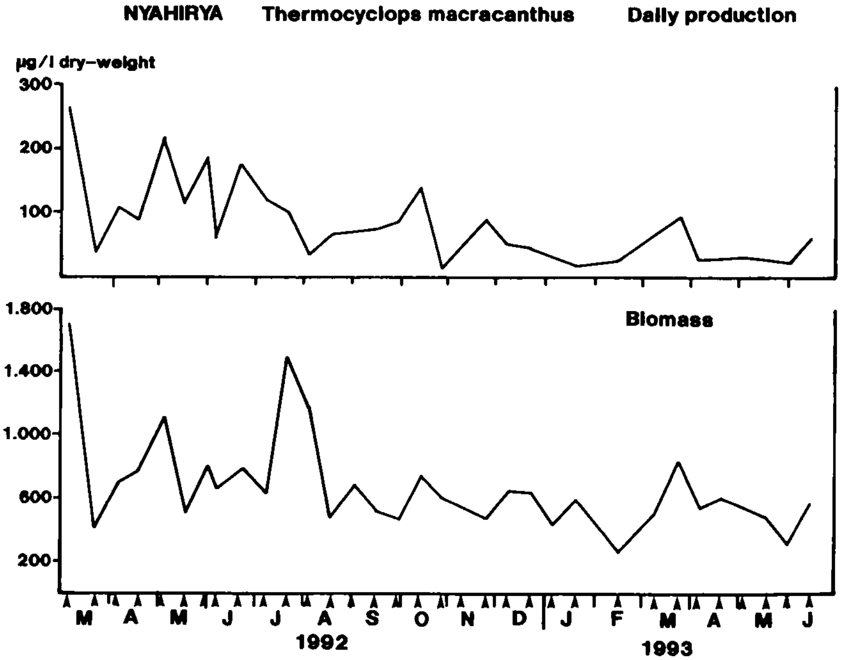


Fig. 49. — Lake Nyahirya 1992/1993, 0 - 10 m, *Thermocyclops macracanthus* mean biomass µg l^{-1} (dw) and mean daily production µg l^{-1} (dw) d^{-1} variations.

4.7. SECONDARY PRODUCTION

Lake Nkuruba's *Thermocyclops* spp. daily production µg $(dw)l^{-1}$ during the investigation period is shown in figure 54. The maximum production peaks occur in March, July and September in the first year and March the following year, the minimum during April, end of May, late July, October to December in the first year and February and April of the following year. Increases in production coincide more or less with increases in biomass. Daily production ranges from 16.48 to 74.0 µg $(dw)l^{-1}$. Annual mean production is 31.84 µg $(dw)l^{-1}$ d^{-1} (n = 24, SD = 15.96). The March-April and June-July production increases are a result of intensified breeding activities. That of September is due to both egg standing crop and post-embryo biomasses. The same is true for production peaks that appear in January and March in the following year.

A dependence of *Thermocyclops spp.* production on phytoplankton biomass is evident (*cf.* fig. 6). Increases in *Thermocyclops spp.* biomass, breeding activities and production are preceded by a decrease in phytoplankton biomass in the first six months of 1992, and an increase in phytoplankton biomass in November-December is followed by an increase in production from February to March the following year.

Mesocyclops aequatorialis daily production is shown in figure 48. Production peaks occur at the beginning of the investigation and repeatedly from June-September in the first year. Another pronounced peak occurs in March in the following year. A dependence of production on egg numbers and total post-embryo biomass is apparent (*cf.* fig. 44). The August peak in the first year is due to intensified breeding activity while that of September of the same year is to both breeding intensification and post-embryo biomass. Low production rates, occurring during April-June of the following year, are due to a decrease in breeding activities and post-embryo standing crop biomass. An increase in production and total biomass in the first and second year is preceded by a decrease in phytoplankton biomass.

Daily production estimate from 12.4.1992 to 29.3.1993 for the species ranges from 0.64 to 27.84 µg(dw) l^{-1}. The annual *M. aequatorialis* daily production mean is 8.15 µg (dw) l^{-1} (SD = 7.39, n = 25).

The production of *Thermocyclops macracanthus* in Lake Nyahirya is shown in figure 49. The atypical big production of 265.3 µg (dw)l^{-1} d^{-1} occurring on 5.3.1992 may be due to an unusually high concentration of adults and their intensified breeding activities (fig. 36). Other production peaks occur in the first year during early and late May, June, October and November, and in March the following year. A production minimum appears in the first year in March, early June, early August, late October and December and January to February in the following year. *T. macracanthus* production peaks are generally preceded by phytoplankton biomass peaks (fig. 6). The low production rate in July of the first year is due to a decrease in the breeding activities despite high post-embryo biomass prevailing at the time. The reason for the increase in *T. macracanthus* production and phytoplankton biomass in the first year may be due to nutrient enrichment from the hypolimnion supposedly due to the tectonic movement of the basin. Earthquakes are a common feature affecting the region.

The annual *T. macracanthus* daily production mean estimated from 5.4.1992 to 22.3.1993 is 87.11 µg (dw)l^{-1} (n = 25, SD = 53.80), and the annual production range is 13.2 to 223 µg (dw)l^{-1} d^{-1}.

The secondary production of the three studied cyclopoid species shows strong dependence on phytoplankton productivity, egg and breeding females densities, post-embryo biomasses and on changing environmental conditions in the lakes.

5. Discussion

5.1. LAKES' PHYSICAL ENVIRONMENTS AND PHYTOPLANKTON PRODUCTIVITY

The distribution and productivity of organisms in an aquatic ecosystem are directly influenced by the state of the physical environments. For planktonic life, temperature, light and dissolved oxygen are physical factors that can clearly limit habitat quality. Anoxic or hypoxic waters can create barriers to plankton distribution or confine it to a defined depth in a water body. Lakes Nkuruba and Nyahirya like other crater lakes in Western Uganda, are meromictic and show permanent stratification with respect to dissolved oxygen and temperature (BEADLE 1963, 1966; MELACK 1978; KIZITO *et al.* 1993; KIZITO & NAUWERCK 1995, 1996). In the tropics, the mixing of lake waters by wind action promotes organic production, e.g. Lake Victoria (FISH 1957, TALLING 1965), Lake George (BURGIS *et al.* 1973). Permanently stratified lakes like Tanganyika and Malawi show evidence of seasonal stirring as a result of seiche movements (BEAUCHAMP 1953, COULTER 1963). The effect of the mixing period on lake circulation is strongly determined by lake morphometry (HECKY & KLING 1987). Mixing in temperate lakes is mainly a function of the changing seasons. In the crater lakes under study, wind action may not be the main cause of the observable sudden mixing that takes place. The crater lakes have a small surface area but a great maximum depth.

Mixing occurs especially during the dry season. This could be a result of evaporative cooling of the surface water. The colder surface water then sinks meeting cooler waters underneath. However, this is not likely to be the only explanation for the mixing events because at times, mixing of the water column also occurs during the rainy season. The lakes' surface temperatures remain relatively warm during the rainy season, mainly because of a reduced evaporative cooling effect. The presence of stable thermoclines in the lakes render them to be less productive than otherwise could be expected from phosphorus concentrations.

Wash-down of nutrients into the lakes by rain runoffs increases photosynthetic activities and dissolved oxygen levels. High dissolved oxygen levels during the dry season (e.g. Lake Nyahirya) in December-January instead may be due to an increase in photosynthesis.

Rainfall and its runoff input nutrients in the lakes and also breaks down standing phytoplankton structures in a way promoting successions of the plankton (HECKY & KLING 1987). Rainfall has been shown in other tropical lakes to enhance organic production through episodal nutrient input by either flowing rivers or direct precipitation (BURGIS 1974, MAVUTI 1990).

The rapid decrease in dissolved oxygen with depth is attributed to increases in respiration rates due to bacterial decomposition.

The observed low secchi disc readings in the actual lakes do confine the euphotic depth to not more than 10 m. Low secchi depths are due to high turbidity in the lakes caused by the presence of detritus and very high densities of bacteria/pico algae (KIZITO *et al.* 1993). This also explains why dissolved oxygen levels get quickly depleted around the position of the oxycline. High turbidities reduce light penetration in lakes. Changes in secchi depth are better correlated with rainfall than phytoplankton productivity. Higher secchi readings obtained during the rainy season are due to an increase in lake transparencies.

The two lakes had been previously classified as mesotrophic mainly because of their phosphorus loading (KIZITO *et al.* 1993). Their phytoplankton biomasses ranged from 0.8 to over 16.0 $\mu g\ l^{-1}$ Chl a. Changing chlorophyll concentration could be a direct consequence of increases in productivity through "Nutrient boosts" from either autochthonous or allochthonous sources like precipitation. The herbivorous zooplankters also exert feeding pressures on the phytoplankton, thereby reducing its standing crop.

Relatively low primary production in the lakes may be caused by limitations like light penetration and required nitrogeneous compounds.

5.2. ZOOPLANKTON HORIZONTAL DISTRIBUTION AND DIEL VERTICAL MIGRATION

5.2.1. Horizontal distribution

Heterogeneous distribution of zooplankton is a widespread phenomenon. Different views and opinions relating to the causes have been advanced mainly by workers from the temperate region, e.g. behaviour of the zooplankton daily periodic migration patterns (SIEBECK 1968, 1980; PREISSLER 1974). NAUWERCK (1978) relates swarm formations to factors like advantages in food finding, predator avoidance and genetic differentiation within a population. BURGIS *et al.* (1973) described it for Lake George as being influenced by flow through and increased fish predation along the shore line. In agreement with the above findings, the crater lakes' zooplankton is not homogeneously distributed. The quantification of the zooplankton from a fixed depth (3 m) introduces some weakness in the actual findings. But, nevertheless, a general picture of the distribution pattern is portrayed. An avoidance of the shoreline is generally observed in most zooplankters. Occasionally this generalization is violated as in the case of Lake Nkuruba where wind blowing in one direction may have exerted some pressure on the underlying water strata.

In the case of Lake Nkuruba, there could possibly be increased predation along the shoreline by *Poecelia reticulata* and littoral invertebrates. Zooplanktivorous feeding habit of this fish has been reported for Lake Naivasha, Kenya, by WHITE (1982) and MAVUTI (1990, 1994). The relatively high correlation existing between *Thermocyclops* spp. and *M. aequatorialis* in Lake Nkuruba points at similarities in niche preferences or interdependences.

Lake Nyahirya's *T. macracanthus* concentration of its adult and copepodide population to the northwest of the lake could be a response to the availability of quality food or accidental swarms. *M. micrura* distribution patterns in the lake could be attributed to a territorial feeding behaviour or swarming of its population.

Ceriodaphnia cornuta in Lake Nyahirya clearly prefers dwelling along the shoreline. This could be because of the presence of organic detritus brought in by rain runoffs from nearby cultivated land on which *Ceriodaphnia* is known to feed (NAUWERCK 1963).

5.2.2. Diel vertical migration

The inhabitation by zooplankton of the anoxic/hypoxic hypolimnion of some Western Uganda crater lakes (BEADLE 1963, KIZITO *et al.* 1993) led the author to expect either the existence of a strong migration behaviour in the lake's zooplankton or an adaptation to withstand anoxic/hypoxic conditions.

Most (DVM) research attempt to provide explanations for ultimate causes of migration patterns in lakes (LAMPERT 1993). DVM can be a fixed or induced behaviour (PIJANOWSKA 1993). It was earlier hypothesized that zooplankton migrates vertically to remain within the optimum light zone (BOWERS 1979). Others such as MCNAUGHT & HASLER (1964), RINGELBERG (1964) and TERAGUCHI *et al.* (1975) correlate it to the rate of changing light intensity. According to ZARET & SUFFERN (1976), BOLLEN (1992), LAMPERT (1993), diurnal migration can also be an evolved mechanism of avoiding predators. Planktonic crustaceans migrating diurnally appear to trade off the benefits of reduced mortality by taking refuge (DUNCAN *et al.* 1993). Diurnal vertical migration may not take place in lakes where predation pressure is not significant (GLIWICZ 1986) and planktonic animals seem to remain in deeper water, surviving on whatever food is available where the risk of visual predation is high in the lit layers (GLIWICZ & PIJANOWSKA 1988). Other planktonic preys adopt the strategy of "better dead than unfed" by remaining at the surface during the day (HUNTLEY & BROOKS 1982, JOHNSON & JAKOBSEN 1987). Others "better hungry than dead" spend the day in deeper waters and ascend to the surface at night (KREMER & KREMER 1988, LAMPERT 1989). Abiotic environment variables like day length, temperature, dissolved oxygen and biotic factors like food presence, crowding and predators influence the zooplankton's physiological state which in turn influences the internal motivation to migrate (RINGELBERG 1980). Very little is known of the genetic constitution of zooplankton as the inducing factor of migration.

Apart from *Chaoborus* larvae and to a lesser extent *Oncocypris*, the results of the present study only reveal a limited migration behaviour of the zooplankton. *Chaoborus* is known to perform diel vertical migration and is adapted to withstand anoxic conditions during day time (JUDAY 1909, WORTHINGTON 1931, DAWIDOWICZ 1993).

Oncocypris only showed moderate migration despite the fact that a great proportion of its population inhabits anoxic waters most of the time. The kind of adaptation to hypoxia remains unclear. Some adaptation in respiration physiology survival for a long time in low oxygen conditions might be involved.

Moina micrura showed some significant nocturnal upwards migration of its population. The explanation for this migration is not very clear but could be associated to some metabolic advantages like moving to better oxygenated surface waters. WORTHINGTON (1931) reported DVM of Lake Victoria Cladocera. WORTHINGTON (1931) and MAVUTI (1992) did not report significant migration of the cyclopoids.

For the cyclopoids, it is known from other studies that the migration behaviour of males, females, copepodides and nauplii within a population often appears to differ substantially (REDFIELD & GOLDMAN 1980, NAUWERCK 1993a).

Thermocyclops spp. of both lakes only showed a gentle descent of their population at sunset. Many instances of reversed migration (downward movement at night) of zooplankton of this kind have been described in literature (for review see BAYLY 1986). Reversed migration can in fact be an indirect effect of the avoidance of larger invertebrate predators that perform normal DVM (LAMPERT 1993). For instance, NEILL (1990) reported migration of diaptomids in the opposite direction, as the predatory larva of *Chaoborus trivittutus* showed "normal" DVM. The cyclopoids of both lakes, except copepodide stages of *M. aequatorialis* and nauplii, descend after sunset, thus avoiding sharing the same space with *Chaoborus* larva which is known to predate on them. *Chaoborus* appears to be the main predator in the pelagic of the lakes.

The apparent non-migration behaviour of *T. macracanthus* nauplii at a depth of 8 m in Lake Nyahirya may reflect their feeding habits and preferences. This is about the position of the oxycline which is characterized by the presence of high densities of pico alga/bacteria and flagellates which may be a preferred food by the nauplii. This means that they are adapted to withstand the hypoxic condition there, or perhaps, they can perform occasional migration upwards to replenish their oxygen supplies.

In Lake Nkuruba, the presence of a zooplanktivorous fish, *Poecelia reticulata,* does not appear to influence the zooplankton migratory behaviour significantly. This is likely to be due to the fact that the fish distribution is only confined to the shoreline of the lake and does not appear to spread to the pelagic (CHAPMAN, pers. comm.).

5.2.3. Temporal and average depth distribution

Unfortunately, continuous studies of this kind have not been conducted on tropical African lakes. Most studies have only treated the quantitative aspects and do not touch the temporal and vertical distribution of the zooplankton (e.g. BURGIS 1971, 1973, 1974; BURGIS *et al.* 1973; GRAS & SAINT-JEAN 1983; HART 1987; MAVUTI 1983, 1994). These studies have been conducted on large and relatively shallow lakes that do not show permanent stratification. A differentiation between tolerance and preference is a pre-request when vertical distribution of different species is seen in relation to ecological factors, such as oxygen and temperature. Tolerable conditions must therefore be present in a lake for a species to occur. And values of temperature and oxygen tension found within these layers define the tolerance levels for each species (LARSSON 1971).

Work from temperate lakes therefore provides better comparison for spatial and temporal aspects (e.g. NAUWERCK 1963, 1993a, b; EINSLE 1968; MODER 1986). One important physical parameter that influences zooplankton distribution in temperate lakes is temperature. It varies seasonally and vertically in the water strata, especially for deep lakes. Some meromictic temperate lakes show permanent dissolved oxygen stratification (e.g. LARSSON 1971, NAUWERCK 1993b). In the two studied crater lakes, light and temperature do not seem to govern the vertical distribution of the zooplankton. The main factors are likely to be dissolved oxygen level tolerances, food availability, and to a lesser extent, presence or absence of predators. *Chaoborus* larva is known to selectively feed on crustacean zooplankton (PASTOROK 1980). It is also adapted to stay in an anoxic environment (e.g. JUDAY 1909).

Food organisms (phytoplankton) for herbivores have their maximum distribution in the epilimnion of the lakes (KIZITO *et al.* 1993). It is therefore not surprising that most crustacean zooplankton is concentrated on the epilimnion. Differences in vertical distribution by different zooplankton species may be an adaptation to minimize interspecific competition for space and food. Food preferences by different species vary. This may dictate the way the zooplankton is vertically distributed in the lakes. The majority of the zooplankton in the actual lakes seem to be adapted to an environment with frequently changing conditions of high and low dissolved oxygen. In any case, the present study also demonstrates through laboratory experiments great tolerance to anoxia and hypoxia by the cyclopoids. There is up to now no explanation for the occurrence of zooplankters in the entire water column at the beginning of this investigation. This could have been a result of sudden mixing of the water column. One possible explanation could be that of tectonic movements of the lakes basin. Earthquakes and volcanic activity are common features of the region.

The zooplankton distributed at or below the oxycline, for example the nauplii and *Ceriodaphnia cornuta* from Lake Nyahirya, could be in some way adapted to withstand hypoxic conditions and feeding on the high densities of bacteria and detritus present at this depth.

A similar explanation could hold true for the minor copepodide I-III peak distributed around the oxycline. Apart from the cladocera, whose densities diminish or disappear from the plankton during the dry season, the rest, especially the cyclopoids, shows the continuous presence with fluctuations of their abundances. The cladocera have their best development usually at the beginning and during the rainy season. This could be due to the presence of favourable and quality food conditions. Cyclopoids abundance peaks tend to develop more during the dry season. This tendency has been observed for other lakes (e.g. BURGIS 1971, MAVUTI 1983). It could be that the cyclopoids are able to withstand shorter starvation periods better than the cladocera, so in this regard they can survive longer and accumulate in the lakes plankton especially during the dry season.

Like the cladocera, *Oncocypris* shows its best development during the rains. Presence of quality and preferred food at the time is a more likely explanation. It is also known from large lakes that phytoplankton succession can be triggered off during the rains mainly because of nutrient enrichment which promotes their development (HECKY & KLING 1987).

5.3. LABORATORY CULTIVATION OF CYCLOPOIDS

A species has a competitive advantage over another when the speed of development of embryonic and post-embryonic stages is high (MAIER 1989). Eggs, naupliar and copepodide duration times provide the baseline data that is required for the estimation of production. A literature survey of freshwater copepod embryonic development time is given in HERZIG (1983). Because of possible differences in adaptation, embryonic and post-embryonic development times of zooplankton from tropical water bodies should not be compared directly without reservations with that of related species from higher latitudes. Variation in duration times may be due to experimental conditions but above all to adaptation effects and to genetic differences among populations caused by geographical separation (HERZIG 1983). Information on tropical Africa freshwater zooplankton embryonic and post-embryonic development times is still limited to a few studies, e.g. Lake George (BURGIS 1970, 1971), Lake Chad, (GRAS & SAINT-JEAN 1976), Lake Roux Orange River, South Africa (HART 1985), Lake Awasa (MENGESTOU & FERNANDO 1991), Lake Naivasha (MAVUTI 1994).

5.3.1. Egg development times

The egg duration times of Lake George's *Thermocyclops hyalinus* and *Mesocyclops leuckarti* were reported to be similar (BURGIS 1970). The latter was determined by Einsle (pers. comm.) to be *Mesocyclops aequatorialis*. This confirms KIEFER (1981) and VAN DE VELDE's (1984) revision of the African species of the Genus *Mesocyclops* where *M. leuckarti* was not found. The egg development times of the present study for a temperature range of 20-33 °C are slightly faster than those reported by Burgis but falling within the same range. Similarity of egg development times of Lake George and Lake Nkuruba's *Mesocyclops* may be due to the fact that *Mesocyclops* of the two lakes belong to the same species.

Compared to MENGESTOU & FERNANDO (1991), *M. aequatorialis* egg development times are shorter at 20 °C but longer at 25 ° and 30 °C than those of the present study. The egg duration times of *T. tenellus* from the present study are generally shorter than for *M. aequatorialis*. The average temperature to which the eggs are exposed is the determining factor in their rate of development (ELSTER 1954). A retardation of egg development of *M. aequatorialis* from the present study and also reported by BURGIS (1970) is explained by BOTTRELL *et al.* (1976) to be a common occurrence at a temperature greater than 30 °C. These high temperatures are, however, unimportant for the present investigation because they are never met in the crater lakes.

A detailed knowledge of reproduction biology and interclutch times of planktonic copepods is indispensable for the comprehension of its population dynamics (MAIER 1992). Literature on the subject is reported by SMYLY (1970), WHITEHOUSE & LEWIS (1973) and MAIER (1992).

The presence of equal percentages of both sexes in populations increase their chances of mating. Often several attempts of a male are necessary to transfer spermatophores successfully (HOLMES 1903). This is in agreement with the finding of the present study where mating time of *M. aequatorialis* lasted up to half an hour at 20 °C. The egg clutches produced in culture by the two investigated species are comparatively larger than those observed in the lakes. Better feeding conditions in the cultures than those occurring in the crater lakes could be a possible explanation for the difference.

The production of many successive egg clutches by the females of the studied species without requiring further mating with the male is true for cyclopoid copepods as a group (MAIER 1992, WHITEHOUSE & LEWIS 1973). A temperature range of 20-30 °C appears to be optimum for the egg clutch production for the two species. Very short interclutch times as observed for *T. tenellus* at temperatures greater than 20 °C enable the species to produce a large number of offsprings despite the small egg clutches they are able to make. Although the interclutch time generally appears to be temperature-dependent, other factors like food quality, quantity, physiological state and age of breeding females play a role. This partly explains the long time ranges observed for the two studied species at different temperatures. But for the present study, food was always supplied in abundance, and was therefore considered not to be limiting. Long interclutch periods observed at low temperature (15 °C) may be caused by a lack of adaptation. Overlapping cohorts and generations in cyclopoid population is a consequence of the production of many clutches by breeding females.

5.3.2. Post-embryonic development

BOTTRELL *et al.* (1976) stressed the importance of food as a regulating factor for post-embryonic development. In the present study food was supposed not to be limiting as it was always supplied in abundance. The development times could therefore be assumed to have been mostly temperature-dependent. Post-embryonic development times from higher latitudes were given by MUNRO (1974), GOPHEN (1976), JAMIESON (1980), VIJVERBERG (1980), ABDULLAHI & LAYBOURN-PARRY (1985) and MAIER (1989, 1992).

The mean naupliar development times of 2.0-4.2 days reported by MENGESTOU & FERNANDO (1991) for *M. aequatorialis* from Lake Awasa for a temperature range of 20-30 °C are much faster than those of the present study (5.8-12.8 days for the same temperature range).

BURGIS (1971) reported a development time of 6 days for *Thermocyclops hyalinus* nauplii at a temperature range of 25-27 °C. Her values fall within the same range as the present study, mean 7.1 days and range 5.2-9.0 days.

From the results of the present studies *M. aequatorialis* showed a faster development of its combined naupliar stages at temperatures of 20, 25 and 30 °C than *T. tenellus*. This reveals a more advanced adaptation of *M. aequatorialis* to warm waters than in *T. tenellus*. *T. tenellus* naupliar development times do not seem to change dramatically with increasing temperature. For example, at 15 °C the development time is 18.37 days and at 20 °C it is 16.10 days. A big increase in development time is observed in the case of *M. aquatorialis*, e.g. it is 26.36 days at 15 °C and 12.80 days at 20 °C.

5.3.3. Combined copepodides development times

Males of the investigated species generally developed faster than the females. This is in agreement with the findings of other authors (e.g. MUNRO 1974, GOPHEN 1976, JAMIESON 1980, VIJVERBERG 1980, ABDULLAHI & LAYBOURN-PARRY 1985, ZANKAI 1987 and MAIER 1989, 1992).

Faster development of males may ensure mating success as adult female moults are met by males with already formed spermatophores ready to mate. Faster development could also explain the existence of higher ratios of males in natural populations at different times.

From the findings of the present study the optimum temperature for the development of the combined copepodide stages of *M. aequatorialis* is 25 °C. This relatively high temperature occasionally occurs in the epilimnion of Lake Nkuruba where the species was collected. The combined female copepodide duration time of *M. aequatorialis* was 29 days compared to 13.84 days for *T. tenellus* at 15 °C. The male copepodide did not moult to adult instar. This again confirms that *M. aequatorialis* is less fitted to living in cold waters than *T. tenellus*. In fact, the two species never experience such extremes in temperature changes in the natural condition of the lakes. But they showed good acclimatization to working laboratory temperatures.

5.4. DISSOLVED OXYGEN TOLERANCE LEVELS

Survival experiments can provide useful information about the potential limits of occurrence of a given species (STICKLE *et al.* 1989). The crater lakes' zooplankton is adapted to living in an environment of low oxygen tensions. The present study reveals a considerable tolerance to anoxia/hypoxia by the two species. This could be due to an adaptation of their respiration physiology. However, *T. tenellus* is less adapted to anoxia/hypoxia than *M. aequatorialis*. This finding is reflected in the vertical distribution of the studied species. *T. tenellus* resides near the lake surface whereas *M. aequatorialis* can have its populations distributed even deeper. *M. aequatorialis*' ability to survive for more than 8 days at dissolved oxygen concentration of 0.50 mg l^{-1} is further evidence for the species' greater tolerance to hypoxic conditions.

5.5. CRUSTACEAN ZOOPLANKTON PRODUCTIVITY, BIOMASS FLUCTUATIONS AND PRODUCTION IN THE TWO LAKES

There is convincing evidence that population densities and production rates of the crustacean zooplankton in the two lakes fluctuate mainly with rainfall and mixing rates of the water columns. Nutrient enrichments resulting from either rain runoffs or mixing, directly or indirectly affect the phytoplankton productivity that primarily serves as food resources of the herbivores.

In high latitudes the growing season is very short, and important determinants of seasonal cycles are the length of the growing season and the speed with which the animals can grow (GREEN 1976). Growth in the temperate regions is mostly limited by temperature (MCLAREN *et al.* 1969), although in some instances predation like that of invertebrates may play a role (e.g. HALL 1964, WRIGHT 1965). In the tropics, water temperature does not seem to limit production (HECKY & KLING 1987). The rate of egg production of the zooplankton is an important determinant of population size and is generally found to depend upon environmental temperature and food levels (EDMONDSON *et al.* 1962, WEGLENSKA 1971).

Presence of ingestible phytoplankton is expected to be matched with an increase in egg production (GREEN 1976, HART 1987). In the crater lakes studied, the first seven months were characterized by high phytoplankton biomass and breeding activities of *Thermocyclops*. A decrease in chlorophyll a concentrations of the two lakes was generally followed by a decrease in population densities and biomasses. Total numbers and biomasses of both *Thermocyclops* and *Mesocyclops* tended to develop more during the dry season than the rainy season. This tendency has been also observed for large shallow lakes (e.g. BURGIS 1971, MAVUTI 1983).

BROCKSEN *et al.* (1969) suggested phytoplankton might be low at times of high birth rates because of greater utilization by egg producing adults. This situation was evident for Lake Nkuruba's *Thermocyclops* population during the month of

September in the first year of investigation, when total count densities and breeding activities were high but chlorophylla concentration low. In Lake Nyahirya, the possible presence of ingestible phytoplankton generally seems to match well with an increase in egg production, total counts and biomasses of *T. macracanthus*.

M. aequatorialis' breeding activities and biomasses are observed to increase after a decrease in chlorophyll a concentration, which points to a time-lag in food utilization. Late copepodide and adult stages of *M. aequatorialis* are also known to be partly carnivorous (e.g. FRYER 1957, BRANDL & FERNANDO 1975).

The Cladocera *Ceriodaphnia cornuta* (Lake Nkuruba) and *Moina micrura* (Lake Nyahirya) were generally present in low numbers. No clear seasonal successions were observed during the time of investigation. Similar observations had been reported by BURGIS (1973) for Lake George, Uganda. An exceptional case was during the second year of investigation when *C. cornuta* biomass in Lake Nkuruba reached high values. This could have been a response to favourable food conditions in the lake. The cladocera populations of the two lakes show better development at the beginning and during the rains, and thereafter their numbers drop significantly, or sometimes disappear in favour of the more starvation-adapted Cyclopoids (BURNS 1988). The Cladocera of the two lakes therefore appear to be r′ selected species (see PIANKA 1970).

Phytoplankton successions in large lakes have been reported to start with the rains mainly because of improved nutrient conditions (HECKY & KLING 1987). Favourable food conditions like the presence of ingestible phytoplankton could be present in the lakes from the onset of the rains.

Phytoplankton may not be the only zooplankter's food in the lakes. There is now growing evidence especially from temperate lakes that detritus, organic aggregation and associated bacteria could also be utilized (NAUWERCK 1963, GLIWICZ 1969).

Cyclopoid egg stock increases in the lakes seem to be rather associated with the existence of more breeding females than with the clutch sizes. The variation in clutch sizes of the *Thermocyclops* populations of the two lakes is not remarkable, e.g. Lake Nkuruba 11.43 ± 1.01 and Lake Nyahirya 9.11 ± 1.21. The *Thermocyclops* females of Lake Nkuruba are bigger than those of Lake Nyahirya (tab. 6 and 7). Therefore they may be capable of making larger clutches than those of Lake Nyahirya. A variety of demographic factors, especially adult size with its bearing on fecundity and proportion of breeding animals will affect birth rates (GEORGE & EDWARDS 1974). Low clutch sizes are of further interest as they may suggest that predation is not important as a mortality factor (GREEN 1976).

Calculations of instantaneous birth rates using egg numbers may have overestimated the real values, because the failure to hatch of some eggs is included in the calculation of the estimations of b′.

With small r′ values, birth and death rates would look similar. This partly explains why the estimated birth rates for the three studied cyclopoid species appeared to parallel the corresponding death rates. It also suggests strong density-dependent influences on mortality.

Cyclopoid's relatively high mortalities observed for Lake Nkuruba populations could be a result of predation pressure of *Mesocyclops aequatorialis'* late copepodide and adult stages, *Chaoborus* larvae and zooplanktivore *Poecelia reticulata* (WHITE 1982; MAVUTI 1990, 1994). No data is available on the extent of losses caused by predation. But the relatively short mean turnover times, e.g. 8.51 ± 4.44 days in *Thermocyclops* and 2.85 ± 2.48 days in *Mesocyclops aequatorialis*, strongly support the argument that there exists some significant predation on the cyclopoids of the lakes.

BURGIS (1971) reported a turnover time of 4.2 days for the Lake George's *Thermocyclops hyalinus* population. She proposed predation to be one of the causes for the losses. A mean turnover time of 11.1 days was reported for the Lake Naivasha's *Thermocyclops oblongatus* population. MAVUTI (1994) argued that there was lack of effective predation on the population.

Predation in Lake Nyahirya could only be due to the *Chaoborus* larvae. This might be one explanation for the relatively long turnover time of 12.45 days for the *T. macracanthus* population.

The relationship between the instantaneous population parameters r′ b′ and d′, and environmental factors like rainfall and mixing rates in the lakes may have indirect control over plankton seasonal cycles.

Wider fluctuations of b′, r′ and d′, mainly at the beginning of the investigation, could have been a response on improved food conditions. In Lake Nyahirya especially, there was a population explosion of *T. macracanthus* that occurred earlier, but due to food limitation it was followed by massive mortality. A steady state condition of the *T. macracanthus* population with its limited food reserves seemed to have been attained towards the end of the investigation period. The breeding females then resorted to the production of small numbers of eggs. Production went down but high biomass of the population persisted. The uncropped limnetic *T. macracanthus* in Lake Nyahirya therefore accumulated as it was not effectively predated upon by *Chaoborus*.

The Lake Nkuruba's *Thermocyclops* population did not exceed the carrying capacity of the lake as obviously was the case for Lake Nyahirya's population. The egg stock, biomass and production remained relatively high the following year. The possible presence of more predation in the lake might be responsible for the regulation of the cyclopoid populations' growth and size.

BURGIS (1971) and BURGIS *et al.* (1973) reported qualitative and quantitative continuity of the *T. hyalinus* population in Lake George. Total count densities and biomasses of crater lakes cyclopoids fluctuate considerably. No seasonal successions in cyclopoids species of the lakes occurred.

As a comparison with the results found in the framework of the International Biological Programme (NAUWERCK *et al.* 1980), the following is shown: the annual average P/B estimated for the *Thermocyclops* in both lakes was 0.13

which can be compared with Lake George's 0.08 (BURGIS 1971) and Lake Naivasha's 0.09 (MAVUTI 1994). The P/B of Mesocyclops was found to be 0.4 which seems to be very high. The annual averages of crustacean P/B from temperate and cold lakes are much lower than those of the present study, but at similar temperatures they fall into the same range.

The dry weights of developmental stages and adult instars determined by the present study are higher than those of BURGIS (1974), MAVUTI (1994) and MENGESTOU & FERNANDO (1991) but appear realistic when compared with those reported by DUMONT *et al.* (1975).

Because of the unpredictable nature of the plankton productivity and presence of anoxic/hypoxic hypolimnions, the crater lakes are not suitable for commercial fisheries. BEADLE (1966) reported the occurrence of massive fish kills in nearby Crater Lake Nkugute after a period of good production. The introduced tilapine fishes get stunted and never grow to good commercial sizes (CHAPMAN, pers. comm).

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