IV. Trophic relations

14. Trophic relations between the phytoplankton and the zooplankton

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The study of trophic relations within planktonic populations in Lake Chad is based on gut content analyses of living individuals immediately after capture. They were conducted during the 'Normal Chad' period in March 1967, November 1968 and October 1970 (Gras et al. 1971).

Their interpretation is based on two indices:

— the percentage occurrence of a particular food, that is the ratio of the number of individuals containing it to the total number of individuals under consideration;

— the relative percentage occurrence, that is the ratio of the previous percentage to the entire percentage occurrence of the various foods divided by 100 (Table 1).

14.1 Diet of the main species

14.1.1 *Cladocera, Ostracods and Calanoids*

The first group was represented by eight species (*Diaphanosoma excisum, Moina micrura, Ceriodaphnia affinis, C. cornuta, Daphnia barbata, D. lumholtzi, D.*

Table 1 Percentage occurrence of the algal species in the gut contents of Ostracods, Cladocerans and Calanoids according to morphological and size characteristics. The numbers designating algal species are those mentioned in Fig. 1. The relative percentage of occurrence is indicated in brackets.

Algae	2.3.4.	5	6	7	8.9.10.11.12	13.14	15
Ostracods	8(2)	61(17)	15(4)	8(2)	154(42)	119(33)	0(0)
Cladocera	18(8)	43(10)	27(12)	5(2)	74(32)	58(25)	3(1)
Daphnia	33(10)	64(20)	37(12)	8(3)	100(31)	64(20)	4(1)
Bosmina	7(3)	36(13)	31(11)	9(4)	65(24)	118(44)	4(1)
Calanoids	19(16)	66(13)	62(13)	32(7)	170(34)	58(12)	23(5)

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longispina, *Bosmina longirostris*) and the Ostracods by a single unidentified species. The calanoids were represented by two main species, *Tropodiaptomus incognitus* (most abundant during the observations), and *Thermodiaptomus galebi*. As a rule, observations were conducted only on adults. All these species were phytophagous or sestonophagous (feeding on algae, detritus, bacteria), no animal remains being found in the stomach contents, with the exception, however, of Calanoids where a few remains of Rotifers or crustaceans were observed. As the percentage occurrences of these prey were very low, their ingestion can be considered accidental, as the Calanoids depend primarily on particle filtration.

14.1.2 *Cyclopoids*

Three species were present in the lake: *Mesocyclops* cf. *leuckarti*, *Thermocyclops incisus circusi* and *Thermocyclops neglectus neglectus*.

The male and female adults of the first two species had a carnivorous diet; the small number of algae observed in a few individuals could either have been ingested occasionally, or been present in the guts of the captured prey.

In the copepodids of these two species, a gradual increase in the intake of animal matter was observed from the first stages to the adult stage, while the plant fraction decreased. The change in diet appeared to be gradual and did not occur at a particular stage. Gophen (1977) observed the same variation in diet of the individuals in Lake Kinneret. Therefore the diet of the first copepodid stages may be considered as mixed; that of copepodid stage 5 being almost entirely carnivorous, at least in females with a greater mean size.

Male and female *Thermocyclops neglectus neglectus* were herbivorous and carnivorous. Copepodids of this species were mainly herbivorous, the percentage occurrence of animal remains being very low: 7% for the copepodid stage 5 and 3% for the copepodid stage 4.

14.2 Composition of the gut contents

Cladocerans as a whole ingested unicellular or colonial algae ranging in size from 4 to 7 μm (coccoïd Chlorophyceae and isolated cells of *Oocystis*) up to about 30 μm (colonies or cenobes). The percentage occurrence of large algae (2, 3 and 4 in Fig. 1) was rather high for the whole group (18%) but it varied considerably especially in *B. longirostris* (7%) and the three species of *Daphnia* (33%) (Table 1).

If the consumption of filaments of *Anabaena* appears to be very low (percentage occurrence of 3), small filamentous Cyanophyceae were generally collected and absorbed by all the species of Cladocerans.

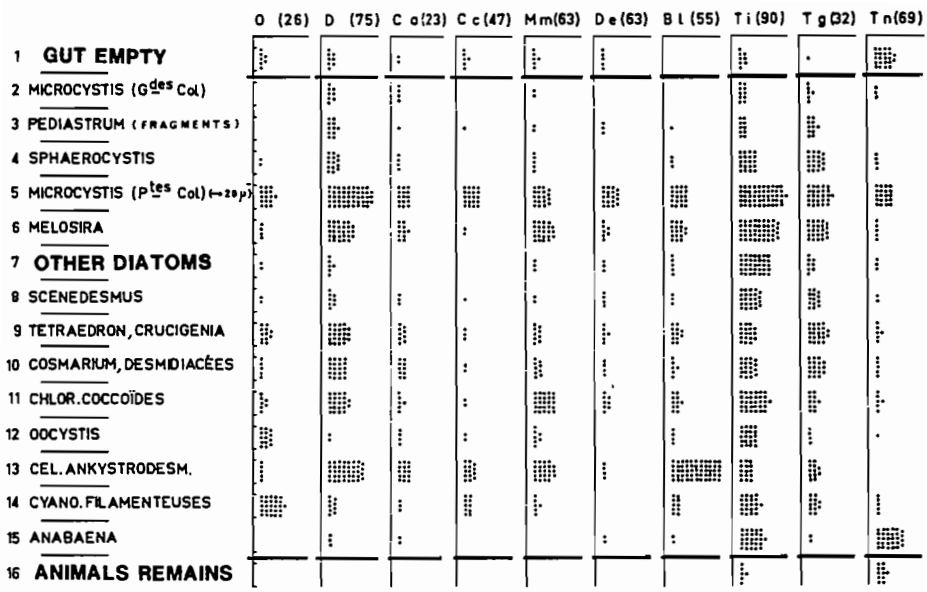

Fig. 1 Occurrence of various planktonic algae in the gut contents of planktonic Crustaceans. The number of individuals of each species examined is given between parentheses. Each point corresponds to the presence of an alga or a group of algae found in the gut contents of an individual of the species concerned; C.c. = *Ceriodaphnia cornuta*; C.a. = *C. affinis*; D. = *Daphnia* (three species); D.e. = *Diaphanosoma excisum*; M.m. = *Moina micrura*; B.l. = *Bosmina longirostris*; O = ostracods; T.i. = *Tropodiaptomus incognitus*; T.g. = *Thermodiaptomus galebi*; T.n. = *Thermocyclops neglectus*.

The algae ingested by the Ostracods ranged from *Oocystis* (isolated cells) and coccoïd Chlorophyceae from 4 to 7 µm, to small colonies of *Microcystis* (from about 25 to 30 µm). Big *Microcystis* colonies (particularly *M. aeruginosa*), *Sphaerocystis* and portions of *Pediastrum* cenobes, rather abundant in the environment during the observations, were not found in the stomach contents. Within the filamentous algae, the small species were the only ones to be ingested; *Lyngbya*, small *Oscillatoria*, *Spirulina laxissima* and Ankistrodesmiform cells, etc ... *Anabaena* was not consumed and the *Melosira* found in the guts was in the form of cell portions, such as occurred in the environment.

The two species of Calanoids under study could be distinguished from the two previous orders by the increased ingestion of large algae whose percentage occurrence reached about 79%. *Tropodiaptomus incognitus* seemed to ingest filaments of *Anabaena flos-aquae* (the percentage occurrence of this algae reached 23% for all observations and 54% during the first series of analyses) but the stomach contents of *Thermodiaptomus galebi* collected at the same stations, included no heterocysts of *Anabaena*, but numerous unicellular algae, both colonial and filamentous.

Animal remains were found in 63% and 67% of the gut contents of adult *Mesocyclops* cf. *leuckarti* and *Thermocyclops incisus circusi* (Fig. 1 and Table 2); the highest predation is on the Cladocerans. In Copepodids with a mixed diet the range of algae found in the digestive tract was roughly the same as that of the filter-feeding species; thus Chlorophyceae, small filamentous and colonial Cyanophyceae and *Anabaena* were observed. Adults of *Thermocyclops neglectus* consumed all zooplanktonic organisms but the highest predation was on the Cladocerans. The percentage occurrence of animal remains was lower in males (12%) than in females (27%). The algae identified in the gut contents were the species that were usually ingested by Cladocerans and Calanoids. The consumption of *Anabaena* was active and undigested heterocysts were often observed in the foregut and the faecal pellets (Fig. 1). The copepodids belonging to this species were predominantly herbivorous: *Microcystis* and *Anabaena* dominated the stomach contents.

14.3 Conclusions

The examination of the gut contents of the microcrustaceans made it possible to specify their diets and to determine the animal or plant groups on which the greatest predation pressure was exerted.

Within the framework of the relations between the phytoplankton and zooplankton, it must first be pointed out that Rotifers (a score of species recorded by Pourriot (1968) in the southern basin) were not considered in this study. Their density was estimated at 44 individuals per liter in 1964–65 (Gras et al. 1967) and at 80.1^{-1} in the archipelago of the southern basin in February 1971. Density ranged from 9 to 14 individuals per liter in 1967–68 (Robinson 1971) and up to 39 (see zooplankton) in the northern basin. These Rotifers fed

Table 2 Percentage occurrence of animal remains, identified or not, in the three Cyclopoid species; *N* = number of individuals examined.

	♀		♂		C5		C4		C3		C1+C2	
Species	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Mesocyclops leuckarti	185	63	51	35	37	45	70	31	88	15	49	6
Thermocyclops incisus circusi	42	67	10	0	–	–		–		–		–
Thermocyclops neglectus	166	27	43	12	30	7	36	3	14	0	6	0

mainly on nannoplankton, small detritus and bacteria with the exception of a predatory species, *Asplanchna brightwelli*, which fed on smaller Rotifers, *Bosmina* and *Ceriodaphnia*; the abundance of this species remained rather low in the lake.

In terms of biomass, however, Rotifers were insignificant when compared to microcrustaceans, at least during the period of 'Normal Chad', so that the filter-feeding species of the last group represented almost the total herbivorous zooplankton of the lake. The same holds true for the next trophic level.

During the 'Normal Chad' period (1964–65, 1971), it can be estimated that the strictly carnivorous species (adults of *Mesocyclops* and *Thermocyclops incisus circusi*) represented from 2.5 to 4% of the total biomass; species which were predominantly carnivorous or herbivorous (Cyclopoids, Copepodids and adults of *Thermocyclops neglectus*) represent from 8% to 16% and the species which were strictly herbivorous-detrivorous made up the remaining 81 to 90%. Thus, approximately 5–8% of the zooplankton stock were secondary consumers, while 92–95% fed on phytoplankton.

The accuracy of these percentages is difficult to evaluate as the rather abundant adults and copepodids of *Thermocyclops neglectus* had a mixed diet and the animal fraction in the gut contents was variable and difficult to estimate.

At the end of the 'Normal Chad' period, in 1972–1973, the percentage of strictly carnivorous species (*Mesocyclops* cf. *leuckarti* and adult *Thermocyclops incisus circusi*) remained in the range from 1.4% to 3.8%, while the population of *Thermocyclops neglectus* with a mixed diet developed and predominated over the herbivorous species during the first half of 1973; therefore, it can be taken that the percentage of plant seston consumed decreased sharply.

After 1973, during 'Lesser Chad', zooplankton density decreased greatly, by about four fifths, and strictly carnivorous species as well as the Calanoids disappeared; the only remaining species were *Thermocyclops neglectus*, with a mixed diet, and the herbivorous Cladocerans.

Finally, it seems that part of the phytoplankton, algae or large colonies and *Anabaena* were not directly ingested by the zooplankton at any stage in the lake. This part of the phytoplankton could be utilized in the form of detritus or bacteria after degradation with the exception of *Anabaena flos aquae*. The latter which represented nearly the entire algal population in low waters seemed to be directly consumed by *Thermocyclops neglectus* (adults and last copepodid stages) and *Tropodiaptomus*, i.e., a little more than 30% of the zooplankton. Then it would be reintroduced into the trophic chain at the level of the zooplankton which fed on the nutritive film deposited on the sediment or on any other substrate.

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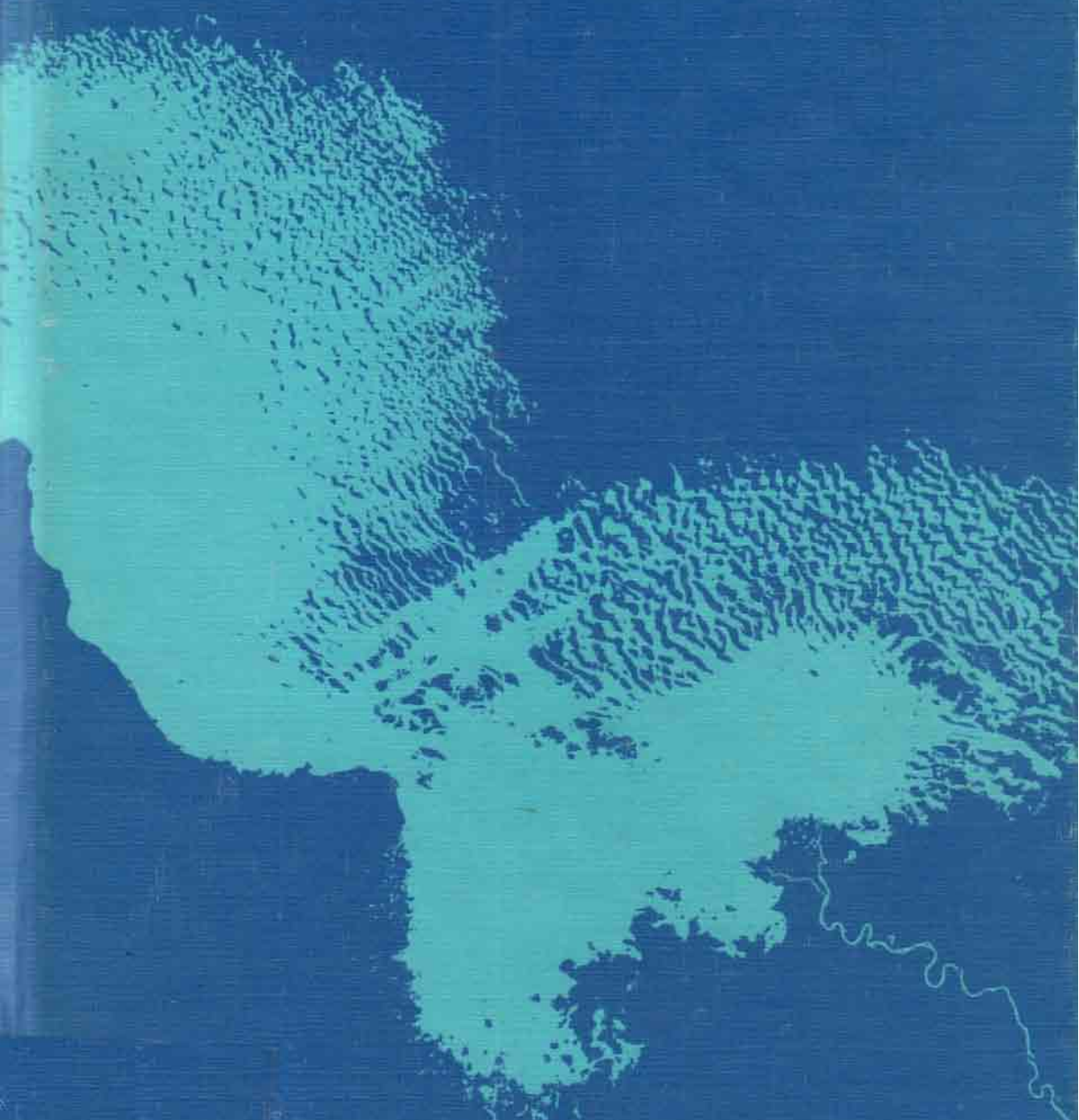

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