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Composition, density and feeding of crustacean zooplankton community in a shallow, temperate lake (Lake Balaton, Hungary)

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Abstract

Composition density and filtering rates of crustacean zooplankton were studied in the open water and among the macrophytes of the oligo-mesotrophic part of Lake Balaton from 1981 to 1983. From the individual filtering rates of the different populations and the densities community grazing rates were derived.

Copepoda made up 79–90% of crustacean plankton community in the open lake and 95–97% of it in littoral zone. Among them the nauplii dominated. At the end of summer 1982, when *Anabaenopsis* was in bloom, the filter-feeding species (*Eudiaptomus, Daphnia*) practically disappeared, being replaced by cyclopoids.

Daphnia had the highest filtering rates followed by those of *Eudiaptomus* and *Diaphanosoma.* Among copepods, the filtering rates in decreasing order were: ovigerous ♀ > all adults > copepodites > nauplii. ♀ > ♂. The filtering rates of the different species varied both seasonally as well as from year to year. In 1983, when the concentration of organic seston decreased, filtering rate increased compared with those in the earlier years. During the water bloom in 1982, the rates decreased by 70% on the average.

The community grazing rate was very low (3% per day) in the open lake and among macrophytes, both in 1981 and 1982; also the share of crustacean zooplankton in grazing was very low. In 1983, together with the improving of water quality, the community grazing rate increased 4-fold. In 1981 and 1983 the rates were influenced by water temperature but in 1982 by seston concentration.

Composition and density of zooplankton community affect the structure and abundance of phytoplankton as a result of feeding, and play a particularly important role in the regulation of nanoplankton (Porter, 1973; Gulati, 1984). Owing to the grazing performance of zooplankton, the densities of certain algal species can significantly diminish, and the whole phytoplankton of the lake can be completely eliminated by zooplankton, which can lead to the improving of water quality (Lampert & Schober, 1978; Horn, 1981; Bangerter *et al.*, 1983; Gulati, 1983). Also the herbivores are known to increase productivity of algae that can pass through their nutrient-rich alimentary canals in viable condition (Porter, 1976). Moreover, the coincidence of certain factors can lead to the developing of algal blooms (Porter, 1977). The effect of zooplankton on algal producitivity may not only differ in different lakes, but also within the same lake. It can change seasonally or more frequently depending on the composition of phyto- and zooplankton (Redfield, 1980). In lakes of low trophy, the share of zooplankton is usually greater in the regulation of algal abundance than in eutrophic lakes (Gliwicz, 1969; Gliwicz & Hillbricht-Ilkowska, 1972; McNaught, 1975; Gulati, 1983; Richman & Dodson, 1983; Muck & Lampert, 1984; Rognerud & Kjellberg, 1984).

The aim of our studies was to obtain answers to the questions: 1. in what degree do the process of eutrophication observed in the lake affect the composition and density of the crustacean zooplankton living in the open water and the littoral zone; 2. what changes are manifest in this regard in the filtering rate of the various species in the different years and seasons; 3. what role is played by the crustacean zooplankton in the regulation of algal abundance.

Description of lake

Lake Balaton is 77 km long, its surface area is 585 km^2, max. depth is 11 m; mean depth is 3.2 m, and the average temperature of water during summer is 23.2 °C (Csoma & Laczai, 1976). Phytoplankton primary productivity in the more eutrophic south-western water area was 830 g C m^{-2} a^{-1} and at Tihany 182 g C m^{-2} a^{-1} at the end of the seventies. In the latter part of the lake it increased 1.8-fold during 5 years (Herodek *et al.*, 1982). In summer, 1982 there was a bloom of the blue-green alga *Anabaenopsis raciborskii* in the south-western part of Lake Balaton, which spread over the whole surface of the lake.

Study stations and methods

The investigations were performed in the north-eastern part of Lake Balaton at the isthmus of the Tihany Peninsula, in the Bozsai Bay undisturbed by recreation, in 1981–1983 (Fig. 1). For studying the open-water samples were collected from the 190–280 cm deep water at about 800–1 000 m distance from the shore. On some occasions in 1981–1982, water samples were also taken from the macrophyte zone of 110–130 cm depth at a distance of 1–6 m from the reed belt.

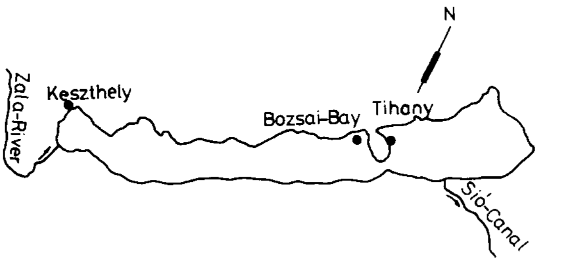

Fig. 1. Lake Balaton with the sampling station (Bozsai Bay).

Crustacean zooplankton composition and density were determined using 20–25 litre water collected with a mud-surface tube sampler of 56 mm diameter suitable for sampling the entire water column. Five or six replicates were determined. In 1983, organic carbon content (POC) was measured by the wet combustion method modified by Ostapenja (1965) in the water samples filtered through a net of 60 μm mesh. In each experiment water temperature was also measured.

For the feeding of crustacean zooplankton in situ seston (< 60 μm) was used as food. From the 20–25 litre water collected by means of the repeated lowering of the mud-surface tube sampler, 1.8–1.9 litre was passed through a nylon gauze of 60 μm mesh to remove zooplankton and large algae. To the filtered sample in the flask 7.98 MBq $NaH^{14}CO_3$ (Hungarian Isotope Institute) was added and it was suspended in the lake at about 0.5 m depth. Time of exposure was 20–24 h. Immediately before the feeding experiment, the labelled suspension (lake water) was shaken thoroughly and poured in 300 ml doses into flasks covered with aluminium foil to prevent further photosynthesis.

Crustaceans were sampled before the feeding experiment also by means of the tube sampler. The feeding experiments were carried out in flasks suspended in the lake. In 1981, the density of crustaceans used in the experiments was ten times the in situ concentration, in 1982 five times greater and from July, 1982 2–3 times greater. Periods of feeding on radioactive food were 3, 5 and 30 min, during winter 5 and 10 min were the shortest periods. In accord with gut passage time (Zánkai, 1983), filtering rates of cladoceran populations and nauplii were determined during winter by feeding for 5 min. In cyclopoid and calanoid copepodites and the adults of *Eudiaptomus gracilis*, for the filtering rate determination feeding periods used were 3 and 5 min in summer, and 5 and 10 min during winter; for adult *Cyclops* feeding time of 30 min was used. Individual filtering rate was calculated as average of the replicates.

Following feeding, the crustaceans were killed in water of 100 °C temperature and after thorough washing kept at c. 5 °C till the end of the experiment. No chemical preservation was used. The crustaceans were sorted according to species resp. developmental stages. First the animals fed for 3 min (nauplius and Cladocera) were sorted and placed in scintillation vials, the adult *Cyclops* specimens were placed last. Namely, the nauplii and Cladocera were placed in the vial 1–3 hours following killing, while the *Cyclops* 5–6 hours later. The samples were counted for nauplii, *Cyclops* and *Eudiaptomus* copepodites + adults, *Daphnia* spp. and *Diaphanosoma.* In 1983, the counts distinguished the various copepodit stages of cyclopoid copepods. Each *Daphnia* spp. was measured in length (from top of the head to the base of the tail spine). The radioactivity of crustaceans was measured in a toluene-based cocktail with a Wallace RACKBETA liquid scintillation counter following treatment with Soluene tissue solubilizer.

$$\text{Individual filtering rate} = \frac{\text{dpm. ind.}^{-1} \times 1440 \text{ min}}{\text{dpm. original susp. ml}^{-1} \times \text{feeding time (min.)}}$$
$$(\text{ml} \cdot \text{ind.}^{-1} \cdot \text{d}^{-1})$$

The daily grazing of species population was calculated as the product of individual filtering rate and animal concentration.

$$\text{Grazing rate} = G = F \times 100 \times \frac{\text{no. of anim.}}{1000 \text{ ml}}$$
$$(\% \ \text{d}^{-1})$$

Results

Of the three years of investigation, 1981 was the coolest and 1982 the warmest (average water temperature was 17 resp. 19.3 °C at noon in May–November). The amount of precipitation was also the greatest in 1982, and the summer of 1983 was the driest. Average temperatures for summer months (June–August) also differed by 1 degree in the two years (in 1981, 22.5; in 1982 23.5 °C). With the exception of July and August, water temperatures measured on the days of investigation were also higher in 1982 than in the other two years (Fig. 2).

In 1983, particulate organic carbon content of water filtered through a net of 60 μm mesh was between 1 and 4.6 mg C $\cdot$ l^{-1} 2.4 mg C $\cdot$ l^{-1} on the average. Highest values were found in spring at the time of the greatest population density of smaller algae. Autumn peaks were likely to be due – besides the quantity of algae – to the stirring up of water by winds and storms on the days preceding and during the experimental period (Fig. 2).

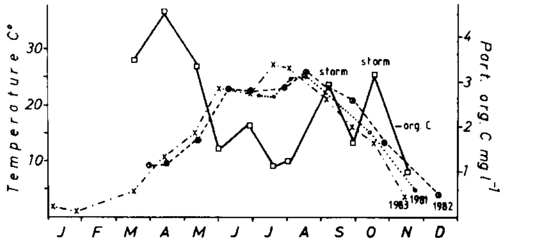

Fig. 2. Temperature of the water in Lake Balaton and the amount of particulate organic carbon in the water (<60μm).

Species composition and abundance of crustaceans

A. Open lake

During each of the three years, crustacean zooplankton community was made up of 1 Calanoida sp. *Eudiaptomus gracilis* (Sars), 3 Cyclopoida spp. [*Cyclops vicinus* Uljanin], *Mesocyclops leuckarti* (Claus), *Acanthocyclops robustus f. limnetica* [Petkovski] and 6 Cladocera spp. Of the latter ones *Diaphanosoma birgei lacustris* [Kořrinek] was represented in greatest number during summer, while *Daphnia hyalina* [Leydig] and *D. galeata* [Sars] in spring and autumn and *D. cucullata* [Sars] in summer. In the summer plankton samples, *Leptodora kindtii* (Focke) was regularly encountered, while *Alona* sp. was recorded only twice (0.3–2 ind. l^{-1}).

The crustacean densities increased from 87 in 1981, to 104 in 1982, to 140 ind. l^{-1} in 1983. The main peak in all the years occurred in August–September, with a spring increase also in 1983. Both in 1982 and 1983, the minimal density of crustaceans was usually observed at the end of winter in March, and that of early summer in June and in the first half of July, resp. (Fig. 3). In winter, the crustacean density was about 100 ind. l^{-1} on the average, in summer it increased by 25–30 ind. l^{-1}.

During the three years, copepods were generally numerically predominant (Figs. 4A, B, C). The proportion of cyclopoid copepodites and adults in the crustacean zooplankton was essentially greater in 1982, the year of algal bloom, than in the other two years (Fig. 4B). At the same time, a new species

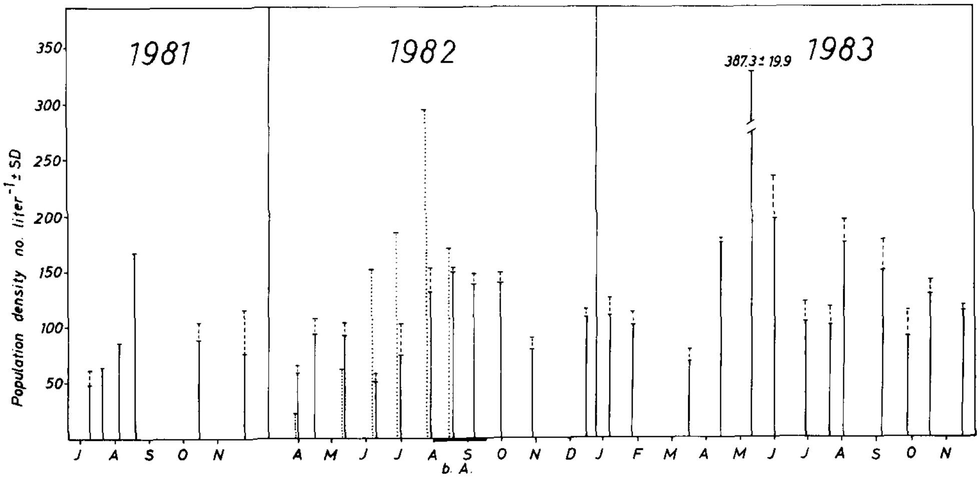

Fig. 3. Means densities with SD of crustacean zooplankton in the open lake (solid line) and among macrophytes (dotted line) during the experimental period; b. A. = bloom of *Anabaenopsis.*

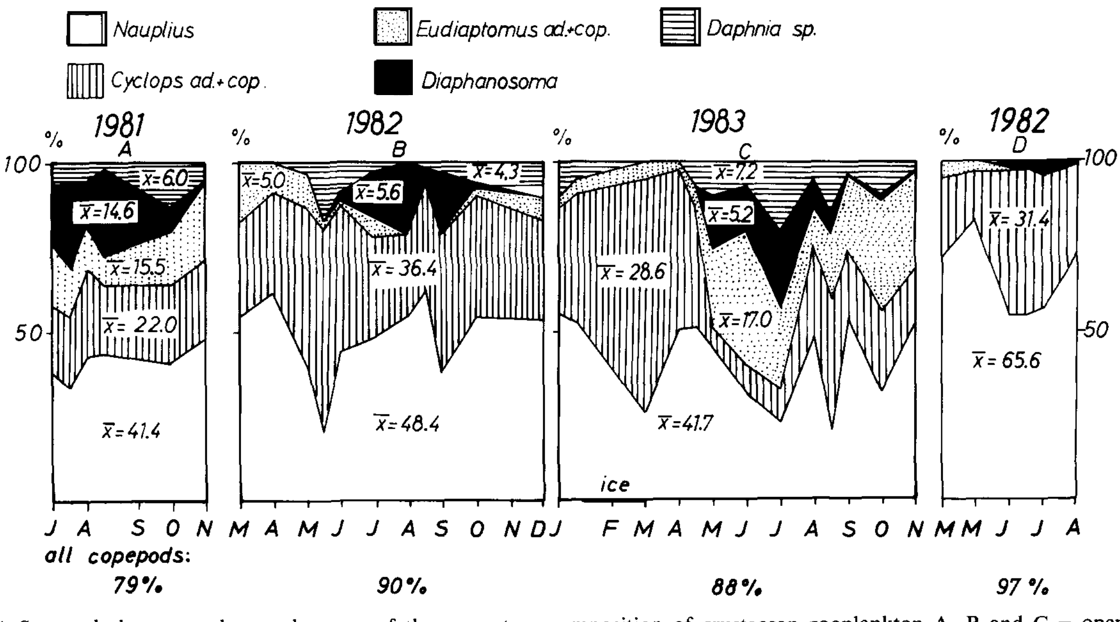

Fig. 4. Seasonal changes and annual means of the percentage composition of crustacean zooplankton A, B and C = open lake; D = among macrophytes.

of cyclopoids, *Acanthocyclops robustus f. limnetica* penetrated the open lake from the macrophytic zone and became numerous there. Relative proportion of *Eudiaptomus* in the crustacean zooplankton essentially differed from those of *Cyclops* during the 3 years. In 1982, their population greatly diminished as early as spring and did not increase until summer next year. In the period of blue-green bloom they practically disappeared from the water (Figs. 4A, B, C).

Of the cladocerans, *Diaphanosoma* only appeared in May–June and disappeared at the end of October, thus its relative proportion in the crustacean zooplankton during the experimental period was not great, reaching, however, during summer in some instances a value as high as 26%. Except in March–April, daphnids were always present in the water, their relative proportion being 5.7% on the average smallest in the period of the water bloom (Figs. 4A, B, C).

Absolute abundance of the members of crustacean zooplankton differed seasonally but annually as well. The number of nauplii being the smallest in general after thawing and at the beginning of summer, and the greatest in April–May and late summer (August–September) (Figs. 5, 6, 7). On the average 36, 51, 61 individuals were found in 1 litre water in 1981, 1982 and 1983, resp.

The mean density of the adults and copepodites of cyclopoid copepods was 21 ind. l^{-1} on the average in 1981, and was practically identical (36–39 ind. l^{-1}) in 1982 and 1983. In the population, the number of copepodites was always greater than that of adult individuals, in 1981 attaining an average value of 14 and in the other two years a value of 28–30 ind. l^{-1}. Detailed analysis of data from 1982–1983 showed that the highest relative proportions of copepodites occurred in both years in May and September and the lowest ones in summer (June–August) (Figs. 6, 7). During winter (between December and March) larval density was constant (28–32 ind. l^{-1}). In 1981, the average number of adults was 6.4, in 1982 and 1983 8.7 ind. l^{-1} (Figs. 6, 7). The majority of adult crustacean were males, occurring in great numbers

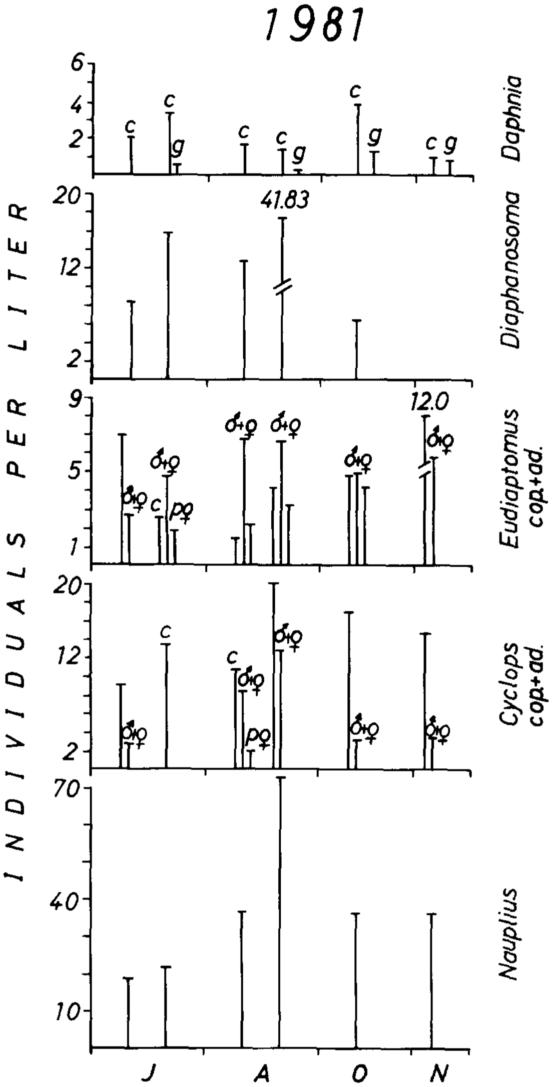

Fig. 5. Abundance of the different crustacean species in 1981. *Daphnia c = D. cucullata, Daphnia g = D. galeata.* Order in the Figs. on *Eudiaptomus* and *Cyclops*: copepodite = c, ♂, ♀, p♀ = ovig. ♀.

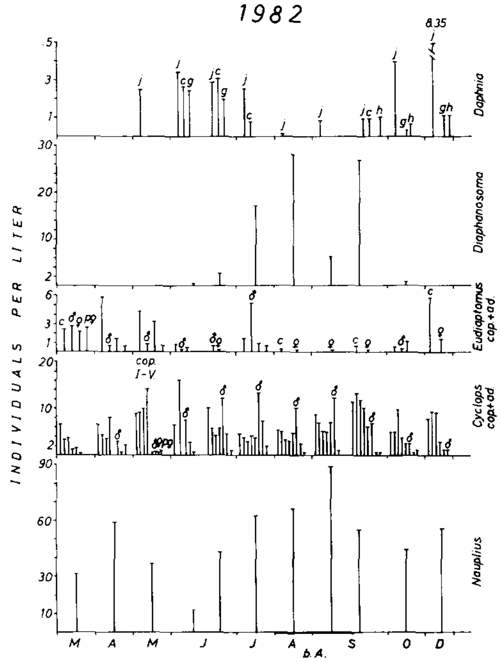

Fig. 6. Abundance of the different crustacean species in the Bozsai bay in 1982. *Daphnia j = D. juvenilis, Daphnia c = D. cucullata; Daphnia g = D. galeata; Daphnia h = D. hyalina;* Order in Fig. on *Eudiaptomus*: c = copepodite, ♂, ♀ p♀ = ovig. ♀. Order in Fig. on *Cyclops*: c = copepodite I–V, ♂, ♀ p♀ = ovig. ♀.b. A. = bloom of *Anabaenopsis.*

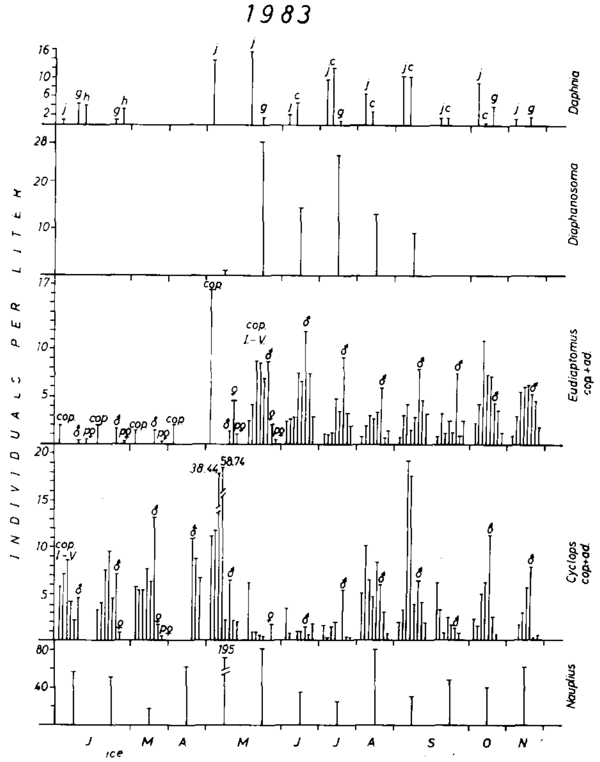

Fig. 7. Same as in Fig. 6 but for 1983.

particularly during summer 1982 and in spring 1983.

Densities of the adults and copepodites of *Eudiaptomus* differed in the three years, being 13, 4.4 and 22.4 ind. l^{-1} on the average in 1981, 1982 and 1983. 57% of the adults were males (Figs. 5, 6, 7).

In 1982, 1982 and 1983, population density of *Diaphanosoma* averaged 17, 12, and 10.5 ind. l^{-1}. Average density of daphnids was both in 1981 and 1982 4.6 ind. l^{-1}, increasing to 12.5 ind. l^{-1} in 1983 (Figs. 5, 6, 7).

B. Macrophyte zone

During spring, the number of crustaceans was essentially smaller among the macrophytes than in the open water, in summer, however, numbers of them were often two times, moreover, seaveral times greater than those collected from the open lake (Fig. 3).

Typical open water species were also collected in the littoral zone, but their numbers were much smaller. The following species were collected only before the reed belt: *Eurycercus lamellatus* (O. F. Müller), *Camptocercus rectirostris Schoedler, Simocephalus vetulus* (O. F. Müller), *Pleuroxus aduncus* (Jurine), *Pleuroxus uncinatus* Baird, *Bosmina longirostris* (O. F. Müller), *Nitocra hibernica* (Brady) and *Limnomysis benedeni* Czer.

From 55–83% of crustacean zooplankton was made up of nauplii (Fig. 4D). Their number was small during spring, later gradually increased, and in summer exceeded 100 ind. l^{-1}. Their maxima occurred in late July (167 ind. l^{-1}), c. three times the open water values. Cyclopoid copepodites and adults occurred in small numbers during spring, reaching gradually a maximal density of 116.5 ind. l^{-1} at the end of July.

Eudiaptomus was always present in the samples, its population density varying between 0.4 and 1.6 ind. l^{-1}. *Diaphanosoma* was found in summer, in June and August only a few individuals (1.1–2 ind. l^{-1}) in July 12 ind. l^{-1}. Daphnids occurred in the water only in June (1.8–2.8 ind. l^{-1}).

Feeding of crustaceans

Individual filtering rate

Individual filtering rates of the various species differed seasonally with age, place and year of collection, and in response to changes in food supply. The largest individual filtering rates were achieved by *Daphnia* species, followed by *Eudiaptomus* and *Diaphanosoma* (Tables 1, 2). Large daphnids filtered more water than the smaller ones. In the case of copepods – based on the average values – the filtering activity decreased as follows: ovigerous ♀ > adults > copepodites > nauplii. ♀ > ♂. Of the cyclopoid copepodites the feeding rate of last stage copepodites was the highest on the average, that of the stage I copepodites being the lowest (Tables 1, 2). Of the copepodites of *Eudiaptomus*, also the older specimens filtered the greatest volume of water, while filtering rates of stage I–III specimens were identical (Table 1).

In the open water, cladocerans were represented by daphnids and *Diaphanosoma*, their filtering rate being 11.1–0.48 ml·ind.$^{-1}$ d^{-1}, 2.1–0.4 ml·ind.$^{-1}$ d^{-1} (Table 1), respectively. *Alona* also consumed labelled food in each experiment, the amount of activity taken up by this crustacean often being considerable.

Individual filtering rates of cladocerans encoun-

Table 1. Seasonal fluctuations in individual filtering rates of crustacean zooplankton species and larval stages in the open lake, $ml \cdot ind.^{-1} \cdot d^{-1}$(mean ± SDM).

Species	Sample No.	Spring 21.3 – 20.6	No.	Summer* 21.6 – 20.9	No.	Algal bloom 10.8 – 20.9	No.	Autumn 21.9 – 20.12	No.	Winter 21.12 – 20.3	Year
Diaphanosoma			10	0.60 ± 0.04			2	1.77			1981
birgei lacustris	2	0.39	5	0.67 ± 0.12	6	0.16 ± 0.05	5	0.95 ± 0.14			1982
	4	1.44 ± 0.22	14	2.08 ± 0.18			1	1.27			1983
Daphnia hyalina							2	3.96			1982
(1.1 – 1.7 mm)	3	6.88 ± 1.66					1	5.39			1983
D. galeata			2	10.91			2	1.52			1981
(1.3 – 1.8 mm)	3	1.75 ± 0.36	2	3.40			2	4.25			1982
	4	6.65 ± 1.14	2	11.09			4	5.14 ± 1.68	2	4.83	1983
D. cucullata			8	2.59 ± 0.50			1	1.22			1981
(1 – 1.6 mm)	3	1.65 ± 0.10	3	2.01 ± 0.61			2	5.05			1982
			8	5.21 ± 1.82			3	1.30 ± 0.17			1983
Daphnia sp.			4	0.94 ± 0.26			2	0.50			1981
juv.	6	0.48 ± 0.13	4	0.68 ± 0.11	1	0.39	4	1.25 ± 0.23			1982
(0.4 – 0.9 mm)	5	2.83 ± 0.71	7	2.83 ± 0.76			4	1.67 ± 0.46	1	4.75	1983
Nauplius			8	0.13 ± 0.02			4	0.06 ± 0.01			1981
	4	0.11 ± 0.01	4	0.12 ± 0.06	2	0.11	3	0.14 ± 0.08			1982
	3	0.10 ± 0.01	4	0.16 ± 0.02			3	0.12 ± 0.02	3	0.14 ± 0.02	1983
Eudiaptomus			8	0.51 ± 0.12			6	0.27 ± 0.08			1981
gracilis	7	0.39 ± 0.18	1	1.14			3	1.77 ± 0.42			1982
cop.all	17	1.53 ± 0.18	43	1.68 ± 0.17			35	1.51 ± 0.22	4	1.70 ± 0.38	1983
cop. I.	2	0.93	8	1.44 ± 0.30			1	1.58			1983
II.	4	0.98 ± 0.13	10	1.46 ± 0.28			6	1.60 ± 0.44			1983
III.	5	1.33 ± 0.35	10	1.29 ± 0.18			8	0.97 ± 0.24			1983
IV.	6	1.97 ± 0.27	14	1.66 ± 0.36			10	1.16 ± 0.37			1983
V.	5	2.04 ± 0.30	14	1.95 ± 0.35			8	1.50 ± 0.33			1983
Eudiaptomus			11	0.60 ± 0.11			6	0.46 ± 0.04			1981
gracilis	14	0.66 ± 0.25	3	1.07 ± 0.17	2	0.04	6	4.18 ± 0.79			1982
ad.all	10	3.05 ± 0.30	28	2.19 ± 0.31			16	1.40 ± 0.22	4	2.20 ± 0.79	1983
♂	9	0.55 ± 0.31	2	0.90							1982
	6	3.30 ± 0.48	16	2.24 ± 0.47			8	1.35 ± 0.37	4	2.20 ± 0.79	1983
♀	9	0.88 ± 0.38	1	1.39	2	0.04	6	4.18 ± 0.79			1982
	4	2.68 ± 0.09	12	2.11 ± 0.36			8	1.46 ± 0.26			1983
ov. ♀			9	0.85 ± 0.19			3	0.67 ± 0.05			1981
	5	0.50 ± 0.18	2	2.68			1	0.38			1982
	3	8.74 ± 0.31	11	3.38 ± 0.78			8	3.26 ± 1.15	2	2.76	1983
Cyclops sp.			6	0.09 ± 0.02			7	0.15 ± 0.07			1981
cop.all	30	0.16 ± 0.04	26	0.23 ± 0.08	20	0.03	33	1.00 ± 0.16			1982
	30	0.93 ± 0.12	50	1.03 ± 0.14			29	1.62 ± 0.24	35	0.69 ± 0.11	1983
cop.I.	9	0.10 ± 0.03	6	0.14 ± 0.09	4	0.02	7	0.57 ± 0.19			1982
	7	0.69 ± 0.19	10	1.27 ± 0.25			5	0.84 ± 0.40	8	0.59 ± 0.15	1983
II.	7	0.08 ± 0.04	6	0.14 ± 0.09	4	0.02	7	0.54 ± 0.17			1982
	7	0.75 ± 0.18	10	0.66 ± 0.28			3	3.19 ± 0.99	7	0.64 ± 0.17	1983
III.	7	0.21 ± 0.07	7	0.33 ± 0.20	4	0.02	8	0.76 ± 0.18			1982
	8	0.67 ± 0.14	9	0.66 ± 0.23			3	2.83 ± 0.92	7	0.58 ± 0.12	1983
IV.	7	0.22 ± 0.11	6	0.23 ± 0.10	4	0.03	6	1.38 ± 0.26			1982
	9	1.02 ± 0.28	11	0.88 ± 0.18			8	1.09 ± 0.24	6	0.59 ± 0.14	1983
V.	2	0.35	8	0.28 ± 0.18	4	0.05	5	1.95 ± 0.65			1982
	6	1.43 ± 0.42	11	1.60 ± 0.41			11	1.66 ± 0.36	7	1.070 ± 0.37	1983
Cyclops sp.			6	0.15 ± 0.06			3	0.12 ± 0.01			1981
ad.all	21	0.35 ± 0.05	18	0.07 ± 0.02	5	0.02	8	2.30 ± 0.83			1982
	25	1.75 ± 0.44	31	1.14 ± 0.25			9	1.17 ± 0.45	15	0.76 ± 0.28	1983
♂	15	0.31 ± 0.06	9	0.08 ± 0.03	7	0.03	5	1.51 ± 0.73			1982
	12	2.00 ± 0.69	21	1.31 ± 0.36			8	1.13 ± 0.50	11	0.81 ± 0.38	1983
♀	9	0.49 ± 0.08	9	0.05 ± 0.03	2	0.04	3	3.62 ± 1.83			1982
	13	1.51 ± 0.58	10	0.79 ± 0.19			1	1.50	4	0.63 ± 0.23	1983
ov. ♀			2	0.34							1981

Table 1. Continued.

Species	Sample No.	Spring 21.3 – 20.6	No.	Summer* 21.6 – 20.9	No.	Algal bloom 10.8 – 20.9	No.	Autumn 21.9 – 20.12	No.	Winter 21.12 – 20.3	Year
	8	0.22 ± 0.10	6	0.12 ± 0.06	2	0.02	3	1.33 ± 0.71			1982
	10	2.50 ± 0.89	10	1.46 ± 0.44			2	2.60	2	0.99	1983
Cyclops vicinus ad.	13	1.67 ± 0.71	7	0.89 ± 0.25			9	1.17 ± 0.45	15	0.76 ± 0.28	1983
ov. ♀	7	2.97 ± 1.25	4	1.67 ± 1.05			2	2.6	2	0.99	1983
Mesocyclops leuckarti ad.	11	1.91 ± 0.58	24	1.22 ± 0.32							1983
ov. ♀	3	1.39 ± 0.38	6	1.33 ± 0.36							1983

* without algal bloom.
SDM = standard deviation of the mean.

Table 2. Seasonal fluctuations in individual filtering rates of crustacean zooplankton species and larval stages among macrophytes, $ml \cdot ind.^{-1} \cdot d^{-1}$ (mean ± SDM).

Species	Sample No.	Spring 21.3 – 20.6	No.	Summer* 21.6 – 20.9	No.	Algal bloom 10.8 – 20.9	No.	Autumn 13.10	Year
Eurycerus lamellatus			3	6.68 ± 2.26					1981
Camptocercus rectirostris			1	16.01					1981
Simocephalus vetulus			4	6.01 ± 1.56					1981
Pleuroxus uncinatus			5	0.60 ± 0.22					1981
Diaphanosoma			3	1.54 ± 0.65			1	1.92	1981
birgei lacustris	1	0.99	3	0.86 ± 0.47	1	0.06			1982
Daphnia cucullata			2	5.53					1981
			1	5.09					1982
D. galeata	1	2.11							1982
Daphnia sp.juv.	1	0.63							1982
Nauplius	3	0.16 ± 0.02	3	0.11 ± 0.03	2	0.20			1982
Eudiaptomus gracilis			3	1.41 ± 0.45			2	0.90	1981
ad. all	6	1.03 ± 0.14							1982
Eudiaptomus gracilis cop.			1	0.42			2	0.26	1981
Cyclops sp.ad.all			2	0.16			1	0.34	1981
	11	0.46 ± 0.16	17	0.21 ± 0.05	10	0.06 ± 0.02			1982
Cyclops sp.cop.all			4	1.45 ± 1.20			2	0.12	1981
	19	0.34 ± 0.08	27	0.28 ± 0.06	9	0.06 ± 0.006			1982
cop.I. – II.	6	0.41 ± 0.23	7	0.12 ± 0.04	4	0.05 ± 0.01			1982
III.	3	0.64 ± 0.45	7	0.20 ± 0.05	2	0.05			1982
IV.	7	0.27 ± 0.08	7	0.28 ± 0.09	1	0.10			1982
V.	4	0.44 ± 0.14	6	0.56 ± 0.19	2	0.06			1982

* Without algal bloom.
SDM = standard deviation of the mean.

tered among the macrophytes (*Eurycercus, Simocephalus, Camptocercus*) did not essentially differ from those of daphnids, the feeding rate of *Pleuroxus* being nearer to that of *Diaphanosoma* (Table 2). *Nitocra hibernica* (Harpacticoida) recovered on four occasions from the water samples collected in the littoral zone did not consume labelled food. The more frequent *Limnomysis benedeni* Czer., however, consumed algae on each occasion.

The filtering activity of crustaceans, particularly the cladocerans, was greater among the macrophytes than in open lake in 70% of the experiments. The daphnids and the *Diaphanosoma* filtered 1.8 times more water in the littoral zone than in the open water (Tables 1, 2). This fact suggests that the filtering rate is influenced by the diversity and concentration of food.

Seasonal averages of individual filtering rates showed that the most intensive feeding was achieved by cladocerans in summer and autumn, by *Eudiaptomus* in spring and by *Cyclops* in autumn (Table 1).

Individual filtering rate significantly fluctuated annually. In 1983, filtering rates were higher than in the preceding years. In 1982, during the bloom of *Anabaenopsis*, the individual filtering rate of the species diminished by 70% on the average (Tables 1, 2).

Community grazing rate

In 1981 the summer mean of zooplankton community grazing rates was only 3.2% $\cdot$ d^{-1}, decreasing to one half this by November (Fig. 8A). Grazing maxima occurred in mid-August, related to doubling of the density of total crustacean zooplankton (Fig. 3), especially those of nauplii and *Diaphanosoma* (Figs. 5, 8A). During summer, the major filter-feeders were cladocerans ($\bar{x}$ = 1.9%), *Diaphanosoma* predominating ($\bar{x}$ = 1.1%). The feeding rate of *Cyclops* was about 1/3 that of *Eudiaptomus*.

In March end 1982, although the crustacean standing crops was low because of the intensive in-

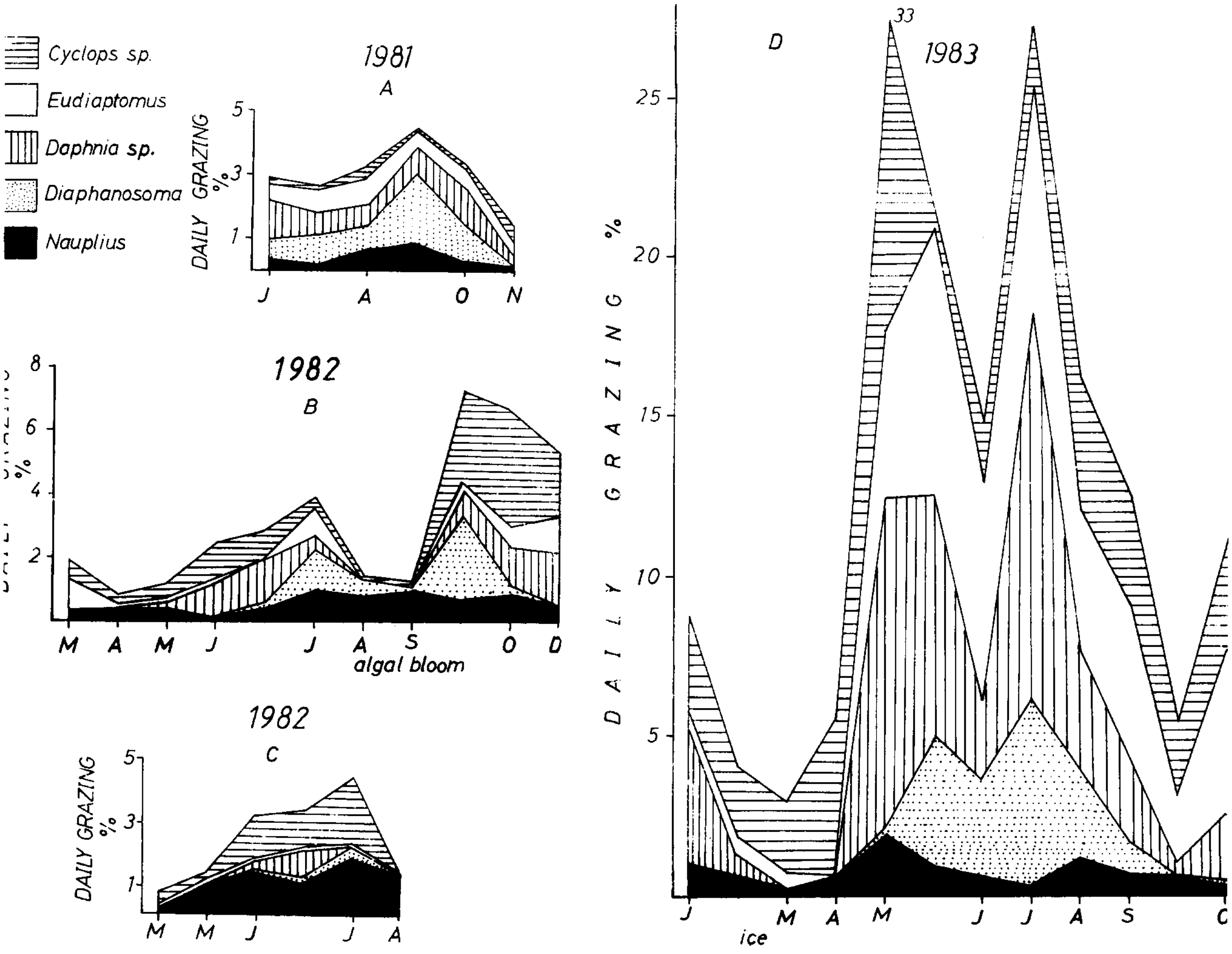

Fig. 8. Seasonal fluctuations in community grazing rates of crustacean zooplankton in 1981–1983. A, B, D = open lake; C = in the littoral zone.

dividual filtering rate, community grazing rate approached 2% · d^{-1} (Fig. 8B). Though crustacean plankton community increased in April and May (Fig. 3), especially *Cyclops* spp., algal grazing rate was only 1% per day. Though in early summer (June) population density of crustaceans diminished, their grazing rate increased due to the multiplication of daphnids and *Cyclops* . Summer grazing maximum of 4% was observed at the end of July, both due to 40% increase in the density of crustaceans (Fig. 3), and the increase of individual filtering rates. During the water bloom, the number of crustaceans were greater than earlier (Fig. 3), the community was dominated by nauplii, *Cyclops* and *Diaphanosoma*. In early September, population density of the latter species fell to one quarter (Fig. 6). Owing to the low individual filtering rate (Table 1), however, community grazing rate diminished to 1.4−1.2% (Fig. 8B). In September end, after the cessation of algal bloom, crustacean population of about identical density filtered 5−6 times greater volume of water than during the mass production of *Anabaenopsis*. The rise of grazing rate was due particularly to the numerous *Diaphanosoma* (27 ind. l^{-1}) as well as cyclopoid copepodites and adults (59 ind. l^{-1}). By the end of October, population density of crustaceans had essentially diminished (Fig. 3). At that time, *Diaphanosoma* became rare in the community, and the numbers of *Cyclops* also diminished to one half, while the numbers of daphnids and *Eudiaptomus* doubled (Fig. 6). For the greater community grazing rate the small population of *Cyclops* was responsible, since the feeding activity of the population was two times greater on the average than at the end of September. During December, despite the new increase of crustacean zooplankton density and the two to three-fold increase in number of filter-feeding species (*Daphnia* and *Eudiaptomus*), community grazing rate was lower because of the average diminishing of individual filtering rates.

In 1982, studies in the littoral zone which parallel with those ran in the open water showed that in spite of the differences in crustacean zooplankton composition (Fig. 4D) community grazing rate was comparable with that in the open lake (Fig. 8C).

In 1983, early January crustacean plankton grazing rate exceeded the maximum that occurred after the water bloom of 1982, and was more than 3% higher than in mid-December (Fig. 8D). Since population density of crustaceans was completely identical at the two timepoints and the number of cladocerans was also nearly the same, the differences in grazing activities can be accounted for by the greater filtratin rates of daphnids in early January. Before freezing at the end of January and immediately after thawing in March (water temperature 4.5 °C), the lower grazing rate must primarily be attributed to the absence of Cladocera, resp. the more than 30% diminution of nauplii in March. The grazing rate of 5.6% · d^{-1} achieved in April mainly due to *Cyclops* increased to 33% at the beginning of May, with 1/3 contribution of *Daphnia* population. The *Cyclops* sp. consisted mainly of stage III and IV copepodites of *C. vicinus* having high filtering rates (Table 1). At the end of May, *Diaphanosoma* population increased and the relative proportion of cladocerans in community grazing increased to 53%. The grazing rate of the *Eudiaptomus* also rose up to 39%, but that of the *Cyclops*, however, decreased from 46% to 4% in the 20 days between the two examinations due to a 10-fold decrease in population density (Fig. 8D). The diminution of the community grazing rate at the end of June was caused by the decrease of cladocerans; an increase in the grazing rate to 27% · d^{-1} in mid-July, occurred because of a considerable increase of their numbers. In August and September numbers and filtering rates of cladocerans diminished and in the autumn principally *Eudiaptomus* and *Cyclops* consumed algae (Fig. 8D).

The averages community grazing rates of 2.9 and 3.2% in 1981 and 1982 were comparable, the share of cladocerans and *Eudiaptomus* being only 36 and 15% of the population but 78 and 40% of grazing, respectively. In 1983, community grazing rate was a higher by order of magnitude on the average (13.4%) in which the real filter-feeders, that contributed to less than one third of the population, had a share of 57%.

Discussion

Changes in the composition of crustacean zooplankton

Water quality in the Lake Balaton is not uniform. On the basis of studies on phytoplankton and zooplankton composition, the lake was divided into three different water quality areas, of which the part of the lake at Tihany is the less eutrophic (Zánkai & Ponyi, 1971; Ponyi, 1977). Algological and bacteriological investigations performed here regularly, however, suggest that the earlier water quality conditions did not remain unchanged even at Tihany, and the changes point to eutrophication (Herodek *et al.*, 1982; Tóth, 1982). Water quality deterioration was particularly accelerated in the eighties, reaching its peak in the water bloom of *Anabaenopsis* in July, 1982 (Tóth & Padisák, 1984). In the vegetation period the average chlorophyll-a concentration was 9.3 mg · m^{-3} in 1981 but reached a value of 20.4 mg · m^{-3} in 1982 (Herodek, pers. commun.). Compared with 1977, the increase in concentrations is 1.5 to 3.3-fold (Herodek *et al.*, 1982). In 1983, chlorophyll-a concentration fell from 16 mg · m^{-3} in late spring to 4.1 mg · m^{-3} in summer. Thus, phytoplankton composition and quantity differed in the three years.

Zooplankton composition and density usually change during the productivity changes of a lake. Passing from oligotrophy to eutrophy, Calanoida are gradually replaced by Cladocera (McNaught, 1975; Lampert, 1977; Munro & Bailey, 1980; Richman & Dodson, 1983; Muck & Lampert, 1984; Gulati, 1984; Rognerud & Kjellberg, 1984), and among the copepods the cyclopoid will dominate (Patalas, 1972; Hillbricht-Ilkowska *et al.*, 1979; Gulati *et al.*, 1984; Rognerud & Kjellberg, 1984).

However, an increase in trophy may not essentially be accompanied by the increase of Cladocera, only the species dominance shifts. Species indicative of oligotrophy disappear, or at least significantly decrease (Rognerud & Kjellberg, 1984). Phytoplankton biomass affects the zooplankton biomass. The correlation between them is positive and significant in eutrophic, meso-eutrophic and deep stratified lakes (Patalas, 1972; McCauley & Kalff, 1981; Herzig, 1979). In shallow lakes, however, the low phytomass is not suggestive of a low zooplankton biomass (Herzig, 1979), moreover, with the increasing of trophy the zooplankton/phytoplankton biomass ratio decreases (Gulati, 1983; Rognerud & Kjellberg, 1984). This also holds true of Lake Balaton.

According to investigations performed in 1977, the ratio of zooplankton (dry weight) to phytoplankton (wet weight) biomass was 0.1 in the whole eutrophic area of the lake, while in the oligo- and mesotrophic regions 0.6 (Ponyi, unpublished data; data on algae: Vörös, 1980). On the basis of literature (Tamás, 1955, 1974; Zánkai & Ponyi, 1972; Ponyi, 1975) Herzig (1979) claimed that the water of Lake Balaton at Tihany was still oligotrophic in the middle of the sixties. Accordingly, during the whole year Copepoda were in majority in the crustacean zooplankton community as compared with Cladocera (Table 3). Though the ratios

Table 3. Percentage composition of crustacean zooplankton in the last 50 years at Tihany.

Year	Winter Clad./Cop. %		Summer Clad./Cop. %		Winter Eud./Cycl. %		Summer Eud./Cycl. %		Summer Daph./Diaph. %		Author	Remarks
1936–38	2.0	98.0	15.2	84.8	98.9	1.1	68.7	31.3	34.2	65.0	Sebestyén *et al.* 1951	Without nauplii
1944–45; 1947; 1949	6.8	93.2	20.0	80.0	45.3	54.7	29.2	70.8	46.9	50.1	Sebestyén *et al.* 1953	Without nauplii
1951–52; 1955–59	4.0	96.0	31.2	68.8	67.0	33.0	50.9	49.1	23.0	75.3	Sebestyén 1960	Without nauplii
1965–67	-	-	23.4	76.6	-	-	55.7	44.3	19.0	80.4	Ponyi & Zánkai 1972	With nauplii
1972–73; 1977	2.2	97.8	32.4	67.6	87.9	12.1	44.4	55.6	23.4	72.4	Ponyi/unpublished data/	With nauplii
1981	-	-	24.9	75.1	-	-	37.9	62.1	13.8	86.2	Present work	Without nauplii
1982	8.0 (1982–1983)	92.0 (1982–1983)	16.2	83.8	12.1 (1982–1983)	87.9 (1982–1983)	6.2	93.8	28.6	71.4	Present work	Without nauplii
1983			27.3	72.7			61.1	38.9	69.1	30.9	Present work	Without nauplii

for the single decades were different, it was evident that in the seventies the population density of cladocerans increased as eutrophication increased; their abundance increases, however, remained far behind the increase of trophy characterized by primary productivity. The planktonic copepods responded more to the changes of water quality. *Cyclops* preceded the *Eudiaptomus* during summer (Table 3).

In 1981, but especially in 1982, crustacean zooplankton composition changed further with the deterioration of water quality. In the planktonic crustaceans, the number and relative proportion of *Eudiaptomus*, and of the cladocerans those of *Daphnia* substantially diminished. During the water bloom of 6 weeks, in 1982, they practically disappeared from the water (Figs. 6, 7, Table 3). The rare-fraction of filter-feeders can be brought into connection with their feeding behaviour, in addition to predation by fishes and their larvae (Ponyi & Zarok, 1984).

The Calanoida as nanophytoplankton feeders have a preference for oligo- and mesotrophic waters (McNaught, 1975; Gulati, 1978, 1983; Richman & Dodson, 1983; Muck & Lampert, 1984). Their relative proportion in the crustacean plankton increases only if chlorophyll concentration does not exceed 6 mg $\cdot$ m^{-3}, above which they diminish (Rognerud & Kjellberg, 1984). Gulati (1984) claims that the density of *Eudiaptomus* decreased by 70% in Loosdrecht Lakes during the increase of trophy, and the greatest feeding activity is achieved by this plankter only at food concentrations less than 1 mg C $\cdot$ l^{-1}. In laboratory experiments using various algae, the threshold feeding concentration for *Eudiaptomus* was found to be 0.07–1.1 mg C $\cdot$ l^{-1} (Zánkai & Ponyi, 1974; Muck & Lampert, 1984); it was lower than determined for *Daphnia* (McNaught, 1975).

The concentration of organic seston ($<320\,\mu m$ mesh) which during summer of the seventies was 1 mg C $\cdot$ l^{-1} (Zánkai & Ponyi, 1976), increased to 2.4 mg l^{-1} by the end of 1981, but remained at this level in May, 1983, except for a value of 5.8–7.3 mg C $\cdot$ l^{-1} during water bloom. Contrary to that in laboratory experiments the natural food present in the filtered water also comprised algae and detritus particles, which for their size or other reasons were not eaten by *Eudiaptomus gracilis*, though were measured into the amount of seston. The measured C values, however, exceeded the food niche 'optimal' for *Eudiaptomus gracilis* in this period (0.07–1.1 mg C $\cdot$ l^{-1}). Therefore, the increase in the food concentration itself may have caused population decrease of *Eudiaptomus*. In late spring, 1983, parallel with the improving of water quality, the quantity of seston decreased, the population density of *Eudiaptomus* increased. An inverse relationship was found between the quantity of organic seston ($< 60\mu m$) and density of *Eudiaptomus* ($r = -0.682$; $n = 9$; $t = 6.148$; $P < 0.001$). The density of *Eudiaptomus* during summer 1983 was 60% higher than in the thirties, when the water was oligotrophic (Sebestyén *et al.*, 1951).

Daphnia species which is more adapted to eutrophic water quality (McNaught, 1975; Richman & Dodson, 1983; Muck & Lampert, 1984) decreased in Lake Balaton when phytoplankton density was the highest, and increased when the quality of water improved considerably.

Similar phenomena have been reported by Adalsteinsson (1979), Edmondson & Litt (1982), Kerfoot & Parnell (1983) and Rognerud & Kjellberg (1984). A decrease in numbers can only partly be accounted for by the marked increase of *Anabaenopsis* filaments. Because of which the filtering activity of daphnids is reduced, and the degree of food rejection increased, causing a decrease in the rate of reproduction (Webster & Peters, 1978; Porter *et al.*, 1982). The negative effect of filamentous algae on the course of life of daphnids is well known (Gliwicz, 1980; Porter & Orcutt, 1980; Lampert, 1981). There are, however, evidences indicating that blue-greens, if their size is suitable, are just as readily eaten by *Daphnia* as other favourite species; moreover, daphnids can be maintained in culture with such food (Gliwicz & Siedlar, 1980; de Bernardi *et al.*, 1982; Lampert, 1981). It has been established by Holm *et al.* (1983) that filaments of blue-greens shorter than 1.5 mm are eaten by daphnids. The filaments of *Anabaenopsis* were shorter, and their size did not prevent the *Daphnia* to eat them. It is even more difficult to explain the decrease of the population density of *Daphnia* in 1981, and in the water bloom-devoid period of 1982, as well as their great increase in summer 1983. It is likely that the daphnids have become specialized in feeding medium density food of good quality (Richman & Dodson, 1983), and adjusted their carapax gape to higher phytoplankton concentration. In such a case, however, the food uptake decreases, leading to the diminution of the population density (Gliwicz & Siedlar, 1980).

Population density of *Diaphanosoma* was nearly identical in the summers of 1982 and 1983, meaning that it was not influenced by the differences is quantity and composition of phytoplankton. On the contrary, Einsle (1978) and Faafeng & Nilssen (1981) observed the disappearance of *Diaphanosoma* during the increasing of trophy. It is likely that its multiplication in Lake Balaton was made possible by its ability to preselect food by means of its narrow carapace opening (Gliwicz, 1977).

The species composition of cyclopoids in 1982 as well as changes in 1983 indicate water quality changes. In summer of 1982 the plankter *Acanthocyclops robustus f. limnetica*, numerous in the open lake, was known earlier only from the littoral regions of Lake Balaton, and in the sixties from the open water of the eutrophic area, resp. (Ponyi, 1977). The appearance of this species in the open lake was attributed by Einsle (1978) to the increased trophy of the water area.

Simultaneous with the expansion of *Acanthocyclops, Mesocyclops* virtually disappeared. This species had been for many decades the single dominant cyclopoid species in the open water of the north-eastern part of Lake Balaton from May to September (Sebestyén *et al.*, 1951; Sebestyén, 1953; Ponyi, 1965, 1968). Its diminution was principally due to competition with *Acanthocyclops* for food, since the adults and the older copepodites of both the species are carnivorous, preying on *Eudiaptomus* nauplii and copepodites. During *Anabaenopsis* bloom, the *Acanthocyclops* was feeding on *Diaphanosoma*, when *Eudiaptomus* was absent. Parallel investigations on the productivity, development, production of both the cyclopoids also indicate the absolute dominance of *Acanthocyclops* (Vijverberg & Richter, 1982). The decrease of *Mesocyclops* was also observed by Einsle (1978) during the increase of *Acanthocyclops*. In late autumn of 1983 when the amount of organic seston carbon decreased to 1.5 mg $\cdot$ l^{-1}, *Acanthocyclops* was finally replaced in the open water by *Mesocyclops.*

Grazing rate

Individual filtering rates differed significantly both seasonally and annually, too. Compared with the available literary data, they hardly differ in case of cladocerans, but those *Eudiaptomus* in Lake Balaton are, however, lower than in other lakes (Table 4).

The feeding rates of crustacean zooplankton community are more intensive during summer than in other periods (Haney, 1973; Gulati, 1978; Gulati *et al.*, 1982; Thompson *et al.*, 1982). The grazing rate in Lake Balaton was also the highest during the summers of 1981 and 1983, but in 1982 the peak shifted to autumn owing to the mass growth of blue-green (Fig. 8A–D). The effect of temperature on community grazing rate is a debated question. Some authors (Haney, 1973; Lampert & Taylor, 1984) claim that there is no or some small correlation between the two factors, while Nauwerck (1959) and Gulati *et al.* (1982) found direct correlation between filtering rate and temperature. In Lake Balaton the filtering rate of *Eudiaptomus* showed significant changes when the increase or decrease of temperature was greater than 10 °C (Zánkai & Ponyi, 1976). It seems that in 1981 and 1983 the community grazing rates followed temperature changes ($r = 0.89$, 0.61 resp. $0.05 > P > 0.01$), in 1982, however, no such correlation was found.

Feeding of crustacean zooplankton community differs even within the single water body, and its rate changes according to the degree of trophy (Gulati, 1984). Haney (1973) found high grazing rates under eutrophic conditions, while in oligotrophic waters only low ones. Other authors (Gliwicz & Hillbricht-Ilkowska, 1972; Gulati *et al.*, 1982, 1984; Gulati, 1983) believe, that zooplankton grazing rates are especially important in waters of low trophy, while in shallow continuously stirred up lakes of high trophy their role is insignificant. During the first two years of investigation, the community grazing rate was very low in Lake Balaton, particularly during summer (Fig. 8A–C). Values similarly low have not been determined even in waters of 10 mg C $\cdot$ l^{-1} seston content, or at most in other seasons (Gulati *et al.*, 1982). In 1983, on the other hand, the average yearly community grazing rate of 13.4% was identical to the grazing rate determined for the clear L. Vechten during investigation of several years (Gulati *et al.*, 1982).

In Lake Balaton both the extremely low and the greater community grazing rates can be related to the quantity and quality of seston. From May 1981

Table 4. Individual filtering rates of crustacean zooplankton species in various lakes.

Species	Size /mm/	Filtering rate $ml.ind^{-1}.day^{-1}$	$\bar{X}$	Lakes	Authors
Diaphanosoma	-	1.15 – 1.44	1.33	L. Vechten	Gulati (1978)
birgei lacustris	0.9 – 1.4	0 – 5.7	1.6	Heart L.	Haney (1973)
	-	0.39 – 2.08	1.15	Balaton (open lake)	Present work
	-	0.99 – 1.92	1.33	Balaton (among macrophytes)	Present work
Daphnia hyalina	1.0 – 1.6	5.7 – 29.3	15.8	Blelham Tarn (enclosure)	Thompson *et al.* (1982)
Daphnia hyalina	1.0 – 1.6	3.1 – 30.7	11.75	Blelham Tarn (enclosure)	Thompson *et al.* (1982)
Daphnia hyalina	–		4.5	L. Erken	Nauwerck (1963)
D. cucullata + *hyalina*	–	2.4 – 4.7	3.75	L. Vechten	Gulati (1978)
D. hyalina	1.2 – 1.7	2.4 – 18.2	10.3	L. Balaton	Zánkai (1983)
D. hyalina	1.1 – 1.7	3.96 – 6.88	5.41	L. Balaton (open lake)	Present work
D. galeata	1.5 – 1.7	1.9 – 20.8	6.4	Heart L.	Haney (1973)
D. galeata	–	2.5 – 20.0	–	Lawrence L.	Haney & Hall (1975)
D. galeata	1.4	1.0 – 5.5	–	Wintergreen L.	Haney & Hall (1975)
D. galeata	0.91 – 1.29	3.84 – 10.1	8.34	George Lake	Bogdan & McNaught (1975)
D. galeata	1.2 – 1.6	4.8 – 18.7	9.2	Balaton L.	Zánkai (1983)
D. galeata	1.3 – 1.8	1.52 – 11.09	5.5	Balaton L. (open lake)	present work
D. cucullata	–	0.24 – 0.96	–	Frederiksborg Slotssø (only bakt.plankt.)	Riemann & Bosselman (1984)
D. cucullata	–	0.28 – 1.31	–	Loosdrecht Lakes	Gulati (1984)
D. cucullata	1.2 – 1.6	3.1 – 13	7.8	Balaton L.	Zánkai (1983)
D. cucullata	1.0 – 1.6	1.22 – 5.21	2.72	Balaton L. (open lake)	present work
D. cucullata	–	5.09 – 5.53	5.31	Balaton L. among macrophytes	present work
Eudiaptomus gracilis				Blelham Tarn	Thompson
(ad. + cop. V.)		4.4 – 6.6	–	(two enclosures)	*et al.* (1982)
ad. + cop. I – IV.		2.7 – 4.4	–	(two enclosures)	*Thompson* *et al.* (1982)
Eudiaptomus gracilis		4.4 – 7.1	–	L. Vechten	Gulati (1978)
Eudiaptomus gracilis		1.09 – 1.97	–	L. George	Kibby (1971)
Eudiaptomus gracilis		0.83 – 2.4	–	L. George	Kibby (1971)
Eudiaptomus gracilis ad.		0.04 – 2.93	–	Balaton L.	Zánkai & Ponyi (1976)
Eudiaptomus gracilis ad.		0.46 – 4.18	1.76	Balaton L. (open lake)	present work
Eudiaptomus gracilis cop.		0.27 – 1.77	1.17	Balaton L. (open lake)	present work

to May 1983, organic seston contents were 2.4 mg $C \cdot l^{-1}$ on the average, considerably in excess of that concentration at which the crustacean zooplankton achieves its maximal filtering activity (Gulati, 1983).

Summary

The composition, biomass and feeding of crustacean zooplankton community were studied in the north-eastern water area of lower trophy (generally mesotrophic waters) in the open water and in the littoral zone at Tihany in Lake Balaton during 1981 – 1983.

In these years, open water crustacean zooplankton was made up of *Eudiaptomus gracilis, Cyclops vicinus, Mesocyclops leuckarti, Acanthocyclops robustus f. limnetica*, three *Daphnia* sp. *(D. hyalina, D. galeata, D. cucullata), Diaphanosoma birgei lacustris, Leptodora kindtii* and *Alona* sp. Among macrophytes the following species: *Eurycercus lamellatus, Camptocercus rectirostris, Simocephalus vetulus, Pleuroxus uncinatus* and *aduncus, Bosmina longirostris, Nitocra hibernica* and *Limnomysis benedeni* were also regularly found besides open water species.

In the open lake, crustacean zooplankton density differed from year to year on the average, changing from 87 to 140 ind $\cdot$ l^{-1} with an average density of 147.4 ind $\cdot$. l^{-1} among macrophytes in 1982.

During the three years, copepods dominated the crustacean zooplankton, their relative proportion in the open water being 79–90%, among macrophytes 95–97%. Nauplii predominated, contributing 41–48% to the crustacean community on the average (36–61 ind $\cdot$ l^{-1}), and in the littoral zone 55–83% (16–167 ind $\cdot$ l^{-1}). Adults and copepodites of *Cyclops* always exceeded in numbers those of *Eudiaptomus*, particularly during the summer algal bloom in 1982. *Diaphanosoma* was most abundant in 1981 and *Daphnia* in 1983.

Compared to earlier decades, the composition of crustacean zooplankton showed great changes in 1981–1982. Parallel with the deterioration of water quality, the number of *Eudiaptomus* and daphnids greatly decreased in 1982, practically disappearing from the water during the six weeks of water bloom. At the same time, there was an increase in the number of cyclopoids and the *Acanthocyclops robustus f. limnetica* of the littoral zone was found to enter the open water, replacing the previously dominant cyclopoid, *Mesocyclops leuckarti*. In late spring, 1983, organic seston decreased, the densities of *Eudiaptomus* and daphnids increased again, *Acanthocyclops* disappeared from the open lake and *Mesocyclops* again dominated.

Of all crustaceans the daphnids had the highest filtering rate, followed by *Eudiaptomus* and *Diaphanosoma*. In the case of copepods, the order of individual filtering rates was: ovigerous ♀ > all adults > copepodites > nauplii. ♀ > ♂.

Individual filtering rates varied seasonally, those of cladocerans being the highest in summer and in autumn, that of *Eudiaptomus* in spring and those of *Cyclops* in autumn. In 1983, the filtering rate of the different species were higher than in the previous year. During the blue-green bloom the filtering rates of different species decreased by 70% on the average.

Community grazing rate averages were similar in 1981 and 1982 (2.9 and 3.2% $\cdot$ day^{-1}). In 1983 the average of community grazing rate was 13.4% $\cdot$ day^{-1}. In 1981 and 1983, rates were the highest during summer; in 1982 peak values shifted to autumn owing to the algal bloom. In 1981 and 1983, community grazing rate was influenced by temperature, and in 1982 no such influence was observed. During the given period of investigation both the quantity and quality of seston essentially affected community grazing rate.

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