INSTITUTE OF ECOLOGY-POLISH ACADEMY OF SCIENCES

EKOLOGIA POLSKA

Vol. XIX Warszawa 1971 No. 30

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THE INFLUENCE OF VARIOUS CONCENTRATIONS OF NATURAL FOOD ON THE DEVELOPMENT, FECUNDITY AND PRODUCTION OF PLANKTONIC CRUSTACEAN FILTRATORS

(Ekol. Pol. 19: 427–473). The paper is a study of the dependence among the concentration of natural food and the development, growth and fecundity rates of planktonic crustacean filtrators (*Daphnia cucullata*, *D. longispina*, *Diaphanosoma brachyurum*, *Chydorus sphaericus*, *Eudiaptomus graciloides*) which dominate in the pelagial of Mikołajskie Lake. On the basis of the obtained data the production of zooplankton community in various thermal and trophic conditions was calculated. The obtained results allowed for a precise quantitative evidence of a limiting significance of food in various natural situations, and to show various intensities of this dependence for different species which feed on various kinds of food.

The planktonic crustacean filtrators are an important link in the production of freshwater ecosystems. As they are the primary consumers, directly utilizing primary production, they decide to a large extent about the character of the energy flow through ecosystem. Therefore the analyses of the causes and mechanisms deciding about their ecological efficiency and the production in aquatic environment are of a great importance. These are the most essential problems in order to understand the functioning of biocenosis and quantitative regularities in ecosystems.

The most common methods of estimating the production of zooplankton crustaceans are based on the biomass increases and changes of numbers of animals. In order to calculate the production with these methods the following quantitative data are necessary: development length, growth rate, fecundity and reproduction and the dependence of these parameters on the environmental conditions, mainly on the thermics and trophy.

Generally the temperature is assumed to be a basic factor deciding about the rate of development, growth and on fecundity of planktonic filtrators in the environment. As far as the trophic factor is concerned, it is assumed that it is of some significance only in low food concentrations. This has been assumed on the grounds that the majority of information on this subject were obtained in laboratory experiments, in conditions quite different from the natural ones. In such experiments the natural food concentration, its species composition, accessibility and food selectivity of planktonic filtrators are not taken into consideration (Węgleńska 1970). Not much is known about what the planktonic filtrators consume in the nature, and whether the regularities found in simplified laboratory conditions are the same as in nature.

This paper aimed at finding the dependence among the abundance of natural food and the development rate, rate of growth and reproduction of planktonic crustacean filtrators dominating in the pelagial of Mikołajskie Lake. Two basic problems in this paper were solved due to the experiments and field observations: 1) Is the quantity of food available for planktonic crustacean filtrators sufficient for their optimal development and growth ; 2) How and to what extent the fluctuations of the abundance of food in nature can influence the production of this community in Mikołajskie Lake, which is a typical eutrophic one for the temperate climatic zone.

I. MATERIAL AND METHODS

1. Laboratory experiment

The experimental investigations of the influence of various concentrations of natural food on the rate of reproduction, development and growth of planktonic crustacean filtrators were carried out in summers of 1965 and 1966. The individuals of the following five species were chosen for the experiments: *Daphnia cucullata* (G.O. Sars), *D. longispina hyalina* (Leydig), *Diaphanosoma brachyurum* (Lièvin), *Chydorus sphaericus* (O.F. Müller) and *Eudiaptomus graciloides* (Lilljeborg). They represent typical microfiltrators with a preference of food particles smaller than 1 micron in diameter (e.g. *Ch. sphaericus*), as well as typical macrofiltrators consuming more intensively food particles with a diameter over several micrones (e.g. *E. graciloides*) (Rodina 1957, Malovickaja and Sorokin 1961, Gliwicz 1969b). The chosen species are the dominants in the pelagial of Mikołajskie Lake and have a decisive share in the production of the whole community of planktonic filtrators in this environment (Hillbricht-Ilkowska, Gliwicz and Spodniewska 1967, Hillbricht-Ilkowska and Węgleńska 1970).

a. Condensing of food

A lake water from the epilimnion of Mikołajskie Lake was used in the experiment. It contained natural seston with a real food of planktonic filtrators (cells of nannoplankton and bacteria), and also the macrophytoplankton. Macrophytoplankton is not directly consumed by planktonic filtrators due to the large size of its cells (Gaevskaja 1949, Suščenija 1958). The presence of macrophytoplankton can have, however, an important influence on the numbers of zooplankton and its food. On one hand it can be the source of vitamins and other substances stimulating or inhibiting the growth and development, which are excreted to the environment (Fritsh 1953, Braginskij 1955, Jørgensen 1956, 1962, Shiraishi and Provasoli 1959), and on the other – it can be a substratum for the development of bacteria (Mazepova 1952, Ulhmann 1954).

A required food concentration was obtained according to the modified method of Dodson and Thomas (1964) of filtering the lake water void of zooplankters through a bacterial membrane filter Coli 5. The applied method allowed to obtain any food concentration without losses of sedimentating cells of algae and bacteria on the filter, and without the destruction of delicate cell structures, thus eliminating the main cause of the changes in the natural food composition.

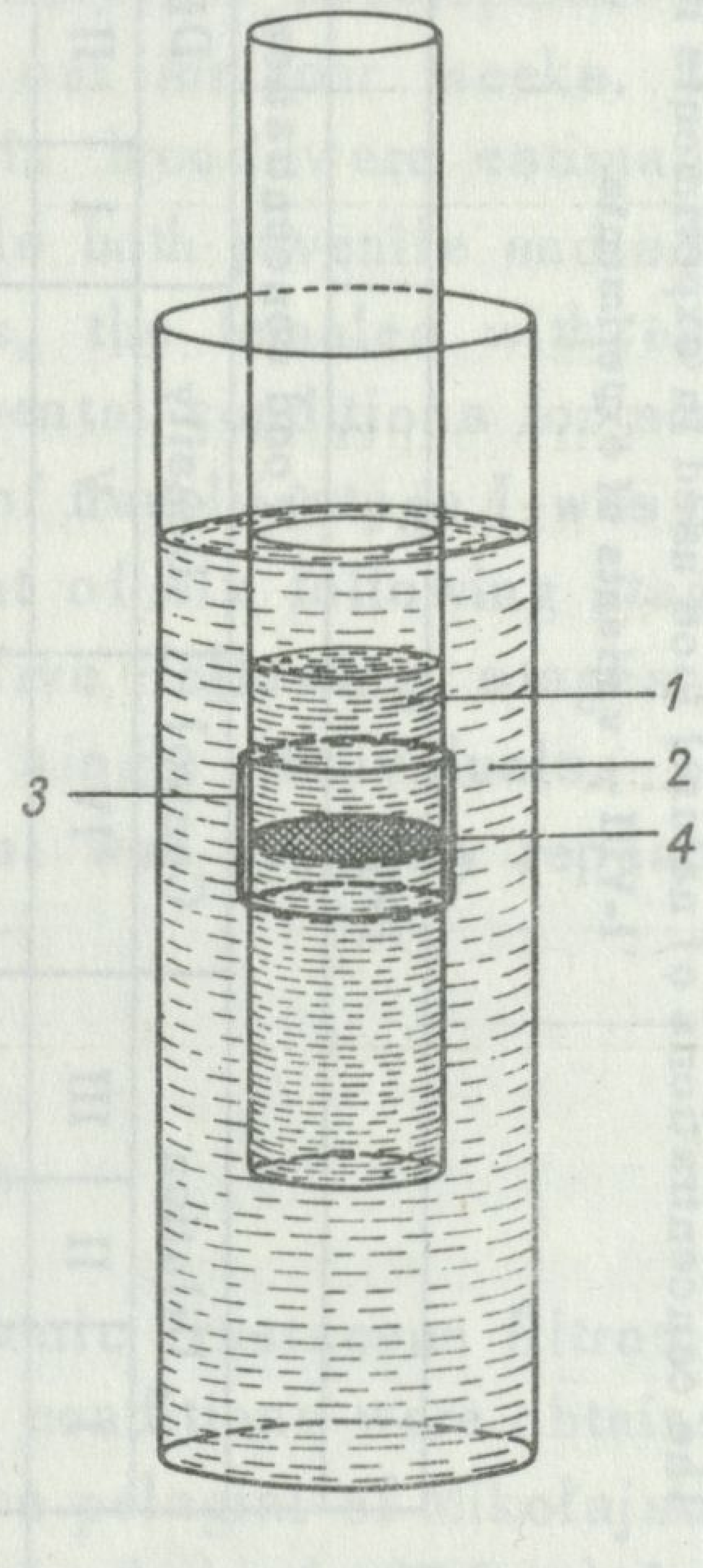

Fig. 1. The schemae of an apparatus for the condensation of natural food
1 – filtrate, 2 – lake water, 3 – rubber tube, 4 – membrane filter

The lake water was checked under the microscope, and the zooplankters were removed with the pipette before the filtration. The apparatus shown in Figure 1 consists of two plexiglass tubes. One of them, 150 cm long, with the diameter 5.5 cm was filled with lake water, and then the second one, 100 cm long with diameter 3.5 cm was put into it. The lower opening of the inside tube was closed with the bacterial membrane filter. The filtration in these comunicating vessels was continued till the water levels in both tubes were level.

Tab. I

The concentrations of natural food used in experiments in 1965 and 1966

I-VIII – variants of experiments

	Food concentration (in mg/l)												
	1965					1966							
	Dilution			Control	Density	Dilution				Control	Density		
	I	II	III	IV	V	I	II	III	IV	V*	VI	VII	VIII
Nannoplankton	0.04	0.09	0.18	0.36	0.72	0.01	0.04	0.10	0.20	0.40	0.80	1.60	4.00
Bacteria	0.61	1.20	1.90	3.00	3.80	0.40	0.68	0.90	1.40	2.10	2.90	3.50	6.00
Total	0.65	1.29	2.08	3.36	4.52	0.41	0.72	1.00	1.60	2.50	3.70	5.10	10.00

*Concentration of natural food in waters of Mikołajskie Lake.

The required dilution of natural food was obtained by adding the filtered water, i.e. without phytoplankton and bacteria, to the lake water. An everyday exchange of lake water in all variants of the experiments prevented the depletion of food and quantitative and qualitative changes. The quantity of food available for planktonic filtrators was analysed after each change of water. Nannoplankton was counted under the microscope in the known volume of water. The species were not determined, but three size classes were distinguished: < 3, 3–10 and > 10 microns. Macrophytoplankton was not counted, because as already mentioned it does not form a direct food of planktonic filtrators. The bacteria were counted directly on membrane filters (Razumov 1947). Only a total number of bacteria was estimated. The biomass of nannoplankton cells and bacteria was estimated on the basis of their volume. Assuming that the specific weight of bacteria and phytoplankton is 1, the volume of 1 micron is 10^{-9} mg wet weight. It was calculated, that the average volume of cells in each size class of nannoplankton is relatively: 6, 220 and 6280 cubic microns (for the sake of simplification it was assumed that all forms were sphaerical). The volume of a single bacterial cell was assumed to be 1 cubic micron (acc. to the data of Kuznecova and Romanenko 1963 and Rodina 1965).

The concentrations of food used in various experimental variants in 1965 and 1966 are presented in Table I.

b. Zooplankton cultures

The cultures of individuals of investigated species were carried out in glass jars containing 50 ml of lake water with required food concentration, one individual per bottle. The bottles were filled up and corked, which prevented the contact of air with animals. The bottles were kept in a water bath, and the temperature was controlled by a thermostat. A constant temperature was maintained: 18°C in the first year of the investigations, 17°C in the second year.[1] The adult females of the investigated *Cladocera* species, caught in the pelagial of Mikołajskie Lake, were kept for some days in the water with an appropriate temperature and food concentration, and thus adapted themselves to the experimental conditions. Juvenile individuals hatched from the eggs produced by these females were used further in the experiments. Everyday observations of the length of embryonic and postembryonic development and of the growth rate and the fecundity were carried out for four weeks. The number of moultings, broods and number of eggs in brood were estimated. After each moulting the body length of all individuals both juvenile and adult ones was measured[2]. In the case of *E. graciloides*, the females with eggs caught in the lake were also adapted to the experimental conditions for some days. After the hatching of juvenile ones, a couple of nauplii stage I was put into each bottle, and then the length of development of six following stages was determined. The length of development of five following stages of copepodits was estimated from the cultures of single individuals. The experiment lasted 45 days. Each experimental variant was paralelly repeated 10 times.

2. Field observations

The data on the numbers and production of planktonic crustacean filtrators and on the quantities of their potential food in natural conditions were obtained from the quantitative plankton samples collected in the pelagial of Mikołajskie Lake (eutrophic, holomictic, mean depth 11.7 m, maximal depth 27.0 m) from 22 July to 30 August 1964. The quantitative samples were collected everyday for 40 days with the help of a 5 liter plankton sampler of Bernatowicz's type. The samples were collected from epi-, meta- and hypolimnion separately.

The samples in epi- and metalimnion were collected every one metre starting from the surface, in hypolimnion samples were collected every 3 or 4 metres

[1]Mean temperature of epilimnion of Mikołajskie Lake in the period of experiments.

[2]The body length of *Daphnia cucullata* and *D. longispina* was measured from the top of the head to the base of spinae, the body length of *Eudiaptomus graciloides* did not include saete furcales.

down to 2 metres above the bottom. The sampling took place during the summer stagnation. The numbers of individuals in hypolimnion were very low (only single individuals of genera *Cyclops* and *Acanthocyclops* were found) due to the oxygen deficit. Therefore only the epi- and metalimnion samples were precisely analysed. The samples were condensed to 50 ml by filtration through the plankton net with the mesh size 40 microns. Then the samples were fixed with 4% formalin and elaborated according to the method of Hillbricht-Ilkowska and Patalas (1967). The following were estimated in each sample: numbers of juvenile and adult individuals, total number of eggs (all eggs in the sample were counted), number of females with eggs, and the size of individuals (on the basis of measurements of tens of individuals of each species).

Paralelly to zooplankton samples, the 100 ml samples of lake water for the estimation of phytoplankton numbers were collected from every one metre in epi-, meta- and hypolimnion separately, every 3–4 days. The number of phytoplankton organisms was determined according to the method of Spodniewska (1967). The number of bacteria was estimated on the basis of samples collected at the surface and from the depth 2, 5, 10 and 15 m. The temperature was measured simultaneously with sampling, and in epi- and metalimnion it was on the average 18 to 21°C.

3. Production calculations

The production of dominating species of planktonic filtrators in the pelagial of Mikołajskie Lake (*Daphnia cucullata, D. longispina, Diaphanosoma brachyurum, Chydorus sphaericus, Bosmina coregonii*[3] and *Eudiaptomus graciloides*) was estimated by a "calculating" method (Vinberg, Pečen and Šuškina 1965) on the basis of the rate of weight increase of particular individuals of particular species, and the changes of their numbers in the environment. According to this method the production (P_{WT_I}) of a population of the investigated species for the periods of time (T_I) between successive samplings can be expressed by the formula:

$$P_{WT_I} = \left[\frac{N_e \cdot W_e}{t_e} + \frac{N_I \cdot \Delta W_I}{t_I} + \frac{N_{II} \cdot \Delta W_{II}}{t_{II}} \right] \cdot T_I ,$$

[3]Production of *Bosmina coregonii* (Baird) was calculated as a product of average biomass and daily biomass turnover. It was assumed that a daily turnover of *B. coregonii* biomass equals the mean daily turnover of the biomass of the remaining four species of *Cladocera*.

Production (P_{WT_I}) for the whole period of time (T_I) (in this paper equals to 40 days) is a sum of partial productions determined for the successive periods of sampling interval, i.e.:

$$P_{WT_{(40)}} = P_{WT_I} + P_{WT_{II}} + P_{WT_{III}} + \ldots \text{ and so on,}$$

where: N_e – number of eggs, N_I and N_{II} – number of individuals of all successive distinguished developmental stages, i.e. nauplii and copepodits (*Copepoda*), or juvenile and adult individuals (*Cladocera*), W_e – the weight of eggs equal to the weight of the juvenile individuals of *Cladocera* and *Copepoda*, ΔW_I and ΔW_{II} – a total weight increase of individuals of successive developmental stages, i.e. the difference between the initial weight of the given stage, and the initial weight of the following stage, t_e – length of the egg development, t_I and t_{II} – length of the development of individuals of the successive stages in particular thermical and trophic conditions, $\frac{\Delta W_I}{t_I}$ (etc.) – a daily weight increase of particular stage.

The rate of weight increase of individuals in particular stages was calculated separately for each sample knowing the life span and development of particular stages and the weight of individuals in various periods of their life. When establishing the length of the development of eggs and young larval stages of the planktonic filtrators, the data of Šuškina (1964) and Pečen (1965a) on the dependences of the development length on temperature were used, and the own data from the already described experiments on the development length dependences on the food concentration. The average life span of an adult *Cladocera* was calculated on the basis of measurements of the body length of individuals, assuming that growth rate of the body length of individuals after reaching the maturity is about three times slower than growth rate of the juvenile forms (Patalas in press, Węgleńska 1968). The following formula was used:

$$\bar{t}_a = \frac{3t_j \cdot (\bar{L}_a - L_{oa})}{L_{oa} - L_{oj}},$$

where: $\bar{t}_a$ – average life span of an adult individual, t_j – the length of development of the juvenile form, L_{oj} – the initial body length of the juvenile form, L_{oa} – the body length of individual at the moment of reaching maturity, $\bar{L}_a$ – average body length of an adult individual in the investigated population.

The weight of individuals in particular developmental stages and of an adult ones was calculated on the basis of measurements of the body length by the formulas of the relation: length – weight (acc. to the literature data). The weight of *Cladocera* individuals was calculated according to the formulas of Pečen (1965b): $W = 0.052 \cdot l^{3.012}$ for *Daphnia*, $W = 0.092 \cdot l^{2.449}$ *for Diaphanosoma* and $W = 0.124 l^{2.181}$ for *Chydorus*, where: W – weight of body in mg, l – length of body in mm. In order to calculate the individual weight of *E. graciloides* the formula of Klekowski and Šuškina (1966) was applied: $W = 55 \cdot l^{2.73}$, where: W – weight of body in micrograms, l – length of body in mm.

II. THE INFLUENCE OF FOOD ON THE LENGTH OF DEVELOPMENT, FECUNDITY AND THE GROWTH RATE OF PLANKTONIC CRUSTACEAN FILTRATORS IN THE LABORATORY INVESTIGATIONS

1. The length of development

The influence of various concentrations of natural food on the length of embryonic and postembryonic development of the investigated species was analysed.

The length of embryonic development of the investigated species was constant in the majority of experiments, and for *Daphnia cucullata*, *D. longispina* and *Diaphanosoma brachyurum* it was 3 days, for *Chydorus sphaericus* about 2.5 days, and for *Eudiaptomus graciloides* 4 days (Tab. II and III). Only the

The length of embryonic development (in days) of five species of planktonic filtrators at 17°C with different concentrations of natural food (1966)

Tab. II

Species	Food concentration (in mg/l)							
	Dilution				Control	Density		
	0.41	0.72	1.00	1.60	2.50	3.70	5.10	10.00
Diaphanosoma brachyurum	3.2	3.1	3.1	3.0	3.0	3.0	3.0	3.0
Daphnia cucullata	3.4	3.2	3.1	3.0	3.0	3.0	3.0	3.0
Daphnia longispina	3.2	3.2	3.1	3.0	3.0	3.0	3.0	3.0
Chydorus sphaericus	3.0	3.0	3.0	2.9	2.9	2.8	2.8	2.8
Eudiaptomus graciloides	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0

very low concentration of food (below 1 mg/l) slowed down the development of eggs of *Cladocera*. The presented results suggest that the length of embryonic development of *Cladocera* depends to very small extent on the feeding of a female in the period before the formation of egg, i.e. on the changes of food concentration in the environment.

The length of development (in days) of three species of planktonic filtrators at 18°C with different concentrations of natural food (1965)
a — embryonic development, b — postembryonic development

Tab. III

Species	Food concentration (in mg/l)									
	Dilution						Control		Density	
	0.65		1.29		2.08		3.36		4.52	
	a	b	a	b	a	b	a	b	a	b
Daphnia cucullata	3.3	9.3	3.0	7.9	3.0	6.9	3.0	6.1	3.0	6.0
Chydorus sphaericus	2.9	5.8	2.5	5.0	2.5	4.6	2.5	4.0	2.5	3.8
Eudiaptomus graciloides	4.0	38.1	4.0	30.9	4.0	26.8	4.0	23.0	4.0	21.6

Detailed results on the length and rate of postembryonic development of *Cladocera* show a positive relation of the length of development and food concentration (Fig. 2 and 3, Tab. III). The development rate quickens and the period before the maturity shortens with the increase of the food concentration. An increase of the food concentration from 0.41 to 2.5 mg/l resulted for an example, in a twice shorter postembryonic development of *D. brachyurum* (Fig. 2).

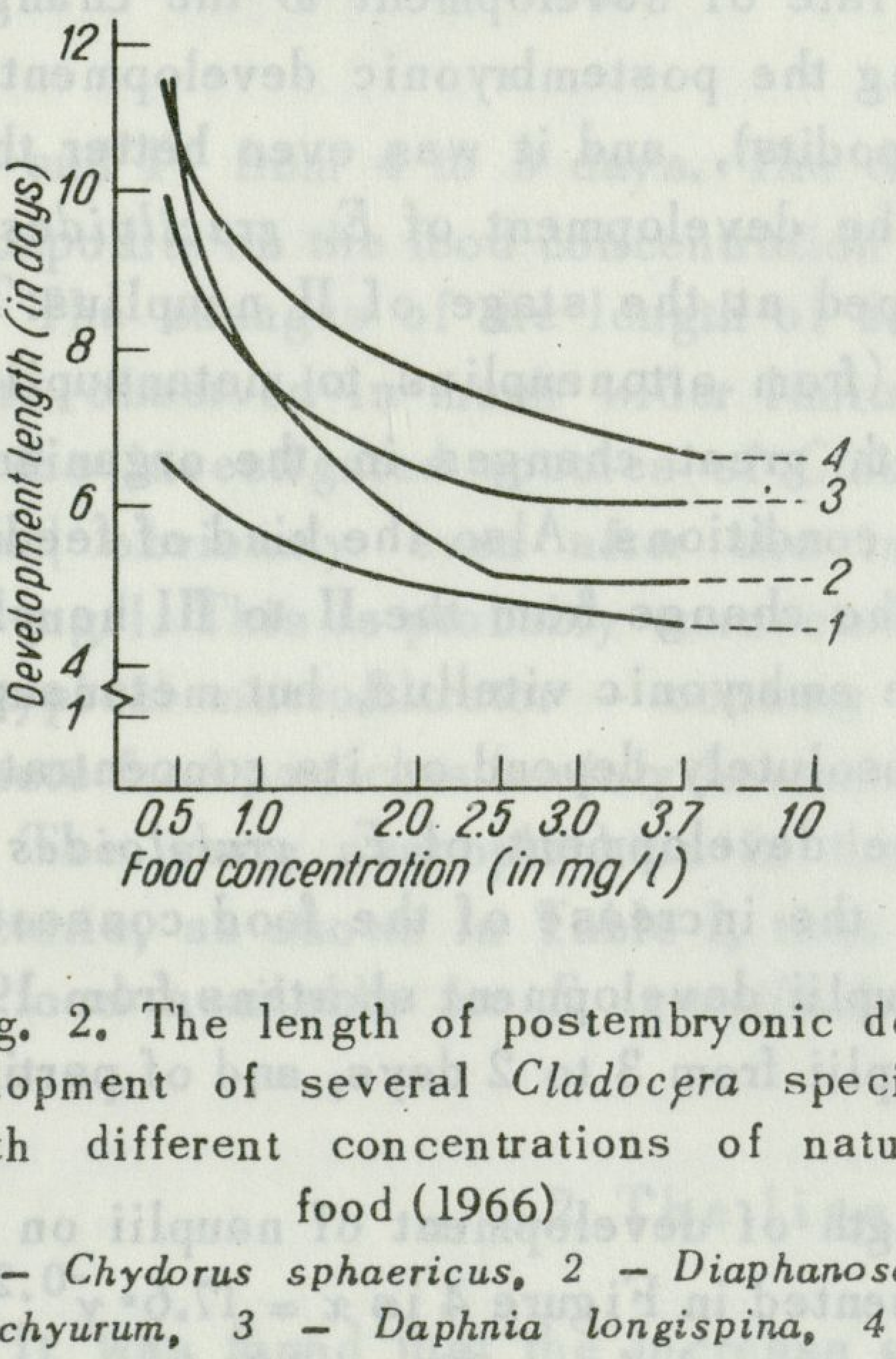

Fig. 2. The length of postembryonic development of several *Cladocera* species with different concentrations of natural food (1966)

1 — *Chydorus sphaericus*, 2 — *Diaphanosoma brachyurum*, 3 — *Daphnia longispina*, 4 — *Daphnia cucullata*

The concentration of natural food in Mikołajskie Lake is 2.5 mg/l

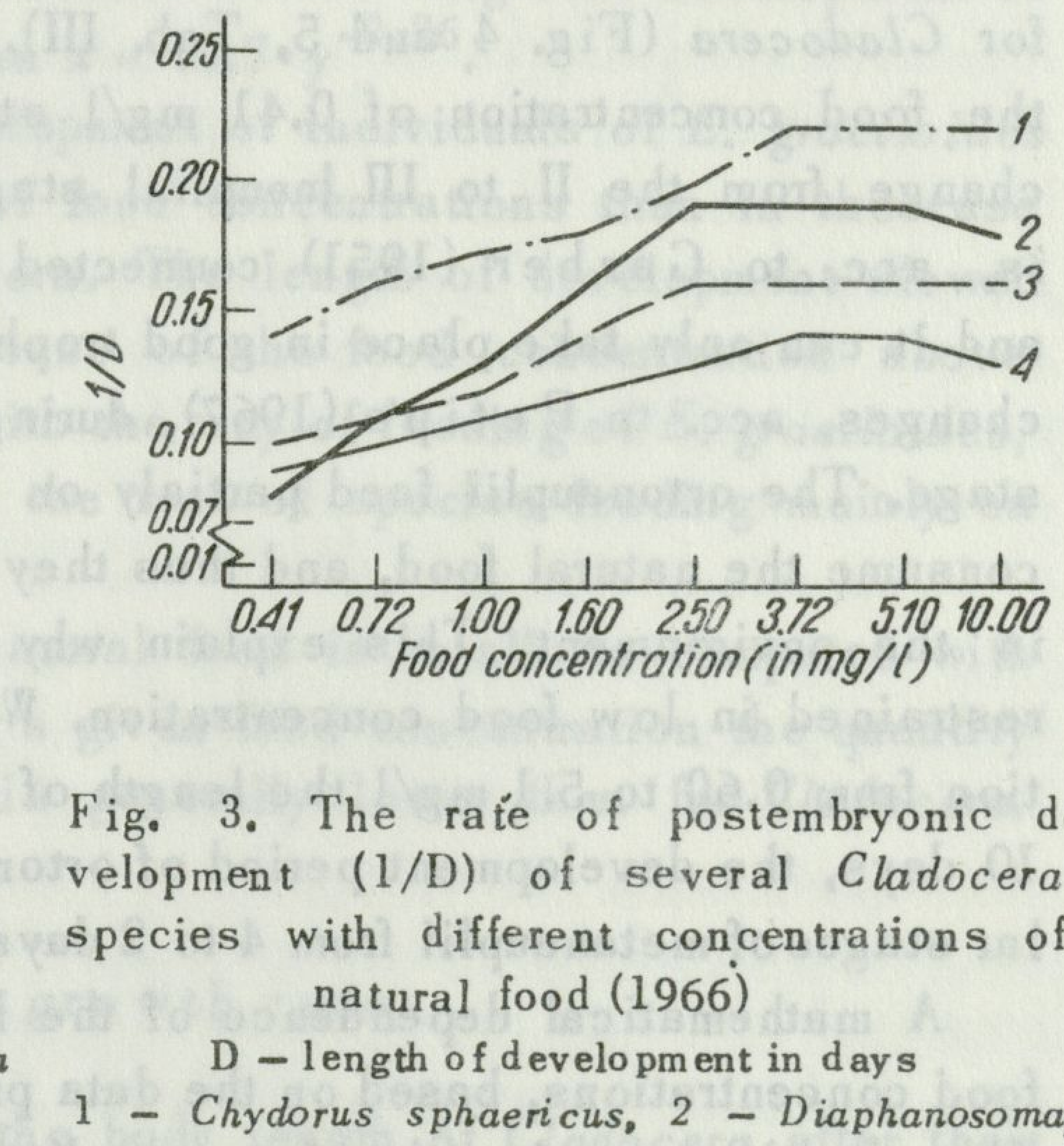

Fig. 3. The rate of postembryonic development (1/D) of several *Cladocera* species with different concentrations of natural food (1966)

D — length of development in days

1 — *Chydorus sphaericus*, 2 — *Diaphanosoma brachyurum*, 3 — *Daphnia longispina*, 4 — *Daphnia cucullata*

The concentration of natural food in Mikołajskie Lake is 2.5 mg/l

The data presented in Figure 2 allow to establish a mathematical relation between the concentration of available food and the length of individuals development, which is a function: $x = f(y)$, where x – development length in days, y – food concentration in mg/l. For *D. cucullata* $x = 9.1 \cdot y^{-0.24}$, for *Ch. sphaericus* $x = 5.7 \cdot y^{-0.18}$, for *D. longispina* $x = 7.8 \cdot y^{-0.27}$, for *D. brachyurum* $x = 7.7 \cdot y^{-0.44}$.

The dependence of the length of postembryonic development of *Cladocera* on a trophic factor is pretty obvious in lower concentrations of food. This dependence decreases together with the increase of the bacterial and nannoplankton numbers, and it can not be observed in their high concentrations. The length of development of *D. brachyurum* and *D. longispina* do not change while increasing the food concentration above 2.5 mg/l (Fig. 2 and 3). An analogous value for *D. cucullata* and *Ch. sphaericus* is 3.7 mg/l. While studying the development rate of *D. brachyurum* and *D. cucullata* individuals, its slight slowing down was observed in the food concentration of 10 mg/l and the period before maturity was then longer (Fig. 3). This phenomenon was probably caused by slowing down of the filtration rate and the disturbance of normal feeding of *Cladocera* due to clogging of the filtering apparatus with large cells of macrophytoplankton, chiefly blue-green algae (Harnisch 1949, Rigler 1961, Burns and Rigler 1967).

A positive relation of the length and rate of development to the changes of food concentrations was observed during the postembryonic development of *E. graciloides* (stages of nauplii and copepodits), and it was even better than for *Cladocera* (Fig. 4 and 5, Tab. III). The development of *E. graciloides* in the food concentration of 0.41 mg/l stopped at the stage of II nauplius. The change from the II to III nauplial stage (from ortonauplius to metanauplius) is, acc. to Garber (1951) connected with great changes in the organisms, and it can only take place in good trophic conditions. Also the kind of feeding changes, acc. to Petipa (1967), during the change from the II to III nauplial stage. The ortonauplii feed partialy on the embryonic vitellus, but metanauplii consume the natural food, and thus they absolutely depend on its concentration in the environment. This explain why the development of *E. graciloides* is restrained in low food concentration. With the increase of the food concentration from 0.60 to 5.1 mg/l the length of nauplii development shortens from 19 to 10 days, the development period of ortonauplii from 3 to 2 days, and of particular stages of metanauplii from 4 to 2 days.

A mathematical dependence of the length of development of nauplii on the food concentrations, based on the data presented in Figure 4 is $x = 17.6 \cdot y^{-0.29}$. The development length of copepodits shortened from 20 to 12 days at an increase of the food concentration from 0.6 to 5.1 mg/l, the development length of copepodits stage I decreased from 3 to 1 day, and of copepodits stage II,

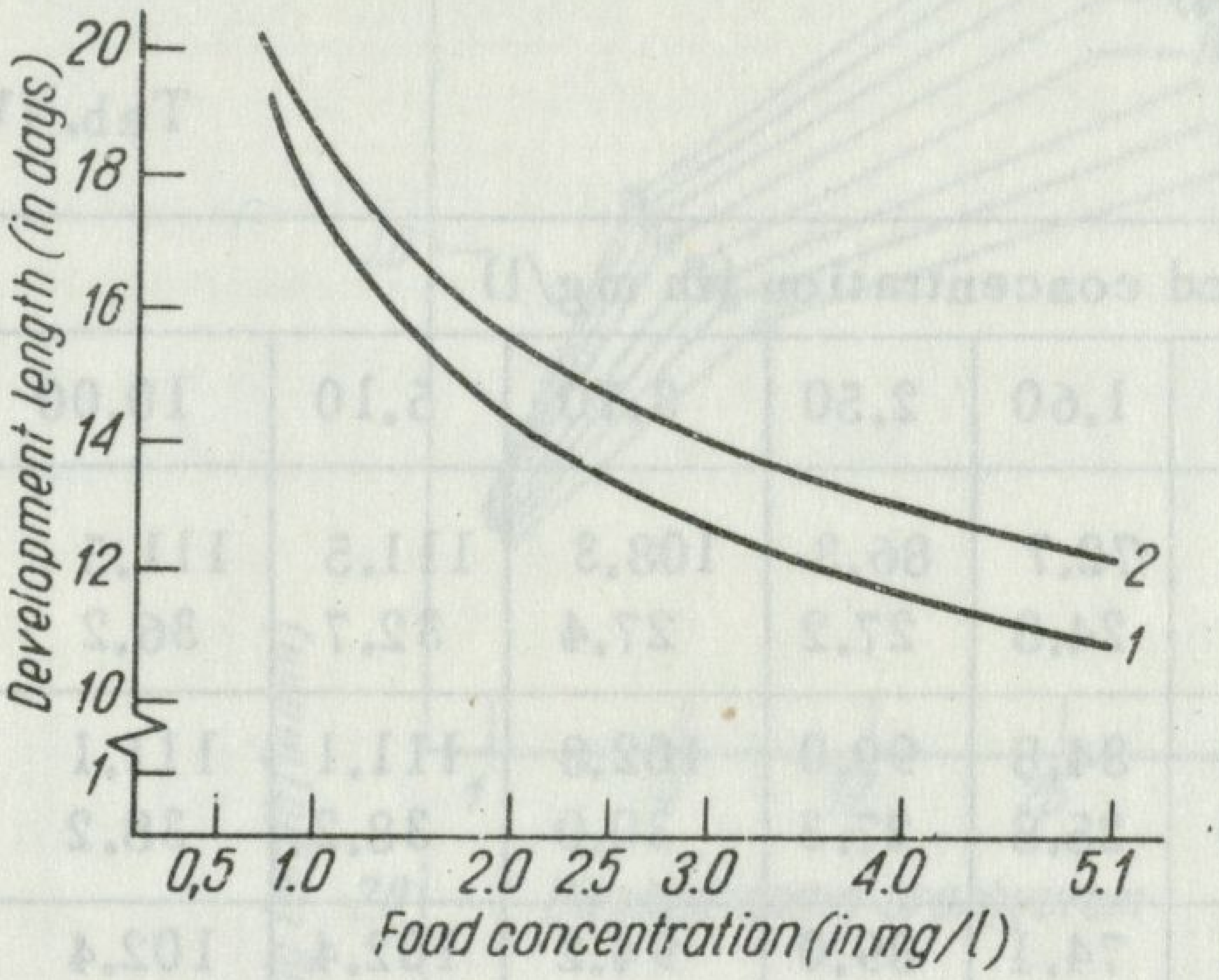

Fig. 4. The length of postembryonic development of *Eudiaptomus graciloides* with different concentrations of natural food (1966)

1 – nauplii, *2*– copepodits

The concentration of natural food in Mikołajskie Lake is 2.5 mg/l

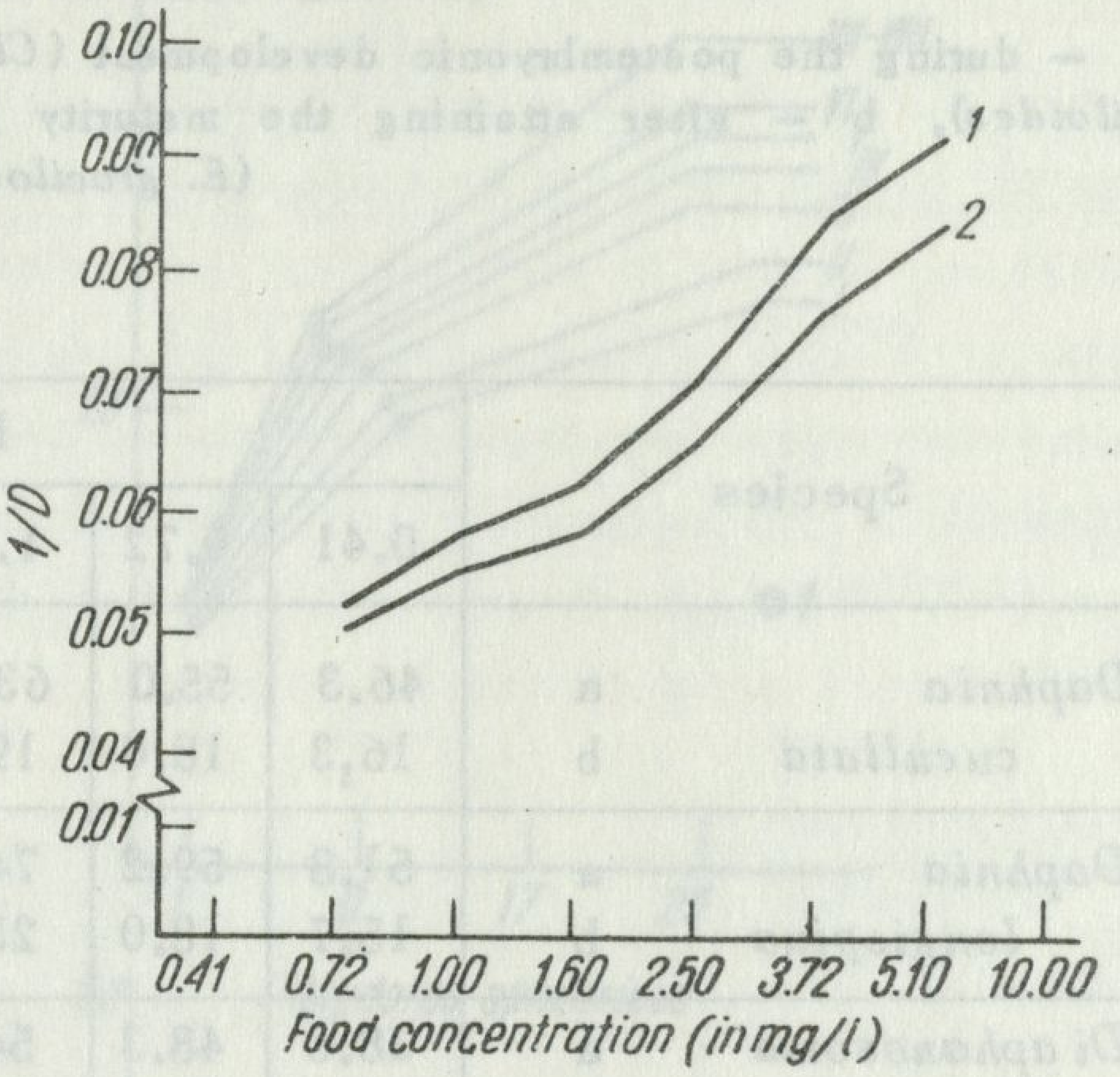

Fig. 5. The rate of postembryonic development (1/D) of *Eudiaptomus graciloides* with different concentrations of natural food (1966)

1 – nauplii, 2 – copepodits

D – length of development in days

The concentration of natural food in Mikołajskie Lake is 2.5 mg/l

III and IV from 4 to 3 days. The dependence of the length of development of copepodits on the food concentration was $x = 18.7 \cdot y^{-0.26}$.

The changes of the length of development of individuals of *E. graciloides* were observed in much wider limits of food concentrations than in the case of the investigated species of *Cladocera*. The length of development slowed down| obviously even after the increase of the food concentration above 3.7 mg/l. This is probably connected with the way of feeding of *E. graciloides*, a typical macrofiltrator – contrary to the rest of species feeding mainly on minute food particles (mainly bacteria).

The share nannoplankton in the natural food is small as compared with bacteria, as shown in Table I, thus in a given food concentration the quantity of food available for *E. graciloides* is generally lower than for *Cladocera*.

2. The linear growth rate

It was found that the increase of the body length of *Cladocera* after their maturity is about 3 times slower than that of the juvenile individuals. This was noticed while analysing the daily increases of the body length (Tab. IV),

The average daily growth rate (10^{-3} mm) of five species of planktonic filtrators with different concentrations of natural food
a – during the postembryonic development (*Cladocera*) and in the stadium of nauplii (*E. graciloides*), b – after attaining the maturity (*Cladocera*) and in the stadium of copepodits (*E. graciloides*)

Tab. IV

Species		Food concentration (in mg/l)							
		0.41	0.72	1.00	1.60	2.50	3.70	5.10	10.00
Daphnia	a	46.3	55.0	63.2	72.7	86.3	108.3	111.5	111.5
cucullata	b	16.3	18.0	19.9	24.8	27.2	27.4	32.7	36.2
Daphnia	a	51.8	59.2	74.6	84.8	99.0	102.8	111.1	111.1
longispina	b	15.7	18.0	23.8	25.8	27.3	30.0	38.2	38.2
Diaphanosoma	a	38.5	48.3	54.1	74.1	89.0	94.2	102.4	102.4
brachyurum	b	12.8	15.9	18.0	24.2	24.8	30.4	33.7	36.3
Chydorus	a	10.2	14.5	18.3	22.0	24.0	30.0	32.5	32.5
sphaericus	b	3.4	4.0	5.0	6.6	7.6	9.0	10.5	10.5
Eudiaptomus	a		9.7	11.7	12.1	14.0	19.5	25.5	
graciloides	b		33.2	41.2	48.7	53.1	71.6	97.0	

which were treated as the index of the rate of growth of investigated species of *Cladocera*. The rate of the increase of the body length of juvenile and adult individuals clearly depended on the food concentration. The rate of growth increased according to the species, from 2 to 3 times together with an increase of the food concentration from 0.41 to 10 mg/l (Tab. IV).

The influence of the trophic factor on the size of body increased with the age of individuals. The measurements of individuals in juvenile developmental stages showed in various concentrations of natural food much smaller differentiation as compared with the adult individuals (Fig. 6). An so e.g. at an increase of the food concentration from 0.41 to 10 mg/l the body length of individuals of *D. cucullata* increased at the moment of their maturity 28%, and after several successive days 47%. The maximal size of individuals was also greater in higher food concentrations (Fig. 6). And so e.g. the maximal body length of *D. brachyurum* in the concentration of food 10 mg/l was 52% longer than the one in 0.41 mg/l. An index of a relative increase of body length, expressed as the ratio of final (maximal) body length of adult individuals to the body length of new born ones, shows also an increasing tendency together with the rise of food concentration (Tab. V). In some variants of the experiment the shortening of the period, in which individuals reached their maximal size in conditions of high food concentration (Fig. 6), was observed. The individuals of e.g. *D. longispina* reached their maximal size after 23 days of life in the

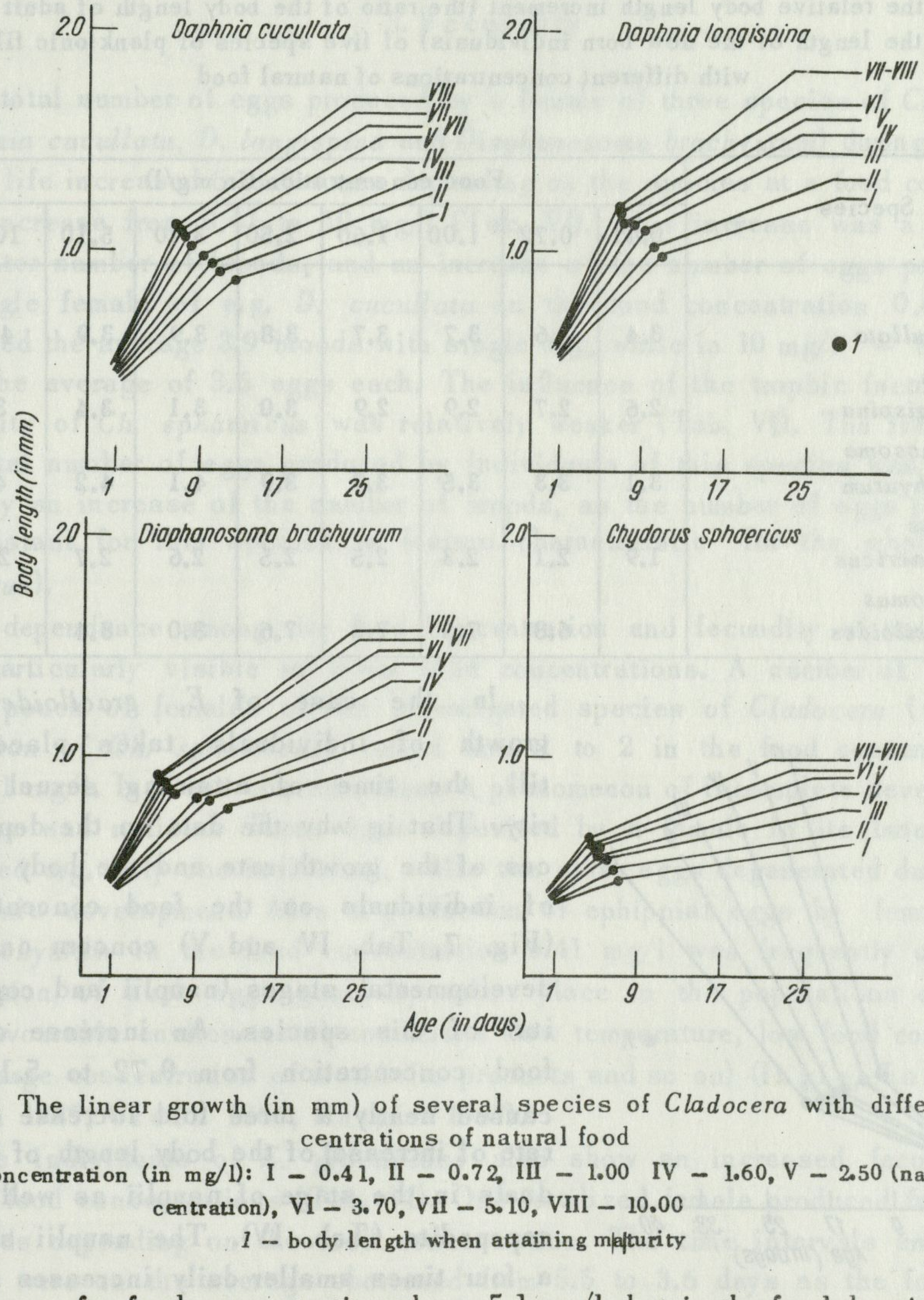

Fig. 6. The linear growth (in mm) of several species of *Cladocera* with different concentrations of natural food

Food concentration (in mg/l): I – 0.41, II – 0.72, III – 1.00 IV – 1.60, V – 2.50 (natural concentration), VI – 3.70, VII – 5.10, VIII – 10.00

1 – body length when attaining maturity

conditions of a food concentration above 5.1 mg/l; but in the food density below 1 mg/l these individuals were growing for the whole 30 days of the experiment. The influence of a trophic factor on the growth rate and on the maximal size of individuals of the investigated species of *Cladocera* was noticed especially in lower food concentrations (below 3.7 mg/l, in the experimental conditions). When a further increase of food concentration was applied, the differences in the growth rate and maximal size among the individuals of the same species were not observed with the exception of *D. brachyurum* and *D. cucullata* (Fig. 6, Tab. IV and V).

Index of the relative body length increment (the ratio of the body length of adult individuals to the length of the new born individuals) of five species of planktonic filtrators with different concentrations of natural food

Tab. V

Species	Food concentration (in mg/l)							
	0.41	0.72	1.00	1.60	2.50	3.70	5.10	10.00
Daphnia cucullata	3.4	3.6	3.7	3.7	3.8	3.9	3.9	4.0
Daphnia longispina	2.6	2.7	2.9	2.9	3.0	3.1	3.4	3.4
Diaphanosoma brachyurum	3.1	3.3	3.5	3.7	3.9	4.1	4.2	4.4
Chydorus sphaericus	1.9	2.1	2.3	2.5	2.5	2.6	2.7	2.7
Eudiaptomus graciloides		6.8	7.5	7.2	7.6	8.0	8.4	

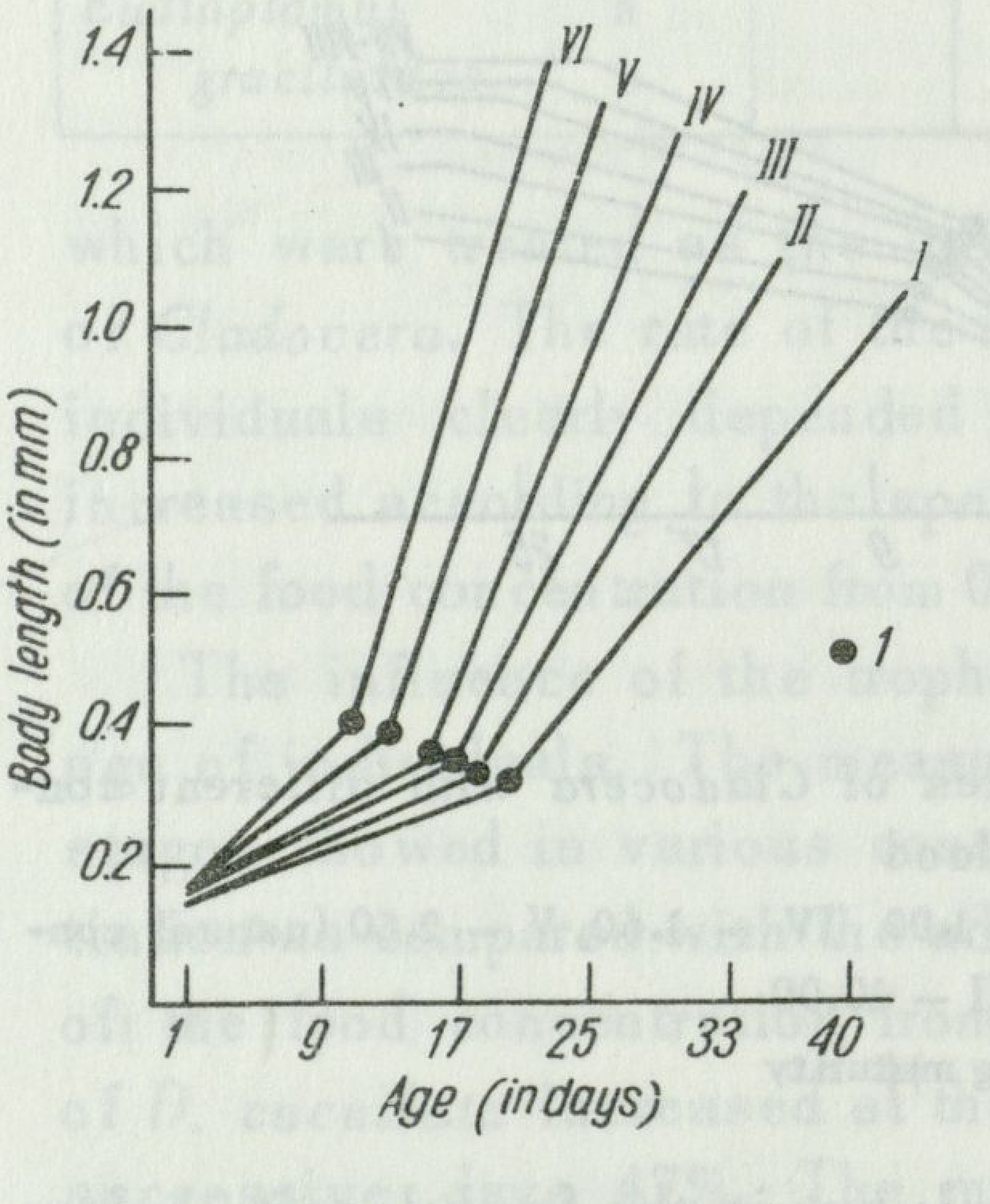

Fig. 7. The linear growth (in mm) of *Eudiaptomus graciloides* with different concentrations of natural food

Food concentration (in mg/l): I — 0.72, II — 1.00, III — 1.60, IV — 2.50 (natural concentration), V — 3.70, VI — 5.10

1 — body length of individuals changing from nauplii to copepodits

In the case of *E. graciloides* the growth of individuals takes place only till the time of attaining sexual maturity. That is why the data on the dependences of the growth rate and the body length of individuals on the food concentration (Fig. 7, Tab. IV and V) concern only the developmental stages (nauplii and copepodits) of this species. An increase of the food concentration from 0.72 to 5.1 mg/l caused nearly a three fold increase of the rate of increase] of the body length of individuals in the stage of nauplii as well as of copepodits (Tab. IV). The nauplii showed a four times smaller daily increases of the body length in all variants of experiment, as compared with copepodits. That is the reason why the differences of the size of nauplii in various food concentrations were smaller as compared with copepodits (Tab. IV, Fig. 7). The increase of the food concentration from 0.72 to 5.1 mg/l resulted in an increase of the body length of nauplii by 25%, while that of copepodits by 40%.

3. Fecundity

A total number of eggs produced by a female of three species of *Cladocera* (*Daphnia cucullata*, *D. longispina* and *Diaphanosoma brachyurum*) during 30 days of its life increased 6 to 8 times depending on the species at a food concentration increase from 0.41 to 10 mg/l (Tab. VI). This increase was a result of a greater number of broods, and an increase of the number of eggs per brood. A single female of e.g. *D. cucullata* in the food concentration 0.41 mg/l produced the average 3.9 broods with single egg, while in 10 mg/l – 8 broods with the average of 3.6 eggs each. The influence of the trophic factor on the fecundity of *Ch. sphaericus* was relatively weaker (Tab. VI). The increase of the total number of eggs produced by individuals of this species was realized only by an increase of the number of broods, as the number of eggs per brood is constant for this species (a feature characteristic for the whole genus *Chydorus*).

A dependence among the food concentration and fecundity of individuals was particularly visible in lower food concentrations. A number of eggs in brood pouch of females of the investigated species of *Cladocera* (with the exception of *Ch. sphaericus*) varied from 1 to 2 in the food concentrations below 1 mg/l. In these concentrations a phenomenon of incomplete development of eggs was noticed. Three eggs deposited by a female in its brood pouch produced e.g. only one individual, while two other eggs degenerated during the embryonic development. Also a production of ephippial eggs by females of *D. brachyurum* in the food concentration 0.41 mg/l was frequently observed. Production of such eggs generally takes place in the populations exposed in unfavourable environmental conditions (low temperature, low food concentration, large concentration of metabolic products and so on) (Ingle, Wood and Banta 1937, Green 1966, Burgis 1967).

The individuals of *E. graciloides* also show an increased fecundity in higher food concentrations (Tab. VI). One fertilized female produced from 1 to 3 broods depending on the food concentration. The time intervals among the broods were on the average shortened from 5.5 to 3.6 days as the food concentration increased. The average number of eggs per one egg sac of an *E. graciloides* female increased from 3.0 to 7.0 with the rise of the food concentration from 0.72 to 5.1 mg/l (Tab. VI).

4. The rate of the increase of individuals biomass

The results on the linear growth and fecundity of individuals of five species of planktonic crustacean filtrators in various food concentrations were used for the calculation of the increase of biomass of particular individuals related

Fecundity of five species of planktonic filtrators kept in individual cultures with different food concentrations
a — number of eggs per one female with eggs, b — number of broods produced by one female during the experiment, c — total number of eggs produced by one female during the experiment
Numbers in brackets show the range of variations

Tab. VI

Food concentration (in mg/l)	*Daphnia cucullata*			*Daphnia longispina*			*Diaphanosoma brachyurum*			*Eudiaptomus graciloides*			*Chydorus sphaericus*		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
0.41	1.0 (1–1)	3.9	3.9	1.2 (1–2)	4.7	5.9	1.0 (1–1)	4.2	4.2				2.0	5.5	11.0
0.72	1.2 (1–2)	5.1	6.2	1.6 (1–2)	5.9	10.1	1.4 (1–2)	5.1	7.3	3.0 (3–3)	1.0	3.0	2.0	6.4	12.8
1.00	1.6 (1–2)	6.0	9.9	2.5 (1–3)	6.0	15.3	1.8 (1–2)	5.9	10.6	3.5 (3–4)	2.0	7.0	2.0	7.0	14.0
1.60	2.1 (1–3)	7.0	14.1	3.2 (2–4)	7.1	23.2	2.3 (2–3)	7.0	16.4	4.5 (3–6)	2.0	9.1	2.0	7.0	14.0
2.50	2.6 (2–4)	8.0	20.8	3.7 (2–5)	8.0	30.1	3.2 (2–4)	8.0	26.1	4.6 (4–5)	3.0	13.8	2.0	7.7	15.4
3.70	3.0 (2–4)	8.0	24.0	4.0 (2–5)	8.0	32.0	3.5 (2–4)	8.0	28.1	5.4 (4–6)	3.0	16.2	2.0	7.7	15.4
5.10	3.3 (2–4)	8.0	27.1	4.2 (3–6)	8.0	34.3	4.0 (2–5)	8.0	32.0	7.0 (5–8)	3.0	21.0	2.0	9.1	18.2
10.00	3.6 (3–4)	8.0	29.5	4.6 (2–7)	8.0	37.4	4.1 (2–5)	8.0	33.2				2.0	9.1	18.2

Increase of the biomass (10^{-4} mg) of individuals of *Diaphanosoma brachyurum* with different concentrations of natural food in 30 days

Tab. VII

Food concentration (in mg/l)	Juvenile individuals	Adult individuals			Total increase of biomass of individual in 30 days	Average daily relative increase of the biomass of an individual*
	Increase of the weight of body	Increase of the weight of body	Weight of eggs	Total increase of biomass		
0.41	379	448	208	656	1035	0.6
0.72	411	680	406	1086	1497	0.8
1.00	411	788	638	1426	1837	1.0
1.60	454	1241	1120	2361	2815	1.3
2.50	454	1543	1820	2361	3317	1.8
3.70	497	1764	1960	3724	4221	2.0
5.10	566	1853	2240	4093	4659	2.2
10.00	566	2080	2310	4390	4956	2.3

*The ratio of daily increase of the weight of body and the weight of eggs of this individual to the initial weight of its body.

Increase of the biomass (10^{-4} mg) of individuals of *Daphnia cucullata* with different concentrations of natural food in 30 days

Tab. VIII

Food concentration (in mg/l)	Juvenile individuals	Adult individuals			Total increase of biomass of individual in 30 days	Average daily rolative increase of the biomass of an individual*
	Increase of the weight of body	Increase of the weight of body	Weight of eggs	Total increase of biomass		
0.41	297	497	84	581	878	1.3
0.72	344	653	126	779	1123	1.7
1.00	386	864	240	1104	1490	2.0
1.60	432	1031	420	1451	1883	2.0
2.50	494	1315	693	2008	2502	2.5
3.70	571	1529	792	2321	2892	2.9
5.10	650	1639	1026	2665	3315	2.9
10.00	650	1906	1102	3008	3658	3.2

*See the reference in Tab. VII.

Increase of the biomass (10^{-4}mg) of individuals of *Daphnia longispina* with different concentrations of natural food in 30 days

Tab. IX

Food concentration (in mg/l)	Juvenile individuals	Adult individuals			Total increase of biomass of individual in 30 days	Average daily relative increase of the biomass of an individual*
	Increase of the weight of body	Increase of the weight of body	Weight of eggs	Total increase of biomass		
0.41	443	523	312	835	1273	0.8
0.72	499	724	610	1334	1833	1.0
1.00	627	971	925	1896	2523	1.3
1.60	667	1278	1794	3072	3739	1.5
2.50	667	1478	2340	3818	4485	1.9
3.70	714	1777	2496	4273	4987	2.1
5.10	822	2415	2652	5067	5889	2.5
10.00	822	2415	2886	5301	6123	2.6

*See the reference in Tab. VII.

Increase of the biomass (10^{-4} mg) of individuals of *Chydorus sphaericus* with different concentrations of natural food in 30 days

Tab. X

Food concentration (in mg/l)	Juvenile individuals	Adult individuals			Total increase of biomass of individual in 30 days	Average daily relative increase of the biomass of an individual*
	Increase of the weight of body	Increase of the weight of body	Weight of eggs	Total increase of biomass		
0.41	28	46	264	310	338	0.5
0.72	35	62	308	370	405	0.5
1.00	50	80	336	416	466	0.6
1.60	50	112	336	448	498	0.6
2.50	62	142	496	638	700	0.7
3.70	62	162	496	658	720	0.7
5.10	68	180	558	738	806	0.8
10.00	68	180	558	738	806	0.8

*See the reference in Tab. VII.

with the changes of food concentrations. The obtained values of individuals production, understood as a total increase of the biomass of particular individual (increase of the weight of body and the weight of produced eggs) during a period of 30 days for *Cladocera*, and 45 days in the case of *E. graciloides*, are presented in Tables VII-XI.

Increase of the biomass (10^{-4} mg) of individuals of *Eudiaptomus graciloides* with different concentrations of natural food in 45 days

Tab. XI

Food concentration (in mg/l)	Juvenile individuals: Increase of the weight of body		Adult individuals	Total increase of biomas in 45 days	Average daily relative increase of the biomass of an individual*
	Nauplii	Copepodits	Weight of eggs		
0.72	24	425	6	455	5.0
1.00	28	664	14	706	4.8
1.60	30	846	36	912	5.0
2.50	30	966	52	1048	5.7
3.70	41	1175	64	1280	7.1
5.10	45	1315	84	1444	8.0

*See the reference in Tab. VII.

The rise of the food concentration resulted in an increase of the biomass of individuals of *Cladocera*, from 2 to 5 times depending on the species (Tab. VII-X), and up to 3 times in the case *E. graciloides* (Tab. XI). The rise of the food concentration, e.g. from 0.41 to 10.0 mg/l resulted in an increase of the biomass of *D. longispina* from 0.12 to 0.61 mg during a period of 30 days. The index of the rate of the individuals biomass increase expressed as an average relative daily increase of biomass, i.e. a ratio of the increase of the weight of body and eggs of an individual to the initial weight of body during 30 days for *Cladocera*, and 45 days for *E. graciloides* (duration of experiments), increased (according to the species) from 1.5 to 3 times together with the rise of the food concentration from 0.41 to 10.0 mg/l (Tab. VII-XI).

The differences in the total increase of the biomass of *Cladocera* found in particular variants of experiment with various food concentrations are smaller for the juvenile than the adult individuals. The rise of the food concentration from 0.41 to 10.0 mg/l resulted in an increase of the biomass of juvenile *D. brachyurum* about 1.5 times, while for the adult individuals – about 6.5 times. For *Cladocera* the total increase of biomass of juvenile individuals was only due to an increase of the weight of body. The biomass increase of adult ones is a sum of the body weight increase and the production of eggs. The production of eggs was in particular variants of experiment from 30 to 80% of the total increase of biomass of adult individuals according on the species (Tab. VII-XI). This causes greater differences in the increase of biomass of adult individuals as compared with juvenile ones. The influence of a trophic factor on a total increase of biomass of individuals is clearly visible in the lower food concentrations (to 3.7 mg/l).

III. THE INFLUENCE OF A TROPHIC FACTOR ON DEVELOPMENT, FECUNDITY AND PRODUCTION OF PLANKTONIC FILTRATORS IN NATURAL CONDITIONS

1. Numbers and biomass of natural food

During the investigated period (22 July to 30 August) the numbers of nannoplankton (the total of all three size classes) varied from 50 to 230 thousands cells/l (Fig. 8). The relatively highest numbers of nannoplankton (on the average 150 thousands cells/l) were noticed in the period from 22 July to 4 August. Later on (from 5 to 20 August) nannoplankton averaged to 80 thousands cells/l and then again increased up to 130 thousands/l on the average.

The most numerous group was the one measuring 3 to 10 microns, the least numerous was that with the largest organisms (> 10 microns) thus confirming the data of Spodniewska (1967). The highest biomass (0.40 mg/l on the average) was found at the maximal numbers of nannoplankton (from 22 July to 4 August), the lowest one (0.19 mg/l on the average) – from 5 to 20 August (Fig. 8).

The numbers of bacteria varied from $1.4 \cdot 10^6$ to $3.4 \cdot 10^6$ cells/ml. Changes of the numbers of bacteria in time were similar to those of nannoplankton (Fig. 8). The maximal numbers of bacteria were observed during the first fortnight of investigations, i.e. from 22 July to 4 August ($3.1 \cdot 10^6$ cells/ml on the average). Minimal numbers occurred from 5 to 20 August ($1.7 \cdot 10^6$ cells/ml on the average) (Fig. 8). During the period of investigations the bacterial biomass considerably varied – from 1.4 to 3.4 mg/l (Fig. 8).

A comparison of the biomass of nannoplankton with that of bacteria confirms the data of Gliwicz (1969a) on the small share of nannoplankton in the food of planktonic crustacean filtrators in the eutrophic lake. The biomass of nannoplankton is only several per cent of the biomass of bacteria, which are a basic food of planktonic filtrators in this type of water bodies.

A total biomass of bacteria and nannoplankton varied from 1.57 to 3.98 mg/l in the investigated period, but three periods different as regarding the food concentration can be distinguished: 1) from 22 July to 4 August, characterized

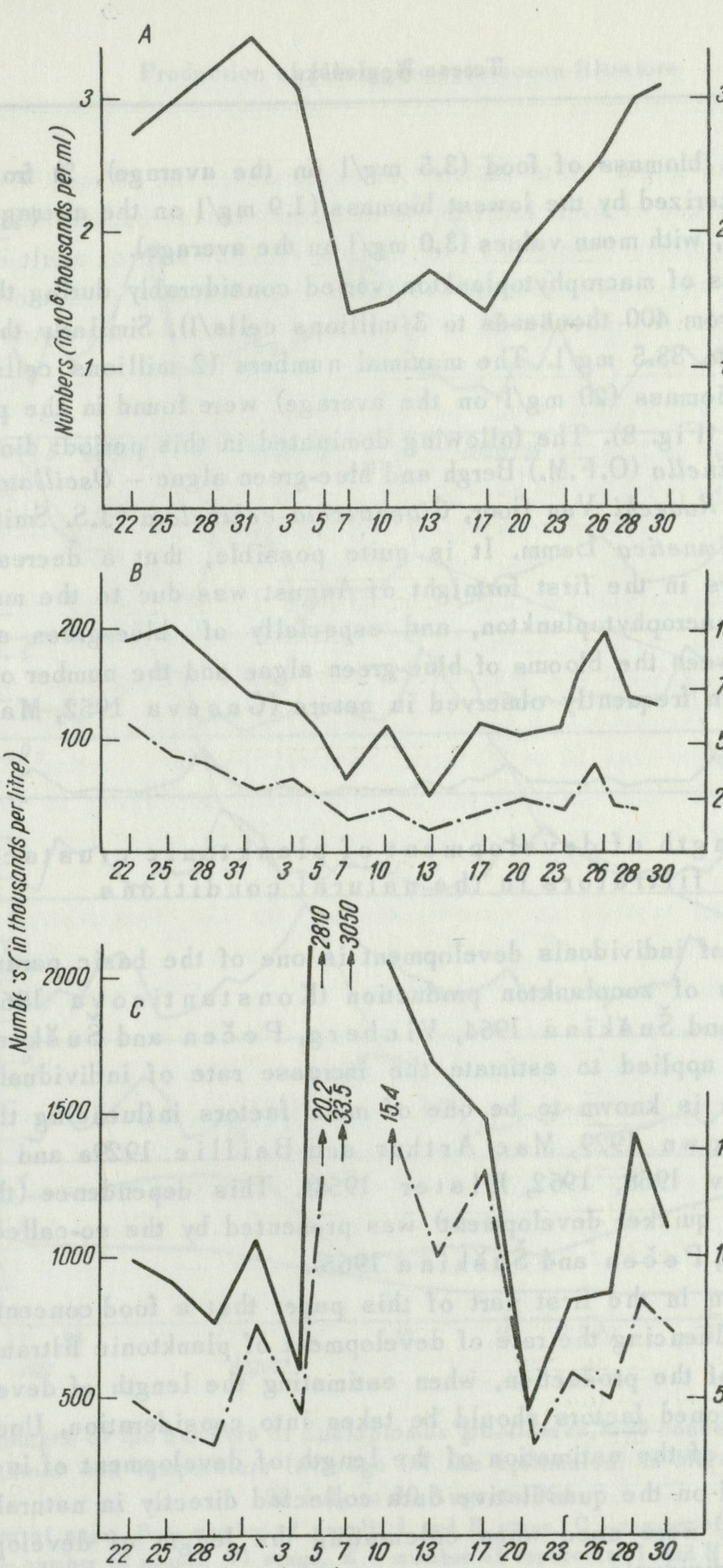

Fig. 8. Changes of the numbers and biomass of bacteria, nannoplankton and macrophytoplankton in the pelagial of Mikołajskie Lake from 22 July to 30 August 1964

A — Numbers and biomass of bacteria, B — Numbers (solid line) and biomass (dashed line) of nannoplankton, C — Numbers (solid line) and biomass (dashed line) of macrophytoplankton by the highest biomass of food (3.5 mg/l on the average), 2) from 5 to 20 August, characterized by the lowest biomass (1.9 mg/l on the average), 3) from 21 to 30 August, with mean values (3.0 mg/l on the average).

The numbers of macrophytoplankton varied considerably during the investigated period (from 400 thousands to 3 millions cells/l). Similarly the biomass varied from 3 to 33.5 mg/l. The maximal numbers (2 millions cells/l on the average) and biomass (20 mg/l on the average) were found in the period from 5 to 17 August (Fig. 8). The following dominated in this period: dinoflagellate *Ceratium hirundinella* (O.F.M.) Bergh and blue-green algae – *Oscillatoria limnetica* Lemm., *O. Radecki* Van Goor, *Gloeotrichia echinulata* (J.S. Smith) Richter and *Lyngbya limnetica* Lemm. It is quite possible, that a decrease of the bacteria numbers in the first fortnight of August was due to the maximal development of macrophytoplankton, and especially of blue-green algae. The antagonism between the blooms of blue-green algae and the number of bacteria is a phenomenon frequently observed in nature (Guseva 1952, Manuilova 1953).

2. The length of development of planktonic crustacean filtrators in the natural conditions

The length of individuals development is one of the basic parameters for the calculations of zooplankton production (Konstantinova 1961, Greze 1963, Pečen and Šuškina 1964, Vinberg, Pečen and Šuškina 1965). This length is applied to estimate the increase rate of individuals weight. The temperature is known to be one of main factors influencing the rate of development (Brown 1929, Mac Arthur and Baillie 1929a and b, Dehn 1937, Monakov 1958, 1962, Elster 1954). This dependence (the higher temperature, the quicker development) was presented by the so-called Krogh's curve (Vinberg, Pečen and Šuškina 1965).

It was shown in the first part of this paper that a food concentration is also a factor influencing the rate of development of planktonic filtrators. Thus in calculations of the production, when estimating the length of development, both these mentioned factors should be taken into consideration. Undoubtedly the best method of the estimation of the length of development of individuals is the one based on the quantitative data collected directly in natural environment. Such data were used when calculating the length of development of *E. graciloides* individuals.

Figure 9 presents the results of everyday quantitative samples collected for the analyses of numbers and age structure of *E. graciloides* population, from the pelagial of Mikołajskie Lake, from 22 July to 30 August 1964. The

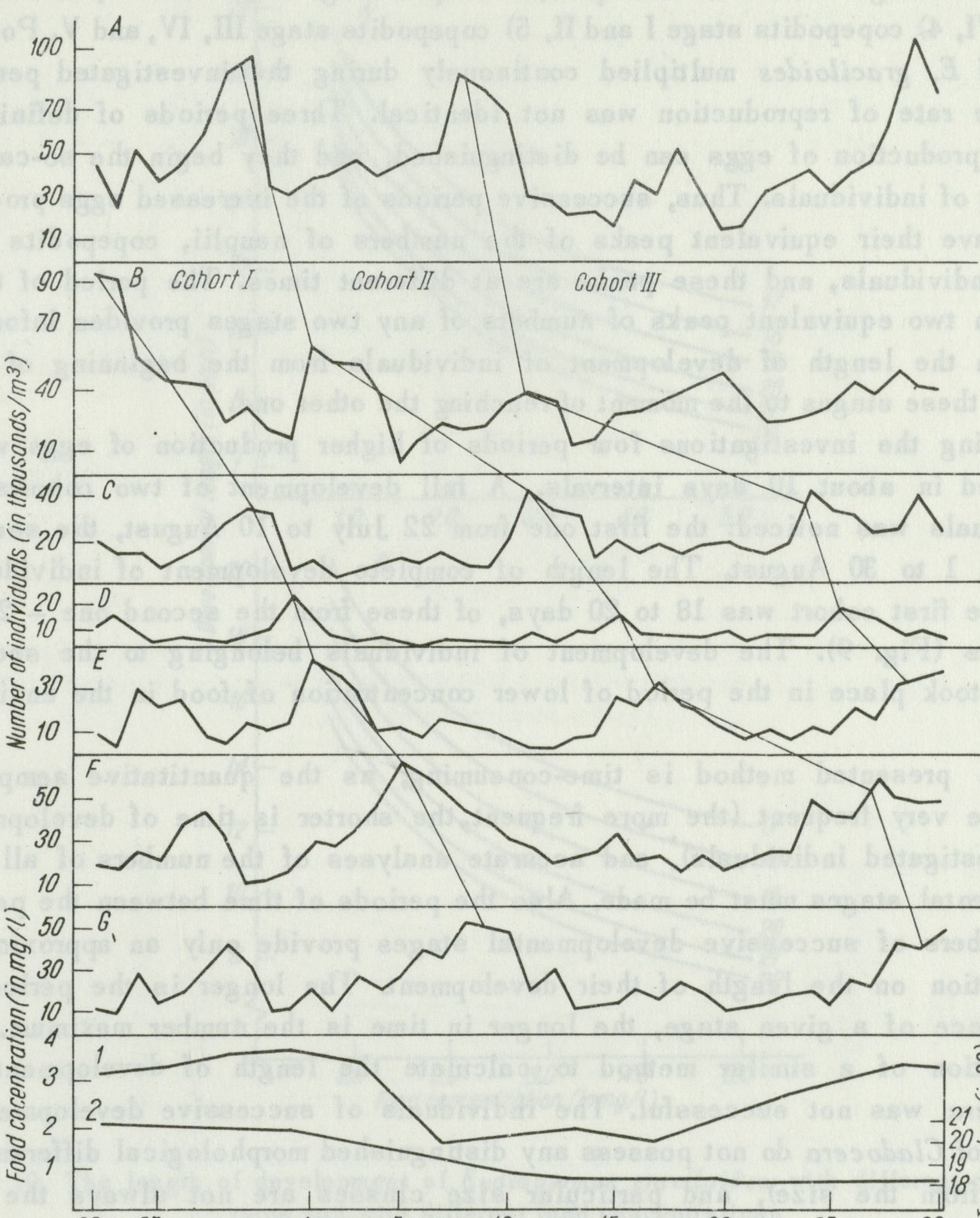

Fig. 9. Changes of the numbers of *Eudiaptomus graciloides*, food concentrations (bacteria, nannoplankton) and temperature (average for the epilimnion) in Mikołajskie Lake from 22 July to 30 August 1964

A — number of eggs, B — number of nauplii I and II stage, C — number of nauplii III, IV and V stage, D — number of nauplii VI stage, E — number of copepodits I and II stage, F — number of copepodits III, IV and V stage, G — number of adult individuals (♀ and ♂)

1 — food concentration, *2* — *temperature*

numbers dynamics of: eggs, particular developmental stages and adult individuals are presented separately. Five developmental stages were distinguished:

1) nauplii stage I and II (ortonauplii), 2) nauplii stage III, IV and V, 3) nauplii stage VI, 4) copepodits stage I and II, 5) copepodits stage III, IV, and V. Population of *E. graciloides* multiplied continously during the investigated period, but the rate of reproduction was not identical. Three periods of definitely higher production of eggs can be distinguished, and they begin the so-called cohorts of individuals. Thus, successive periods of the increased eggs production have their equivalent peaks of the numbers of nauplii, copepodits and adult individuals, and these peaks are at different times. The period of time between two equivalent peaks of numbers of any two stages provides information on the length of development of individuals from the beginning of the first of these stages to the moment of reaching the other one.

During the investigations four periods of higher production of eggs were observed in about 10 days intervals. A full development of two cohorts of individuals was noticed: the first one from 22 July to 10 August, the second – from 1 to 30 August. The length of complete development of individuals from the first cohort was 18 to 20 days, of these from the second one – 28 to 30 days (Fig. 9). The development of individuals belonging to the second cohort took place in the period of lower concentration of food in the environment.

The presented method is time-consuming, as the quantitative sampling must be very frequent (the more frequent, the shorter is time of development of investigated individuals), and accurate analyses of the numbers of all developmental stages must be made. Also the periods of time between the peaks of numbers of successive developmental stages provide only an approximate information on the length of their development. The longer is the period of occurrence of a given stage, the longer in time is the number maximum. An application of a similar method to calculate the length of development of *Cladocera* was not successful. The individuals of successive developmental stages of *Cladocera* do not possess any distinguished morphological differences (apart from the size), and particular size classes are not always the age classes. Also a repeated frequency of periods of higher egg production was not observed for *Cladocera* therefore the cohorts of individuals were not observed. When calculating the production of *Cladocera* it is necessary to apply the laboratory data on the length of development, and the influence of temperature and food concentration on these data should not be neglected.

The laboratory cultures of zooplankton, in order to determine the length of development of its particular components, should be kept in conditions as close to the natural ones as possible. A constant temperature of 17 and 18°C, as well as the natural food characterize the experimental cultures applied in this research. The development of various species of *Cladocera* at a temperature range from 10 to 23°C (with constant food concentration) was investigated

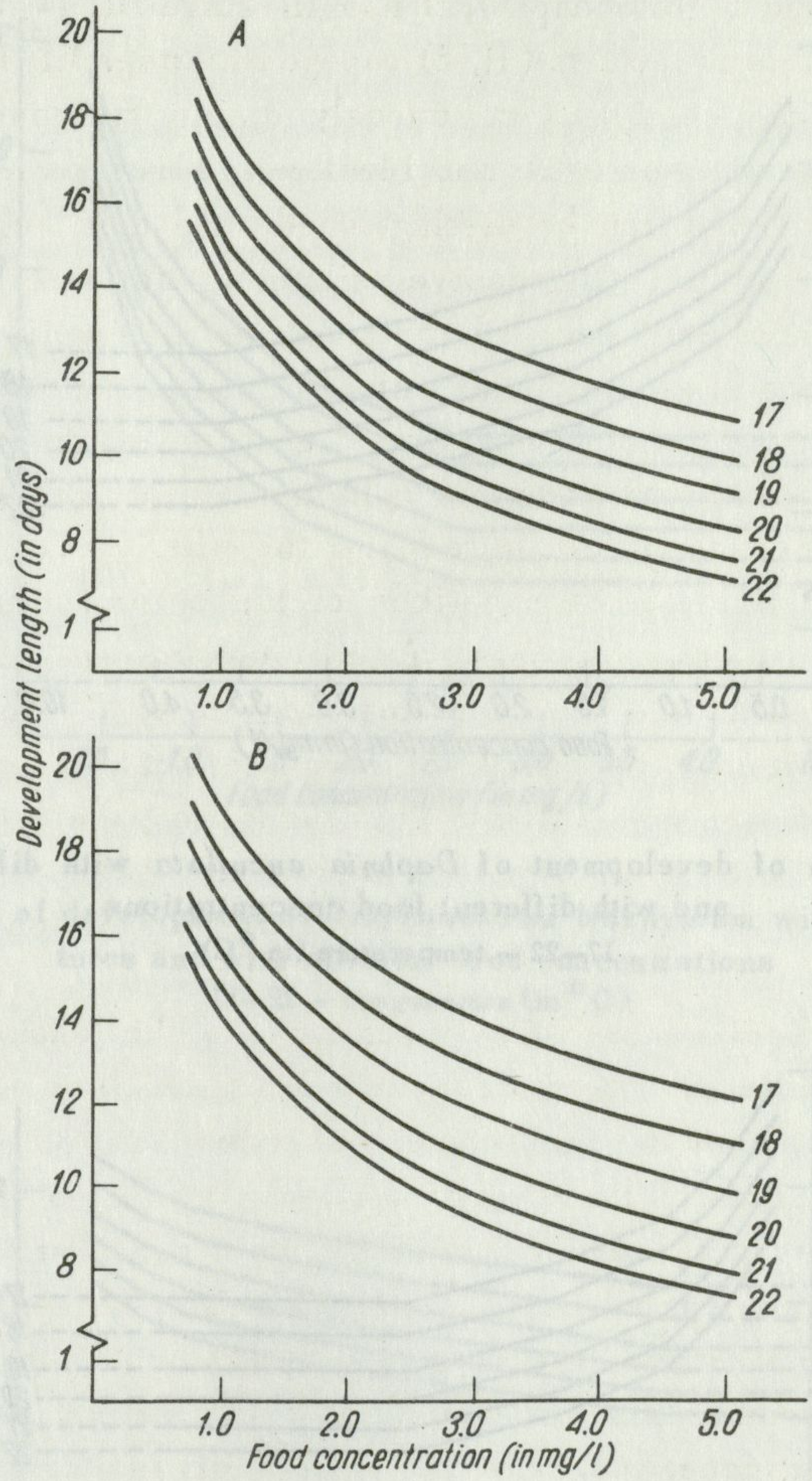

Fig. 10. The length of development of *Eudiaptomus graciloides* with different temperatures and with different food concentrations

A – nauplii, B – copepodits

17–22 – temperature (in°C)

by Pečen (1965a). Similar investigations on *E. graciloides* were carried out by Šuškina (1964). The results of these papers and the own data on the length of development of investigated species in various food concentrations and in constant temperature of 17°C were used for plotting the curves of the development of *E. graciloides, D. cucullata, D. longispina, Ch. sphaericus* and *D. brachyurum* in various food concentrations and various temperatures (Fig. 10–14). It was assumed that a 1°C rise of temperature in the range of optimal temperatures for the development of investigated species (17–22°C) causes a uniform

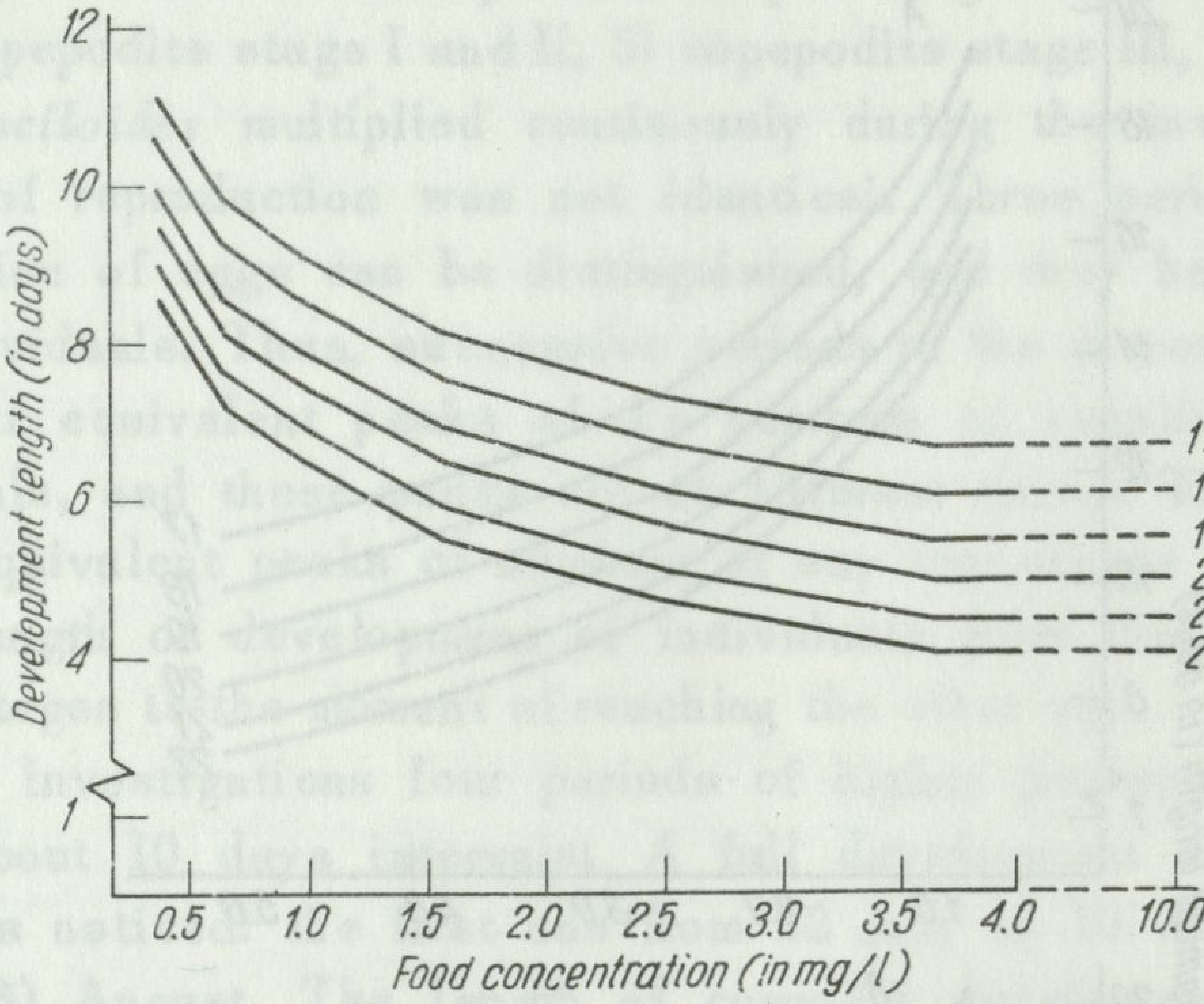

Fig. 11. The length of development of *Daphnia cucullata* with different temperatures and with different food concentrations
17–22 – temperature (in °C)

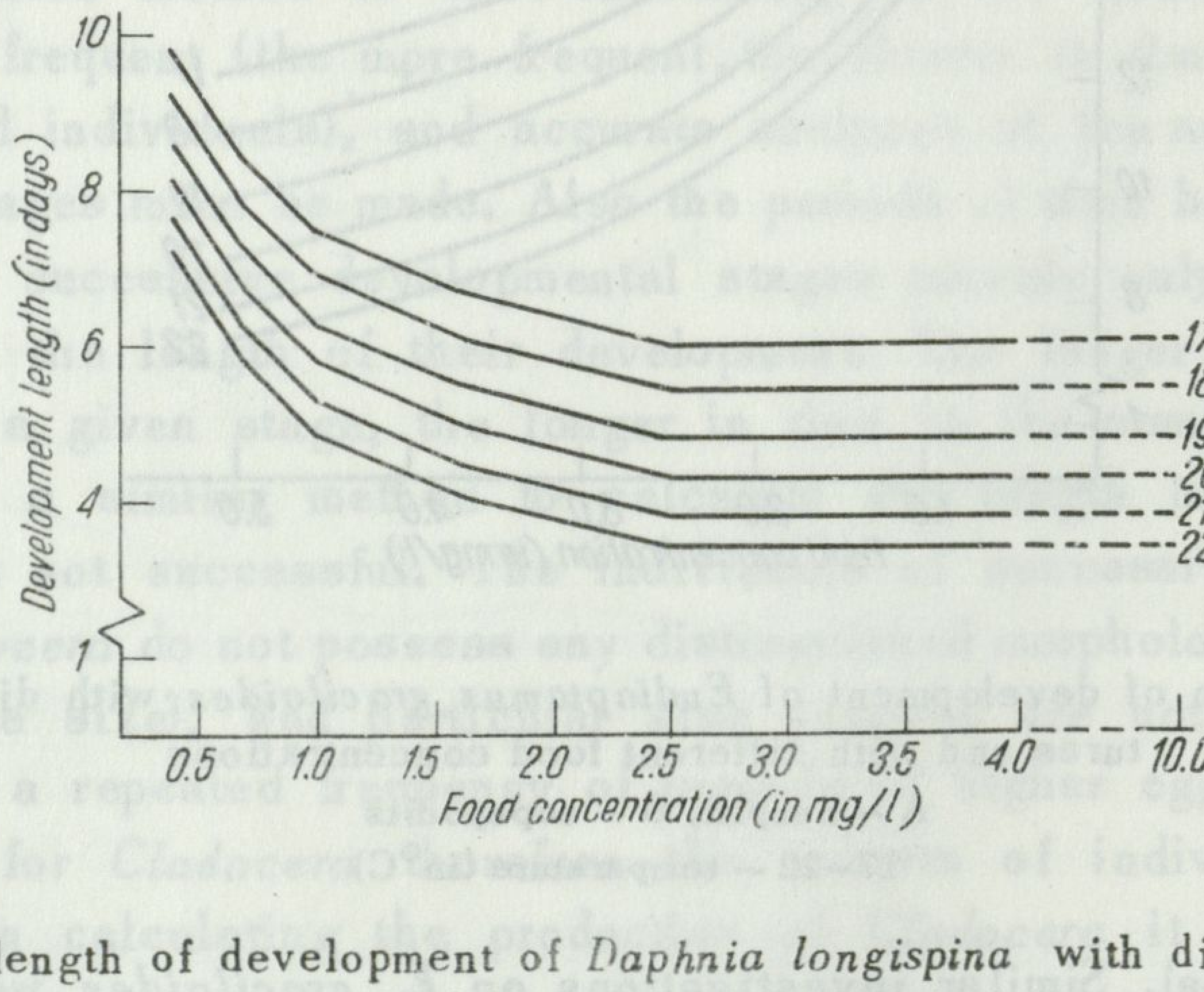

Fig. 12. The length of development of *Daphnia longispina* with different temperatures and with different food concentrations
17–22 – temperature (in °C)

increase of the rate of development in each food concentration. This assumption is confirmed by the preliminary data of Š u š k i n a (1964), obtained when analysing the development of *E. graciloides* in three various food concentrations, and the data obtained in present paper on the length of development of *D. cucullata*, *Ch. sphaericus* and *E. graciloides* at 18°C (Tab. III).

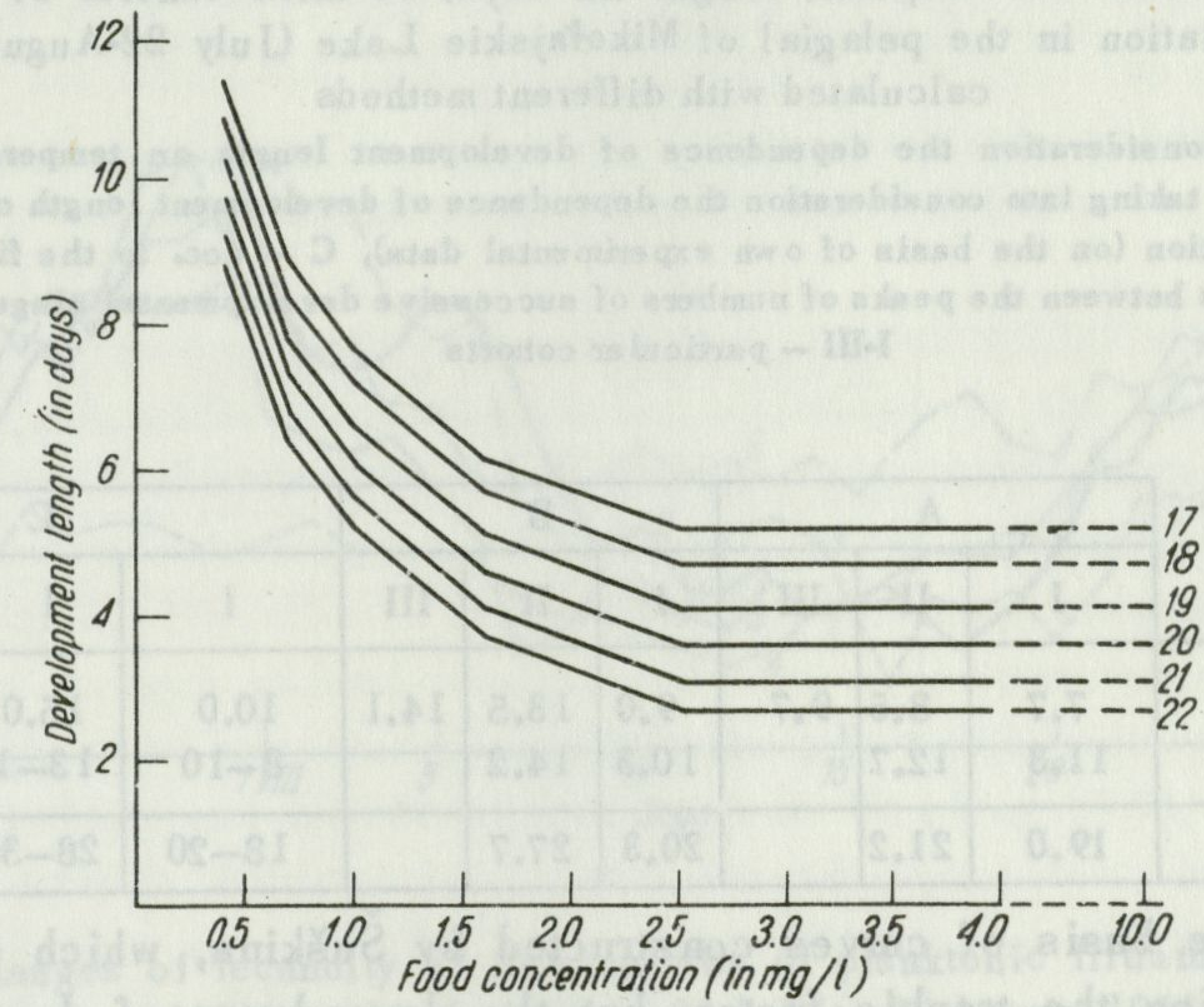

Fig. 13. The length of development of *Diaphanosoma brachyurum* with different temperatures and with different food concentrations
17–22 – temperature (in °C)

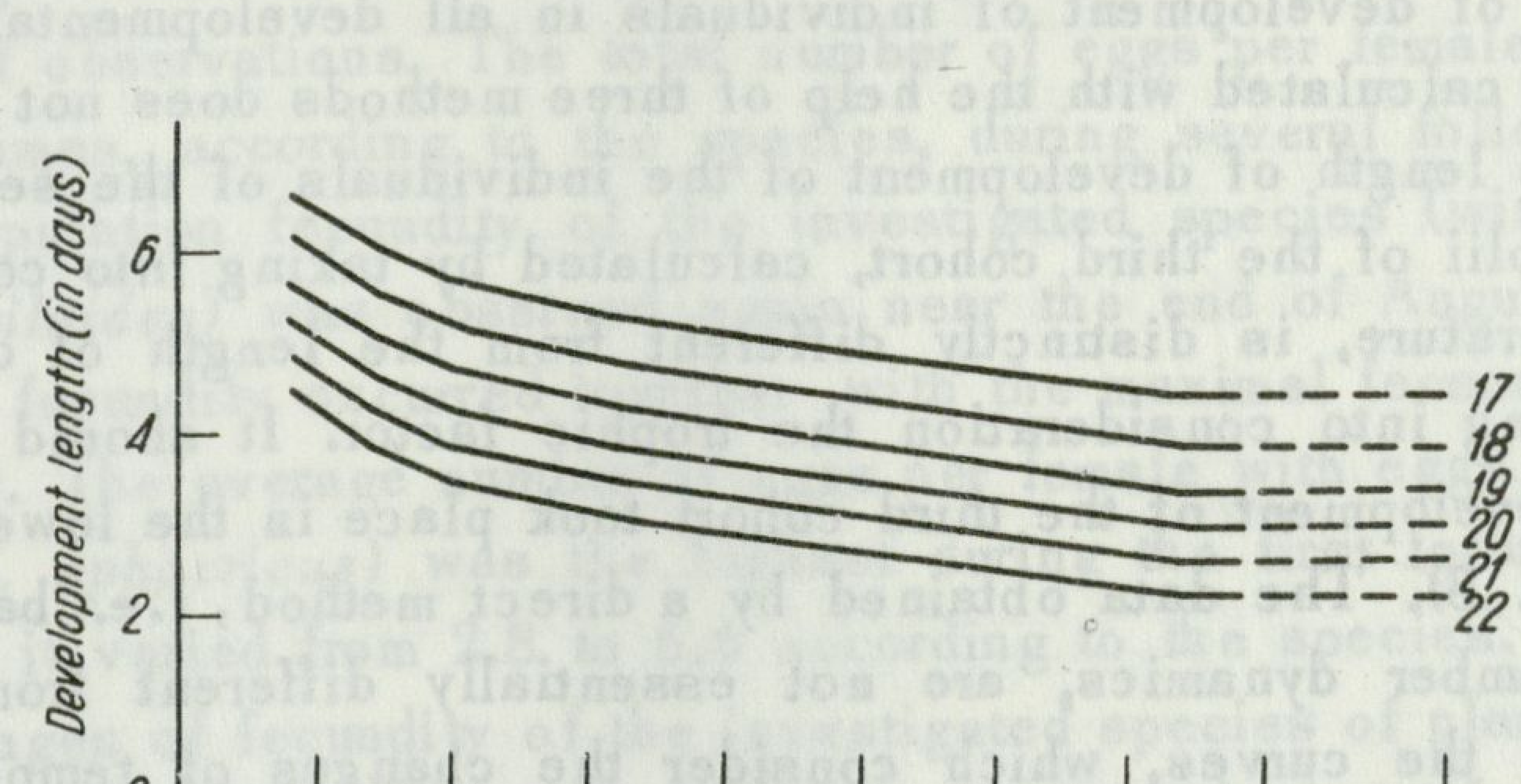

Fig. 14. The length of development of *Chydorus sphaericus* with different temperatures and with different food concentrations
17–22 – temperature (in °C)

Having the data on the quantities of food available and the temperature in the epilimnion of Mikołajskie Lake it is possible to calculate the length of development of individuals using the curves from Figures 10–14. The length of development of three cohorts of *E. graciloides* calculated on the basis of the curves in Figure 10 are presented in Table XII. For the comparison of the length of development of the same cohorts this Table presents the data

The comparison of the development length (in days) of three cohorts of *Eudiaptomus graciloides* population in the pelagial of Mikołajskie Lake (July 22-August 30, 1964), calculated with different methods

A – taking into consideration the dependence of development length on temperature (acc. to Šuškina 1964), B – taking into consideration the dependence of development length on temperature and food concentration (on the basis of own experimental data), C – acc. to the field data (time intervals between the peaks of numbers of successive developmental stages)

I-III – particular cohorts

Tab. XII

	A			B			C		
	I	II	III	I	II	III	I	I	III
Nauplii Copepodits	7.7 11.3	8.5 12.7	9.7	9.0 10.3	13.5 14.2	14.1	10.0 8–10	15.0 13–15	15–16
Total	19.0	21.2		20.3	27.7		18–20	28–30	

obtained on the basis of curves constructed by Šuškina, which do not take into consideration the trophic factor, but the dependence of development on the temperature. The data on the length of development obtained by direct observations of number dynamics in particular developmental stages of the investigated population of *E. graciloides* are also presented.

The length of development of individuals in all developmental stages of the first cohort calculated with the help of three methods does not differ much (Tab. XII). The length of development of the individuals of the second cohort and of the nauplii of the third cohort, calculated by taking into consideration only the temperature, is distinctly different from the length of development calculated taking into consideration the trophic factor. It should be pointed out, that the development of the third cohort took place in the lower food concentration (Fig. 8). The data obtained by a direct method, i.e. based on the analysis of number dynamics, are not essentially different from the data calculated from the curves, which consider the changes of temperature and the trophic factor. The agreement of these results prove that the curves of the dependence of the length of development on the food concentration and the temperature (Fig. 10–14) are the curves characterizing with sufficient accuracy the situations observed in nature.

3. Fecundity and the size of planktonic crustacean filtrators in natural conditions

The course of the changes of a population fecundity (average number of eggs per female) presented on the graph as a mobile average was similar for all investigated species (Fig. 15). The maximal population fecundity (1.3 to

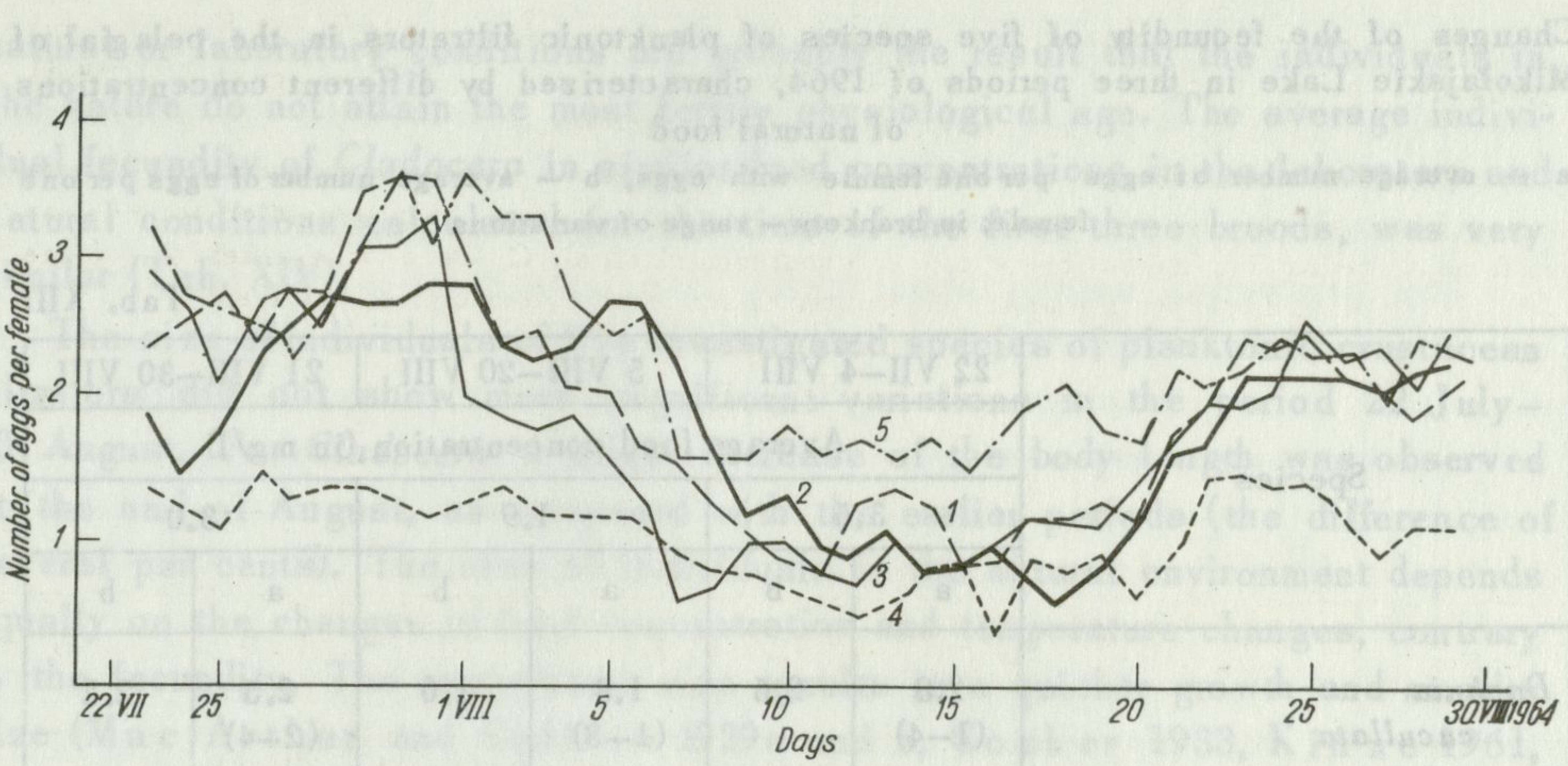

Fig. 15. Changes of fecundity of five species of planktonic filtrators in the pelagial of Mikołajskie Lake from 22 July to 30 August 1964

1 – Daphnia longispina, 2 – Diaphanosoma brachyurum 3 – Daphnia cucullata, 4 – Chydorus sphaericus, 5 – Eudiaptomus graciloides

3.0 eggs per female, according to the species) was found during the first fortnight of observations. The total number of eggs per female decreased from 1.5 to 2 times, according to the species, during several following days. The rise of population fecundity of the investigated species (with the exception of *E. graciloides*) was observed again near the end of August. The maximal population fecundity occurred together with the maximal fecundity of individual (Tab. XIII). The average number of eggs per female with eggs (with the exception of *Ch. sphaericus*) was the highest during the first fortnight of observations, and it varied from 2.8 to 6.4 according to the species. The comparison of the changes of fecundity of the investigated species of planktonic filtrators with the actual biomass of bacteria and nannoplankton in the lake show a distinct positive correlation (Tab. XIII). The above results justify the opinion that the fecundity of individuals is a good index of food conditions in the environment (Manuilova 1948, 1950, 1955, 1958, Burns 1966, Burgis 1967). The obtained results were compared with the data on individual fecundity, which were obtained in the laboratory experiments. In the case of *Cladocera* the number of eggs per female with eggs was slightly lower in the natural environment than in the experimental conditions, althought the food concentrations were similar (Tab. XIV). The individual fecundity of *Cladocera* in the natural conditions was estimated on the basis of number of eggs in brood pouch of females in two or three first broods (assuming, that the average life span of adult individual is several days). The fecundity of individuals in the laboratory

Changes of the fecundity of five species of planktonic filtrators in the pelagial of Mikołajskie Lake in three periods of 1964, characterized by different concentrations of natural food

a — average number of eggs per one female with eggs, b — average number of eggs per one female; in brackets — range of variations

Tab. XIII

Species	22 VII–4 VIII		5 VIII–20 VIII		21 VIII–30 VIII	
	Average food concentration (in mg/l)					
	3.5		1.9		3.0	
	a	b	a	b	a	b
Daphnia cucullata	2.8 (1–4)	2.6	1.8 (1–3)	1.0	2.5 (2–4)	2.2
Daphnia longispina	3.5 (1–5)	2.7	2.2 (1–3)	1.3	3.4 (1–5)	2.1
Diaphanosoma brachyurum	3.1 (2–4)	2.4	1.5 (1–2)	1.2	3.0 (1–4)	2.0
Chydorus sphaericus	2.0 (2–2)	1.3	2.0 (2–2)	0.8	2.0 (2–2)	1.2
Eudiaptomus graciloides	6.4 (3–10)	3.0	4.6 (3–6)	1.8	4.5 (3–6)	2.0

Changes of individual fecundity of Cladocera (average number of eggs per one female with eggs) in natural conditions and in the experiment with different food concentrations (for the period of the first three broods)

Tab. XIV

Species	Food concentration (in mg/l)			
	3.5–3.7		1.6–1.9	
	Natural conditions	Experiment	Natural conditions	Experiment
Daphnia cucullata	2.8	2.7	1.8	1.7
Daphnia longispina	3.5	3.3	2.2	2.3
Diaphanosoma brachyurum	3.1	3.0	1.5	2.0

experiments was estimated on the basis of the number of eggs in brood pouch of females during seven-eight broods. Own observations, as well as the data of Anderson (1932); Anderson and Jenkins (1942), Green (1954, 1955) and Richman (1958) show that a maximal fecundity of *Cladocera* is attained between the fifth and tenth brood, i.e. in the middle physiological age. The differences among the average numbers of eggs per female with eggs in the natural or laboratory conditions are probably the result that the individuals in the nature do not attain the most fertile physiological age. The average individual fecundity of *Cladocera* in similar food concentrations in the laboratory and natural conditions calculated for the time of the first three broods, was very similar (Tab. XIV).

The size of individuals of five investigated species of planktonic crustacean filtrators did not show more significant variations in the period 22 July–30 August. For *Cladocera* a slight increase of the body length was observed at the end of August, as compared with the earlier periods (the difference of several per cents). The size of individuals in the natural environment depends equally on the changes of food concentration and temperature changes, contrary to the fecundity. The temperature rise results in a quicker growth and smaller size (Mac Arthur and Baillie 1929a and b, Cocker 1933, Kinne 1961, Mac Laren 1963). During the present investigations the changes of food concentrations were accompanied by a gradual decrease of temperature (from 21 to 18° C). In such conditions the influence of the changes of food concentration on the size of individuals (found in the laboratory experiments carried out in a constant temperature) was obscured by the drop of temperature. Thus the size of individuals in this situation can not be treated as an index of the food abundance in the environment. This conclusion agrees with the results of Deevey (1960, 1964) and Maghraby (1965) who found that the size of planktonic crustaceans depends to a larger extent on the temperature than on the food concentration.

4. Production of planktonic crustacean filtrators

An attempt was made to estimate the production of the community of planktonic crustacean filtrators dominating in the pelagial of Mikołajskie Lake (*D. cucullata*, *D. longispina*, *Ch. sphaericus*, *D. brachyurum*, *B. coregonii* and *E. graciloides*) on the basis of field materials concerning the numbers, size and fecundity, and the experimental data on the length of development of individuals. The calculations of absolute production value and of the index of a daily production rate[4] of this community was made for three periods considerably differing in their food concentrations by: a) assuming that the food quantity in the natural conditions is not a factor limiting the individuals growth rate, which is always constant in a given temperature, b) taking into considera-

[4] A daily biomass turnover was calculated acc. to the formula $\frac{P_{WT}}{\bar{B}_T \cdot T}$, where: P_{WT} – production of individuals in g/m³, $\bar{B}_T$ – average biomass in g/m³, T – time in days.

tion the influence of the food concentration on the length of development of individuals. In both cases the dependence of the development on the temperature was considered. It is worth underlining that all calculations of zooplankton production found in literature were made according to assumption a.

The production values when taking into consideration the trophic factor or not were quite different for the period 5–20 August, when the food concentration was on the average 1.9 mg/l (Tab. XV). The production calculations according to assumption a give generally much higher results for the whole community than those obtained taking into consideration the influence of a trophic factor on the length of individuals development. The difference for particular species is from 27 to 38%, and 34% for the whole community. The above mentioned food concentration is lower than the one found to be an optimal for all the species in the laboratory conditions. A significant difference between the production values calculated using two methods for the other two periods was found only for *E. graciloides* (to 17%). For other species these differences were either not found, or did not exceed some per cent. That is why the production values calculated in both ways for the community of planktonic crustacean filtrators with the dominance of *Cladocera* differed insiginificantly for the other two periods. These results can be explained by a relatively high food concentration in these two periods. This concentration, high enough for the optimal development of *Cladocera*, is too low for the optimal development of *E. graciloides*. This is due to the different food preference of the latter.

The indexes of daily production rate for particular species and for the whole community calculated by taking the trophic factor into consideration or not are presented in Table XVI. The differences between the results obtained using both methods for the period of low concentration of food in the environment are so distinct as in the case of absolute production values.

IV. DISCUSSION

The results of laboratory experiments and the field observations presented in this paper show that the concentration of the food available is a factor as important for the development, growth and production of planktonic filtrators as temperature. A positive dependence of the length and rate of development on a trophic factor was found for all investigated species in a broad range of food concentrations (from 0.41 to 5.1 mg/l)[5] (Fig. 2–5, Tab. III). The strongest influence of the food density on the length of development was found for the individuals of *E. graciloides* (Fig. 4 and 5). This species is a typical macrofiltrator, consuming the food particles larger than 6 microns (nannoplankton)

[5] These concentrations are lower than those generally applied in the laboratory experiments.

The comparison of production (in g/m^3) of six species of planktonic filtrators in the pelagial of Mikołajskie Lake, calculated using different methods for three periods of 1964 with different food concentrations

a – taking into consideration the influence of temperature on the development length of individuals, b – taking into consideration the influence of temperature and food concentration on the development length of individuals

Tab. XV

Species	22 VII – 4 VIII			5 VIII – 20 VIII			21 VIII – 30 VIII		
	Average food concentration (in mg/l)								
	3.5			1.5			3.0		
	a	b	$\frac{a-b}{b}$ %	a	b	$\frac{a-b}{b}$ %	a	b	$\frac{a-b}{b}$ %
Eudiaptomus graciloides	7.15	6.10	16.0	6.61	4.77	38.7	4.54	3.91	17.0
Daphnia cucullata	9.23	9.02	2.4	3.85	2.86	34.4	1.82	1.72	5.6
Chydorus sphaericus	4.80	4.66	3.0	3.43	2.60	32.0	2.21	2.10	5.0
Diaphanosoma brachyurum	3.67	3.67	0	2.15	1.67	28.8	1.95	1.95	0
Daphnia longispina	4.79	4.79	0	3.75	2.94	27.8	3.09	3.09	0
*Bosmina coregonii**	4.49	4.34	6.9	3.66	2.66	37.5	2.79	2.66	4.8
Total	34.13	32.58	4.7	23.45	17.50	34.0	16.40	15.43	6.2

*Production of *B. coregonii* was calculated as a product of average biomass and the daily biomas turnover.

The comparison of the index of production rate P/B (daily turnover of the biomass) of six planktonic filtrators in the pelagial of Mikołajskie Lake, calculated using different methods for three periods of 1964 with different food concentrations

a – taking into consideration the influence of temperature on the development length of individuals, b – taking into consideration the influence of temperature and food concentration on the development length of individuals, c – average biomass (in g/m³)

Tab. XVI

Species	22 VII – 4 VIII			5 VIII – 20 VIII			21 VIII – 30 VIII		
	Average food concentration (in mg/l)								
	3.5			1.9			3.0		
	Daily P/B			Daily P/B			Daily P/B		
	a	b	c	a	b	c	a	b	c
Eudiaptomus graciloides	0.14	0.12	3.45	0.10	0.07	3.98	0.12	0.10	3.84
Daphnia cucullata	0.25	0.24	2.62	0.20	0.14	1.19	0.18	0.17	1.02
Chydorus sphaericus	0.38	0.36	0.89	0.26	0.19	0.81	0.27	0.26	0.81
Diaphanosoma brachyurum	0.29	0.29	0.88	0.22	0.17	0.59	0.21	0.21	0.90
Daphnia longispina	0.28	0.28	1.19	0.20	0.15	1.16	0.23	0.23	1.29
*Bosmina coregonii**	0.30	0.29	1.07	0.22	0.16	1.04	0.22	0.21	1.27
Total	0.24	0.23	10.10	0.16	0.12	8.77	0.17	0.16	9.13

***It was assumed that a daily turnover of *B. coregonii* biomass equals the average daily turnover of biomass of the four remaining investigated species of *Cladocera*.**

(Malovickaja and Sorokin 1961). The share of nannoplankton in the food biomass of planktonic crustacean filtrators is relatively small. That is why an even small decrease in the abundance of nannoplankton can affect to a greater extent the development of individuals prefering this food, than the analogous decrease of the abundance of bacteria – the development of other four investigated species. The literature does not provide any information quantitatively characterizing the dependence of the length of development on the concentration of the natural food. The only example is a paper by Šuškina (1964) on the experimental investigations of the influence of phytoplankton concentration on the development length of *E. graciloides*. This author investigated the development length of this species at a constant temperature 22°C and in the food concentration from 0.2 to 5.0 g/m³. By an extrapolation of her results to other temperature conditions (with the help of Krogh's curve, showing the dependence of the development length on temperature), Šuškina obtained information of the development length of individuals of this species in three concentrations of phytoplankton: 1) from 0.2 to 1.0 g/m³, 2) from 1.0 to 4.0 g/m³, 3) 5.0 g/m³, at temperatures from 10 to 22°C. The data of Šuškina are very similar (within the range of the same temperatures and similar food concentrations) to the development length of *E. graciloides* found in this paper.

The length of development of individuals is one of basic parameters for the calculations of zooplankton net production. The field data can be the basis for the direct calculation of the development length of only few zooplankton species from the suborder *Cyclopoida* and *Calanoida* (Ravera 1954, Nauwerck 1963, Wright 1965, Elbourn 1966). This is only possible if the multiplication of individuals in populations is limited to only one period, or if during a continuous multiplication there are periods of well marked increase of the eggs production, as it was observed in the case of the analysed population of *E. graciloides*. For the majority of species a direct estimation of development length on the basis of number dynamics is, however, impossible. In such cases there is the necessity of transfering the data of the length of development obtained in the laboratory conditions to natural conditions, taking into consideration the temperature and the quantity of food actually available for the planktonic crustacean filtrators in their environment.

The majority of laboratory experiments dealing with the influence of the kind and concentration of food on the development and production of planktonic filtrators were carried out in conditions far from the natural ones (literature review – Węgleńska 1970). The data from such experiments can not be applied for the production estimations in natural situations. The experiments carried out by the author were made in conditions as close to the natural ones as possible, and that is why the length of development of the investigated species, established with their help, is probably equal to the one in the lake. This conclusion is supported by the data on the length of development of *E. graciloides* from the laboratory experiments and from the analysis of the period of time among the peaks of numbers which were observed in the lake (Tab. XII). However, there is a question, whether the results obtained here have a universal application, i.e. can the curves presented in Figures 10–14 be applied for the estimation of the length of development of individuals in other seasons and in other water bodies? It is difficult to answer this question without special investigations. It seems, however, that in situations with a similar structure of the community of planktonic filtrators as in Mikołajskie Lake (with the domination of microfiltrators) and a similar food composition (prevalence of bacteria on small algae) – and this concerns the majority of eutrophic lakes – the curves presented in this paper can be applied without any restrictions. Thus the establishment of the length of development of planktonic crustacean filtrators will be much easier, as the estimation of the abundance of bacteria and nannoplankton is much less troublesome than carrying the laboratory experiments.

The above concerns the postembryonic development of individuals. The experimental results show that an embryonic development depend only to a very small extent on the changes of food concentrations and it is fairly constant in a given temperature (Tab. II and III). Many experimental works prove that the rate of eggs development depends mainly on the temperature (Wood and Banta 1933, Elster 1955, Eichhorn 1957, Esslova 1959, Malovickaja 1965). The data on the embryonic development obtained in this paper are very similar to those by the quoted authors.

The results of experiments show a distinctly marked influence of a trophic factor on the fecundity of the investigated species. The rise of the food concentration caused an increase of the number of broods, and for the majority of the investigated species also the increase of number of eggs per brood (Tab. VI). The laboratory data were confirmed by the field observations on the lake (Fig. 15 and Tab. XIII), and they prove that the fecundity of individual is a good index of the food abundance in the environment. The results of these observations and experiments agree with the data of many other authors who showed the existence of a positive correlation between the changes of individuals fecundity and food concentrations (Marshall and Orr 1952, Meškova 1952, Comita and Anderson 1959, Edmondson 1962, Edmondson, Comita, Anderson 1962, Hall 1964).

The experiments also showed a marked influence of a trophic factor on the rate of growth and the maximal size of individuals. The rise of the food concentration caused a quickening of the growth rate and an increase of the maximal size of individuals for all investigated species (Fig. 6–7, Tab. IV-V).

The obtained results confirm the ideas of many other authors about the reasons for the differentiation of the size of individuals (Patalas 1954, Czeczuga 1960, Axelson 1961, Tonolli 1961, Wiktor 1961, Węgleńska 1964). The analysis of the growth rate of individuals confirmed the observations of Patalas (in press) and the results of many laboratory experiments (Anderson 1932, Richman 1958, Smirnov 1964, Hrbačkova-Esslova 1962) which showed that the rate of the increase of the body length of adult individuals is about three times slower than that of juvenile individuals (Tab. IV).

The presented results determine the significance of natural food as a factor controling the development growth, fecundity and production of planktonic crustacean filtrators, especially in the low food concentrations. Numerous literature data on the quantities of food available in the natural conditions (Czeczuga 1961, Petrovič 1961, Rodina 1961, Pavoni 1963, Manuilova 1965, Czeczuga and Czerpak 1967), allow to assume that the populations of planktonic crustacean filtrators from the water bodies with a lower trophy do not realize their potential possibilities of growth and development. The experimental investigations of Blažka (1966) on the metabolism of *Dapnia longispina hyalina* (Leydig) kept on natural food from a dam reservoir Slapy and on the culture of *Scenedesmus*, are an interesting example showing a shortage of food in the natural conditions. This author found that the source of energy used in the metabolism of *Daphnia* fed with the culture of *Scenedesmus* are only the fasts and carbohydrates, and the proteins are used as a building material. In the case of the natural food, 40% of metabolism of *Daphnia* is based on proteins. As both these kinds of food are characterized by the same protein contents, the observed differences in the metabolism of *Daphnia* are due to the different quantities of available food. The quantity of food available for *Daphnia* in the surface layers of Slapy reservoir was, acc. to Blažka, a half lower than the quantity of algal food in laboratory experiments. A different efficiency of protein utilization in the metabolism of *Daphnia* had a decisive influence on the production of individuals biomass. In Blažka's experiments the period of renewing the *Daphnia* population kept on the culture of *Scenedesmus* was on the average 1.9 days, and of the one kept on the natural food – 6.5 days.

In happens occasionally that too small quantities of directly available natural food prevent the occurrence of a species of planktonic consumer in particular water body. The example of such situation was shown by Hrbačkova-Esslova (1962). This author kept *Daphnia pulex* (a species typical for small water bodies with a great abundance of nannoplankton) in water from the Slapy dam reservoir, which contained several times lower quantities of nannoplankton, than the natural environment of this species. This experiment showed that there is not enough food in Slapy reservoir for a full development and reaching the maturity by *Daphnia*, as new born individuals were dying after the third or fourth moulting, with symptoms of under feeding. A full development and maturity of *D. pulex* individuals were observed only after giving additional food, i.e. *Chlorella* and *Scenedesmus*.

In the eutrophic water bodies, and among them in Mikołajskie Lake the situation is not so obvious. In the experimental conditions a definitely greater influence of a trophic factor on the growth and development of planktonic crustacean filtrators was observed in the case of diluting than in the case of condensing the natural food (Fig. 2, 4, 6, 7, Tab. II-V). Therefore it can be stated that the food does not limit the development and production of planktonic filtrators in the reservoirs with a more advanced trophy. On the other hand it is known from the data of Spodniewska (1967) and from own observations, that in some seasons the food conditions in Mikołajskie Lake are poorer than these observed during the experiments. The biomass of bacteria and nannophytoplankton can decrease to 1.0 mg/l. The results of experiments show that such food concentrations are not sufficient for an optimal growth and development of planktonic filtrators. When analysing the influence of a trophic factor on the development and production of planktonic crustacean filtrators one should consider not only the quantity of food available, but also the number of individuals in a community of planktonic consumers. There is a lot of data which confirm that the development rate, growth and thus the production have a different course in experiments with individuals than with populations, and with communities of organisms with various density. E.g. Galkovskaja (1963) showed that the indexes of production efficiency are higher for a population culture than for cultures of individuals. It seems that an inverse situation is more frequent, i.e. the decrease but not the increase of such indexes in a population culture as compared with cultures of individuals. The data of Zeilichman and Heinrich (1959), Ivanova (1963), Manuilova (1964) and Heinle (1966) prove that a decrease of quantity of food per individual causes that the growth rate slows down, the fecundity is lower, and the development is longer. These results agree with the results of the experiments on the influence of various densities of *D. brachyurum* individuals on the development rate of this species (Węgleńska 1968) and with the present field observations (Fig. 8, 9, 15, Tab. XV and XVI). The field observations of six species of planktonic crustacean filtrators in Mikołajskie Lake have begun during their summer maximum of numbers (250 thousands/m^3 on the average). It can be assumed that for such a number of individuals even relatively high food concentrations (3.5 mg/l on the average) are not sufficient for the optimal growth, development and production of these species. On the other hand an increase of the numbers of animals and the increase of their consumption can also result in worse food conditions in the lake. Namely, the intensively consumed algae and bacteria are replaced by great numbers of larger forms – macrophytoplankton, not consumed by planktonic filtrators, and inhibiting the bacterial development.

The presented data allow to conclude that the quantity of food available for the planktonic filtrators in the eutrophic lake can be a limiting factor for the development and production of individuals. The limiting significance of food shows a varying degree of intensity for various species utilizing different kinds of food.

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WPŁYW RÓŻNYCH KONCENTRACJI POKARMU NATURALNEGO NA ROZWÓJ, PŁODNOŚĆ I PRODUKCJĘ SKORUPIAKOWYCH FILTRATORÓW PLANKTONOWYCH

Streszczenie

Celem badań prowadzonych w latach 1964–1966 było określenie zależności między koncentracją pokarmu naturalnego a tempem rozwoju, wzrostu i rozmnażania oraz pro-

dukcją skorupiakowych filtratorów planktonowych (*Daphnia cucullata*, *D. longispina*, *Diaphanosoma brachyurum*, *Chydorus sphaericus* i *Eudiaptomus graciloides*) dominujących w pelagialu Jeziora Mikołajskiego. Wyniki eksperymentów laboratoryjnych i obserwacji terenowych pozwoliły na rozwiązanie dwóch zasadniczych problemów: 1) Czy koncentracja pokarmu dostępnego dla skorupiakowych filtratorów planktonowych w środowisku naturalnym jest wystarczająca dla ich optymalnego rozwoju i wzrostu; 2) W jaki sposób i w jakim zakresie obserwowane w naturze wahania ilości pokarmu mogą wpływać na produkcję zespołu skorupiakowych filtratorów planktonowych, występujących w Jeziorze Mikołajskim, typowym dla naszej strefy klimatycznej jeziorze eutroficznym.

Eksperymenty laboratoryjne polegały na hodowli pojedynczych osobników pięciu badanych gatunków w stałych temperaturach (17 i 18°C) i przy różnych koncentracjach pokarmu (od 0,41 do 10 mg/l bakterii i nannoplanktonu) (tab. I). Odpowiednie koncentracje pokarmu uzyskiwano stosując zmodyfikowaną metodę Dodsona i Thomasa (1964) (fig. 1). Analizowano: długość rozwoju embrionalnego i postembrionalnego osobników, tempo wzrostu i płodność (liczbę „kładek" i liczbę jaj w „kładkach"). Obserwacje terenowe polegały na zbieraniu prób ilościowych z pelagialu Jeziora Mikołajskiego, codziennie od 22 lipca do 30 sierpnia. Uzyskano tą drogą informacje o liczebności, płodności i wielkości skorupiakowych filtratorów planktonowych w środowisku naturalnym oraz o ilości ich potencjalnego pokarmu (bakterii i nannoplanktonu).

U wszystkich badanych gatunków obserwowano ogólną prawidłowość: wzrost koncentracji pokarmu powoduje przyspieszenie tempa rozwoju postembrionalnego i skrócenie okresu dojrzewania osobników o kilka bądź o kilkanaście dni (fig. 2–5 i tab. III). Zależność ta szczególnie wyraźnie wystąpiła przy niższych koncentracjach pokarmu. Na podstawie uzyskanych wyników ustalono matematyczną zależność między koncentracją pokarmu a długością rozwoju postembrionalnego osobników. Uwzględniając dane piśmiennictwa o wpływie temperatury na rozwój postembrionalny osobników wykreślono krzywe obrazujące tę zależność (fig. 10–14). Rozwój embrionalny tylko w małym stopniu jest zależny od zmian koncentracji pokarmu (tab. II-III). Na podstawie codziennych pomiarów długości ciała osobników uzyskano informacje o tempie ich wzrostu i maksymalnych rozmiarach. Otrzymane wyniki dowodzą, że wzrost koncentracji pokarmu powoduje przyspieszenie tempa wzrostu i jest pozytywnie skorelowany z maksymalnymi rozmiarami osiąganymi przez dojrzałe osobniki wszystkich badanych gatunków (fig. 6–7, tab. IV-V). Wzrost koncentracji pokarmu stymuluje płodność osobników. Ogólna liczba jaj wyprodukowanych przez jedną samicę w ciągu 30-dniowego lub 45-dniowego okresu życia wzrastała, w zależności od gatunku, od 1,5 do 8 razy. Wzrost ten był wynikiem zarówno zwiększenia liczby „kładek", jak i liczby jaj w poszczególnych „kładkach" (tab. VI). Wyniki dotyczące wzrostu i płodności osobników przy różnych koncentracjach pokarmu wykorzystano do obliczenia przyrostu ich biomasy. Wzrost koncentracji pokarmu z 0,41 do 10 mg/l powoduje, w zależności od gatunku, przyrost biomasy osobników od 2 do 5 razy (tab. VII-XI). Na podstawie bezpośrednich obserwacji terenowych stwierdzono, że wykazane w eksperymentach laboratoryjnych zależności między koncentracją pokarmu a płodnością skorupiakowych filtratorów planktonowych mają taki sam charakter w środowisku naturalnym (tab. XIII-XIV, fig. 15). Płodność osobników jest więc dobrym wskaźnikiem zasobności pokarmowej środowiska. Krzywe obrazujące zależności rozwoju osobników od koncentracji pokarmu i temperatury, wykreślone na podstawie eksperymentów laboratoryjnych, sprawdzono w badaniach rozwoju *Eudiaptomus graciloides* w warunkach naturalnych. Zastosowano metodę polegającą na mierzeniu odstępów czasu między szczytami liczebności poszczególnych stadiów rozwojowych tego gatunku (fig. 9). Długość rozwoju osobników obliczona tą metodą różniła się tylko nieznacznie od długości rozwoju wyliczonej z odpowiedniej krzywej wykreślonej na podstawie danych eksperymentalnych (tab. XII).

W oparciu o dane terenowe dotyczące liczebności, wielkości i płodności badanych gatunków wyliczono produkcję i wskaźnik dobowego tempa produkcji dla całego zespołu skorupiakowych filtratorów planktonowych dominujących w Jeziorze Mikołajskim (tab. XV-XVI). Wyliczenia produkcji wykonane przy uwzględnieniu jedynie wpływu temperatury oraz przy uwzględnieniu wpływu temperatury i koncentracji pokarmu na długość rozwoju osobników różniły się wyraźnie. Największe różnice (34%) obserwowano przy ocenie produkcji całego zespołu skorupiakowych filtratorów planktonowych w okresie najmniejszej koncentracji pokarmu w środowisku (ok. 1,9 mg/l). Uwzględnienie czynnika troficznego jest więc konieczne przy ocenie produkcji filtratorów planktonowych.

W świetle uzyskanych wyników można wnioskować, że w sytuacjach gdy mamy do czynienia z podobną do obserwowanej w Jeziorze Mikołajskim strukturą zespołu skorupiakowych filtratorów planktonowych (dominacja mikrofiltratorów) i z podobnym składem pokarmu (przewaga bakterii nad drobnymi glonami), a dotyczy to wszystkich jezior eutroficznych, koncentracja pokarmu dostępnego dla filtratorów planktonowych w niektórych okresach jest czynnikiem limitującym rozwój i produkcję osobników. To limitujące znaczenie pokarmu może być różne dla poszczególnych gatunków, zależnie od preferowanego przez nie pokarmu.

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