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FOOD SIZE SELECTION AND SEASONAL SUCCESSION OF FILTER FEEDING ZOOPLANKTON IN AN EUTROPHIC LAKE*

ABSTRACT: Filtering rate, feeding rate, fecundity and numbers are more strongly limited by low available food concentrations in some filter feeding crustacean species, while in other species by too high concentrations of large and filamentous algae. The former are distinguished by a lower upper size limit of particles grazed (and a narrower gap between carapace margins in cladocerans), the latter by a higher upper size limit of particles grazed and, as a result, by greater susceptibility to filtration interference by net phytoplankton. A high concentration of net algal forms is discussed as a selectively working factor, modifying the final result of competition between the more and the less efficient filter feeding species in the lake.

Contents

1. Introduction
2. Material and methods
   2.1. Material
   2.2. Filtering rate
   2.3. Body length and width of carapace crevice
   2.4. Numbers, intensity of reproduction and individual production in crustacean populations
   2.5. Numbers and biomass of phytoplankton
   2.6. Non-algal food concentration
3. Results
   3.1. Food size selection among cladocerans
   3.2. Filtering rate for various particle size ranges in *Eudiaptomus graciloides*
   3.3. Filtering rate and its changes through the seasons
   3.4. Filtering rate and population fecundity and numbers
   3.5. Summer reduction in filtering rate and phytoplankton in 1973
   3.6. Fecundity and individual production of filter feeders against seasonal succession of phytoplankton in 1966

1. INTRODUCTION

There are few ecological phenomena which have been described so thoroughly and in such great detail as that of lake zooplankton seasonal succession. The species composition of zooplankton communities undergoes distinct changes throughout the seasons which is most easily observed in eutrophic lakes of the temperate zone. Species or even genera reaching maximum abundance in late spring (e.g., *Daphnia, Bosmina, Eudiaptomus*) usually in summer give way to other forms (e.g., *Diaphanosoma, Ceriodaphnia, Chydorus*), only to regain quite often their temporarily lost dominant position when autumn comes.

However, the mechanisms of these seasonal changes remain overall unexplained. Biotic factors such as food and predation are sometimes thought of as playing a certain role, but more frequently these changes are explained by different spectra of ecological tolerance of the species in relation to abiotic environmental factors undergoing seasonal changes, particularly to temperature (for review see Hutchinson 1967) . Indeed, this factor may be of some importance, but its influence has not yet been proved. On the contrary, it seems that typical summer monacmic species (e.g., *Chydorus sphaericus* (O. F. Müller)) as well as spring-autumn diacmic species (e.g., *Eudiaptomus graciloides* (Lill.) or *Daphnia longispina* O. F. Müller) have the same spectra of temperature tolerance. This is evident from the comparison of the relationship between egg development time and temperature for 13 crustacean species (Bottrell 1975, Bottrell et al. 1976) as well as from the comparison of the relationship between postembryonic development time and temperature for four cladoceran genera (Pečen 1965 after Hillbricht-Ilkowska and Patalas 1967).

Numerous studies on plankton seasonal succession have shown an inverse rather than a direct relationship between the abundance of phytoplankton and zooplankton. This has been explained along the lines of either Harvey's et al. (1935) or Hardy and Gunther's (1935) mutually controversial hypotheses. According to the former zooplankton pressure upon phytoplankton may become sufficiently strong to limit its abundance. According to the latter zooplankton cannot develop in large numbers in the presence of abundant phytoplankton due to chemical inhibition of animals by algal substances excreted into the environment. This controversy is still alive as the phytoplankton is treated as a whole without taking into account its two size fractions, which are both differently sensitive to zooplankton grazing and which both influence the zooplankton in a different way. These fractions are the small nannoplanktonic algae (let us say below 50 μm diameter) available as food for filter feeding animals, and the large net phytoplankton algae (over 50 μm diameter) unavailable as food for filter feeders but in some way influencing the filtering processes of animals.

It may be expected that the positive (small algae) and negative (net algae) effect of both fractions upon various species of filter feeding zooplankton is of different degree. If this is so, both fractions can constitute important factors responsible for the succession of zooplankton species. The work of both fractions upon zooplankton must be connected with the process of food intake by animals, and therefore it was in this process, the process of filtering food suspension from the environment, that these mechanisms were sought.

The aim of this paper is to find out what is the significance of both phytoplankton fractions for the seasonal changes in species structure of planktonic crustaceans and to describe the mechanisms of influence of small (edible) and of large (inedible) algae upon the demography of species forming the planktonic filter feeding community in the lake.

Research was carried out in the well and thoroughly described eutrophic Mikołajskie Lake, where for many years the same sequence of seasonal changes in phyto- and zooplankton was always observed:

a. spring population booms of *Bosmina coregoni* Baird, *Daphnia cucullata* Sars, *D. longispina* and *Eudiaptomus graciloides*, following soon after the decline in high early spring densities of diatoms, in the period of large biomass of nannoplanktonic algae;

b. summer decline or disappearance of these populations, accompanied by development of *Diaphanosoma brachyurum* Liévin, *Chydorus sphaericus* and *Ceriodaphnia quadrangula* O. F. Müller populations and by a mass appearance of large algae, mostly peridinians and blue-greens;

c. autumn return of high numbers of the "spring" species, accompanied by the sharp decrease in numbers of the "summer" species populations and by disappearance of summer algal blooms (Spodniewska 1967, 1974 and unpublished data, Hillbricht-Ilkowska et al. 1972 and unpublished data, Spodniewska, Hillbricht-Ilkowska and Węgleńska 1973, Raczkowska 1974, Węgleńska — in preparation, Gliwicz — unpublished data, Kan — unpublished data).

2. MATERIAL AND METHODS

2.1. Material

Between May and October 1973 twenty-four measurements were made of the filtering rates of all the dominant filter feeding species in respect of various size ranges of food particles. These measurements were carried out in situ in Mikołajskie Lake 4 times a day (at 1,00, 7,00, 13,00 and 19,00 hours) on the following dates: 12 May, 12 June, 18 July, 21 August, 24 September and 23 October 1973. On the same dates and from the same offshore station samples were taken of phyto- and zooplankton used for the microscopic analyses of the numbers and biomass of the dominant algal species and the numbers, age structure, individual size and fecundity of the investigated crustacean species, as well as for the measurements of the distance between carapace margins (crevice width) in cladocerans.

In order to verify the results obtained on the basis of 1973 data use was made of 1966 raw data made available by Dr. Anna Hillbricht-Ilkowska, Dr Irena Spodniewska and Dr. Teresa Węgleńska. The 1966 data, which have already been published in an integrated form in a number of papers (Hillbricht-Ilkowska and Spodniewska 1969, Hillbricht-Ilkowska and Węgleńska 1970, Hillbricht-Ilkowska et al. 1972, Gliwicz and Hillbricht-Ilkowska 1975, Węgleńska — in prepara-

tion), were taken at the same offshore station in Mikołajskie Lake and covered the analyses' results of nannophytoplankton and net phytoplankton numbers and biomass, of the intensity of live algal mass elimination and of numbers, fecundity and productivity of dominant filter feeding crustacean species.

2.2. Filtering rate

Determination of the filtering rate of the crustacean species under more or less natural conditions proved until recently to be plagued with too many obstacles. It was not for 12 years after the first attempts by N a u w e r c k (1959) that H a n e y (1971) was successful in introducing a simple and quick method being a skilful combination of B u r n s and R i g l e r 's (1967) and G l i w i c z 's (1968) methods. H's method allows a quick measurement of the filtering rate of any species in situ by introducing for few minute exposures small amounts of highly radioactive yeast cells (^{32}P) into the experimental chamber closed under water with a segment of the natural plankton community.

However, this method also involves a shortcoming typical of all laboratory methods (a review of laboratory methods can be found in S o r o k i n 1968 and R i g l e r 1971). This method gives the filtering rate of particles, but only of those particles which correspond in size to the experimentally introduced yeast cells (in H a n e y 1971 − Rhodotorula sp. of cell diameter of about 3.5 μm), whereas it renders no information on the filtering rate of larger and smaller food particles.

To obtain also this information a method was used in the present paper which referred to the laboratory methods of B u r n s (1968a, 1969a) and G l i w i c z (1969a), their idea being to introduce into the environment different size indigestible particles of artificial "food" and then, after a short exposure, to measure and count them in the animals' alimentary tracts.

In the present method, which has already been exploited (G l i w i c z 1976a), beads of organic polimer were used, ranging in size between 1 and 110 μm diameter. These perfectly spherical particles were resistant to concentrated acids and were of relatively low specific gravity. They were obtained in the required size distribution (Table I) by the method of interrupted polimerization in the Research and Experimental Institute of the Ceramic Industry, Pruszków, Poland.

Table I. Initial concentration of organic polimer beads of various size ranges in the experimental environment in which animals were exposed for filtering rate measurements

Size of particles (μm diameter)	0	5	10	15	20	25	30	35	40	45	50
Number of particles per ml	3,537	4,702	2,422	430	176	77	42	21	7	3	

The size distribution was chosen so that it would be as close as possible to the particle size distribution of natural lake seston (G l i w i c z 1969a, 1974 and unpublished data). In this way it was attempted to avoid the effect of filtering rate inhibition by having too large a concentration of beads above 15—20 μm diameter, although this effect was not to be avoided completely (see Subsection 4.1). With the same in view, rather low concentrations of beads were used, not exceeding those concentrations of natural seston particles to be found in the environment.

The principle of the method was, in general, to expose the animals in situ to known concentrations of the polimer beads added to the lake water containing natural concentrations of all the seston components, including phyto- and zooplankton. After exposure, which was

shorter than the passage of food through the alimentary tracts, the animals were killed in freshly boiled water (to prevent defecation) and fixed in a 4% formaldehyde solution. Then, within a freely chosen time, they were selected into species and age stages, rinsed in water filtered through Millipore AAWPO47 filters (to get rid of polimer particles on the external animal surfaces) and submerged (in lots of 1–10 individuals) in a small drop of concentrated H_2SO_4, where they were kept for a period of at least 4 hours at a temperature of 50–70°C. After all of the animal tissue had been dissolved by the acid, the beads, insoluble in the acid, were counted in every drop (under 1,250 × magnification) in size ranges of every 5 μm diameter (0–5, 5–10, etc.). Then from the ratio of the average number of beads of a given size range per individual (N_g) to the number of beads of the same range in 1 ml of the experimental environment (N_e – Table I) the filtering rate (F) was calculated for this size range (in ml · ind.$^{-1}$ · 10 min.$^{-1}$, after multiplication by $6 \cdot 10^3$ – in μl · ind.$^{-1}$ hr^{-1}): $F = 6 \cdot 10^3 \cdot N_g \cdot N_e^{-1}$. The filtering rate of a species was calculated as the mean value of F for the beads from size ranges of 0–5, 5–10 and 10–15 μm diameter since these particles were always found in the alimentary tracts of all the species and since particles of all these size ranges were present in the experimental environment in the greatest concentrations (Table I).

Lake water from the depth of 1.5–2 m was exposed in 5-litre capacity glass bottles. They were filled in such a way so that the water together with all the seston would be in the smallest possible contact with the air to avoid air bubbles collecting on animal carapaces and their exposure to an excess of light. With this in mind the bottle containing the suspension of beads in their initial concentration (250 ml suspension with a 20 times larger concentration than in Table I) was forced under the lake surface. When being submerged the bottles remained stopped with a rubber stopper perforated by two glass tubes of 1 cm diameter. The first tube, with one end entering just beyond the stopper, was tapered at the other end with a rubber hose sealed with a clip. The second tube reached the bottom of the bottle, thus being submerged in the initial suspension, while its upper end was connected to a weighed, funnelled rubber hose. When the weighed end was dropped down to the required depth, and the clip removed from the hose of the first pipe, the lake water, forcing its way into the bottle through the second pipe, would cause the air to escape through the first pipe. Once the lake water had filled the submerged bottle and was thoroughly mixed with the initial bead suspension, the perforated stopper was replaced with a glass one. The bottle was then left submerged for the exposure time being occasionally inverted by hand to prevent particle sedimentation.

This way of filling bottles can also be used for other experiments if the initial suspension of beads is replaced, e.g., by ^{32}P marked yeast cells or by a certain number of predatory Leptodora. Also, increased densities of experimental animals (or of phytoplankton) can easily be forced into the bottle if the end of the second pipe is connected to the end of the collecting receptacle of a plankton net of required mesh size, which had previously been vertically or horizontally towed for a given distance and had not been removed from the water. This method of exposing limnetic sections in such bottles seems to be easier and to have less technical obstacles than exposure in Gliwicz's (1968) or Haney's (1971) experimental chambers.

2.3. Body length and width of carapace crevice

Cladoceran body length was measured as the distance between the topmost point of the line of the head dome (without head spine in Daphnia species) and the most posterior point of the carapace (without the tail spine in Daphnia species and Bosmina coregoni), whereas calanoid body length as the distance between the foremost point of the head and the end of furca (without furcal bristles).

The gap between the carapace margins (crevice width) was measured in animals from

quantitative zooplankton samples fixed in 4% formaldehyde solution and transferred to a mixture of glycerine and water. This measurement was carried out as far as possible on animals of similar body length. In *Chydorus sphaericus* the crevice width was measured at its widest point, which corresponds to the middle of the animal carapace. In *Daphnia longispina*, *D. cucullata* and *Bosmina coregoni* the crevice width was measured at a distance of about 0.2 of the total crevice length from its foremost end under the rostrum. This more or less corresponds to the middle of that part of the crevice, through which water is sucked into the filtering chamber. The width measured at this point may be assumed as the average width of the crevice in its "inflow" part (in all three species, particularly in both *Daphnia* species, the crevice is narrower in its foremost and wider in its rear part).

2.4. Numbers, intensity of reproduction and individual production in crustacean populations

All these parameters were determined on material of quantitative net plankton samples (mesh size of $40-50\,\mu m$) taken from depth layers of $0-6$, $6-10$ m, and for some species also from the $10-24$ m depth layer. The samples were taken with a 5-litre capacity Bernatowicz water sampler 4 times in every 24 hours from every 1 m depth (2 samples for each), fixed immediately after straining on the net with 4% formaldehyde solution, and analysed individually or together after integrating for the above mentioned layers. A mercury thermometer, placed in the sampler, was used to measure the temperature of the water.

For each date, a sufficient subsample volume was used to count off at least 100 adult individuals from each species and an equivalent number of eggs and of juvenile individuals. When an insufficient abundance of a species was found in a sample this number was brought down to 20 adult individuals.

The intensity of the population reproduction was defined as mean daily egg production per adult female (P_e). Changes in the mean number of eggs per adult (which is often used as the fecundity indicator) in a given period of time do not necessarily indicate the real changes in the reproduction intensity, as in the same time the duration of egg development may change as a result of change in environmental temperature. The mean daily egg production per female was calculated as $P_e = N_e \cdot N_a^{-1} \cdot D_e^{-1}$ (eggs ind.$^{-1}$ day^{-1}), where N_e is the mean number of eggs per volume unit, N_a is the mean number of adult females in the same volume in the same time, D_e is the duration of egg development in a given temperature. This method of evaluating reproduction intensity for several rotifer species was first applied by Edmondson (1960). For the calculation of P_e values the regression line given by Bottrell (1975) was exploited, illustrating the relationship between temperature and duration of egg development (D_e) in cladocerans and copepods. In the temperature (T) range relevant to the present study ($9-22.5^{\circ}C$) this relationship is nearly identical for all 13 planktonic species, for which Bottrell (1975) had collected data from various sources. Although these 13 species do not include *Daphnia cucullata, Bosmina coregoni, Diaphanosoma brachyurum (Daphnia longispina, Chydorus sphaericus, Eudiaptomus gracilis* Sars are included), it was assumed that all the species analysed would show the same relationship between development time and temperature. Intensity of population reproduction was estimated in the same way for 1966.

The value of daily individual production ($P_{ind.}$) was also calculated for 1966 for every species population for each of 24 dates for which data were available. This value was defined as the sum of daily somatic and generative production of the average individual: $P_{ind.} = P_{pop.}$

$\cdot N_{j+a}^{-1}$ (μg f.w. $\cdot$ ind.$^{-1} \cdot$ day^{-1}), where: $P_{pop.}$ is the daily production of the species population (acc. to W ę g l e ń s k a – in preparation), N_{j+a} is the mean number in species populations (juvenile and adult individuals taken together) in the period for which the $P_{pop.}$ value was determined.

2.5. Numbers and biomass of phytoplankton

The same 1973 samples of net plankton were used to determine the numbers in net phytoplankton species. Neither numbers nor biomass of nannoplanktonic algae was thus determined. From each sedimentarily concentrated sample 10 subsamples were taken, in which every individual of less abundant species was counted, whereas more abundant species were only counted up to 100 cells or colonies per sample. For species biomass (fresh weight) calculation the several years' mean volume of cells or colonies (S p o d n i e w s k a 1974 and unpublished data) was used.

2.6. Non-algal food concentration

The concentration of non-algal food in 1966 was indirectly determined from the rate of increase in non-algal food concentration (live and dead organic material less live algal and animal biomass, i.e., bacteria, detritus and dissolved organic matter) defined as non-phytoplankton and non-zooplankton organic matter increase rate in the surface layer of the lake (0–6 m depth, which in the period of summer stratification corresponds to the epilimnion and which throughout the year encompasses the whole euphotic layer). It was calculated for the same offshore sampling station as cumulation rate of non-algal organic matter $- \Delta NOM = E -$ $- (S + R_H + P_z)$, where: E is the rate of live algal mass elimination in this layer, including organic matter extracellularly released by algae; S is the rate of sedimentation of particulate organic matter falling out from this layer; R_H is respiration rate of heterotrophic organisms in this layer; P_z is net production of non-predatory zooplankton in this layer (all values in the same units: kcal $\cdot$ m$^{-2} \cdot$ day^{-1}). This calculation was based on measured values of phytoplankton biomass and its changes in time, of gross plankton primary production, of respiration of the whole planktonic community, of sedimentation of organic matter, of net production of non-predatory zooplankton excluding protozoans, as well as on several values indirectly calculated from the measured values (details in G l i w i c z and H i l l b r i c h t - –I l k o w s k a 1975). This is why values of ΔNOM, besides bacteria and detritus, also include protozoan biomass and dissolved organic matter, but they do not include inflows (or outflows) of organic material from (into) the lake littoral and lake drainage basin.

3. RESULTS

3.1. Food size selection among cladocerans

For each of the five investigated cladoceran species, it was found that of the various size ranges of food particles, the highest filtering rate was for the smallest particles (0–5 or 5–10 μm diameter) and that it gradually decreased with their increase in diameter (Figs. 1–4, F). Curves of similar shape were obtained for each of the four measurements carried out at various times of the 24-hour period, differing only in the absolute values of F. However, this

does not necessarily mean that each of the individuals had a filtering rate different for particles of various size ranges[1]. It seems rather to be the effect of averaging out the results, as each curve is based on four measurements taken at different times, each measurement being an average of 3–5 samples containing 3–10 individuals which differed considerably in size (Table II). Therefore, there might have been such individuals, among the several tens making up the final average, which had taken only small (e.g., 0–5 or 0–10 μm) particles, as well as those taking in particles from a broader size range (e.g., 0–20 or 0–25 μm) with equal intensity. This could well be the result of the wide range of size of individuals analysed, particularly in the case of *Bosmina coregoni*, for which the most regular decrease of the F value with increase in particle size was observed (Fig. 3, F), and for which the final averages were obtained, from the widest scope of individuals' size (standard deviation of the sample up to 42% of its mean – Table II).

To be sure, the above should not be neglected, but there would appear to be a more important reason than that of individuals' size. It seems that the upper limit of size of food particles entering the filtering chamber is to some extent set by the distance between the carapace margins of a cladoceran in its front part, as this is where the water with food suspension is taken in. Confirmation of this can be found in the percentage distribution of individuals of a given species according to the crevice width (Figs. 1–4, CW). It must be stressed here that no positive correlation has been found between size of individual (body length) and crevice width (CW) for any of the species analysed. Rather a tendency towards negative correlation has been observed for some species, although it has been insignificant at $p = 0.1$. It must also be noted that the percentage distribution of individuals with various crevice width could have been different for live individuals in the lake, that is before they were fixed. However, it should not be assumed that fixing a sample with formaldehyde would affect individuals of the same species to a different degree, if any (*Daphnia pulex* Leydig was not affected at all), in various months. It is plausible to accept that over-time changes in CW value distribution do show the real pattern of changes in the degree of carapace crevice opening among various cladoceran species in the lake, although the CW values should rather be treated as relative data.

Congruency between the F value distribution for different food particle size ranges (left hand side) and the percentage distribution of individuals according to the crevice width (right

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[1] Although it may well be so. In another paper (G l i w i c z – in preparation), there are three probable mechanisms specified which could be crucial for a negative correlation between food particle size and their filtering rate in an individual.

The first is related to the morphological structure of the filtering chamber in typical filter feeding cladocerans. First of all, the gap between the carapace margins (crevice width) in its anterior part (through which water with food suspension is drawn inside the carapace) widens towards the rear. In addition, the fissure between the edges of the first pairs of thoracic limbs (through which water with food suspension enters the filtering chamber) has its wider and narrower places. Both of these increase the chances of smaller particles and decrease the chances of larger particles to enter the filtering chamber.

The second mechanism may be related to constant changes in the degree of opening of both the carapace crevice and the fissure between the limb edges during filtration. This again offers greater chances for smaller particles, as they have a larger space of time to enter the chamber, whereas larger particles can only enter when both the crevice and fissure are fully open.

The third one may in turn be connected with a more active postabdominal rejection of larger than of smaller particles from the filtering chamber, thus again increasing the odds against larger particles.

The same effect should be produced by the work of each of these mechanisms: a more intensive sweeping of smaller rather than of larger particles from the environment by an individual.
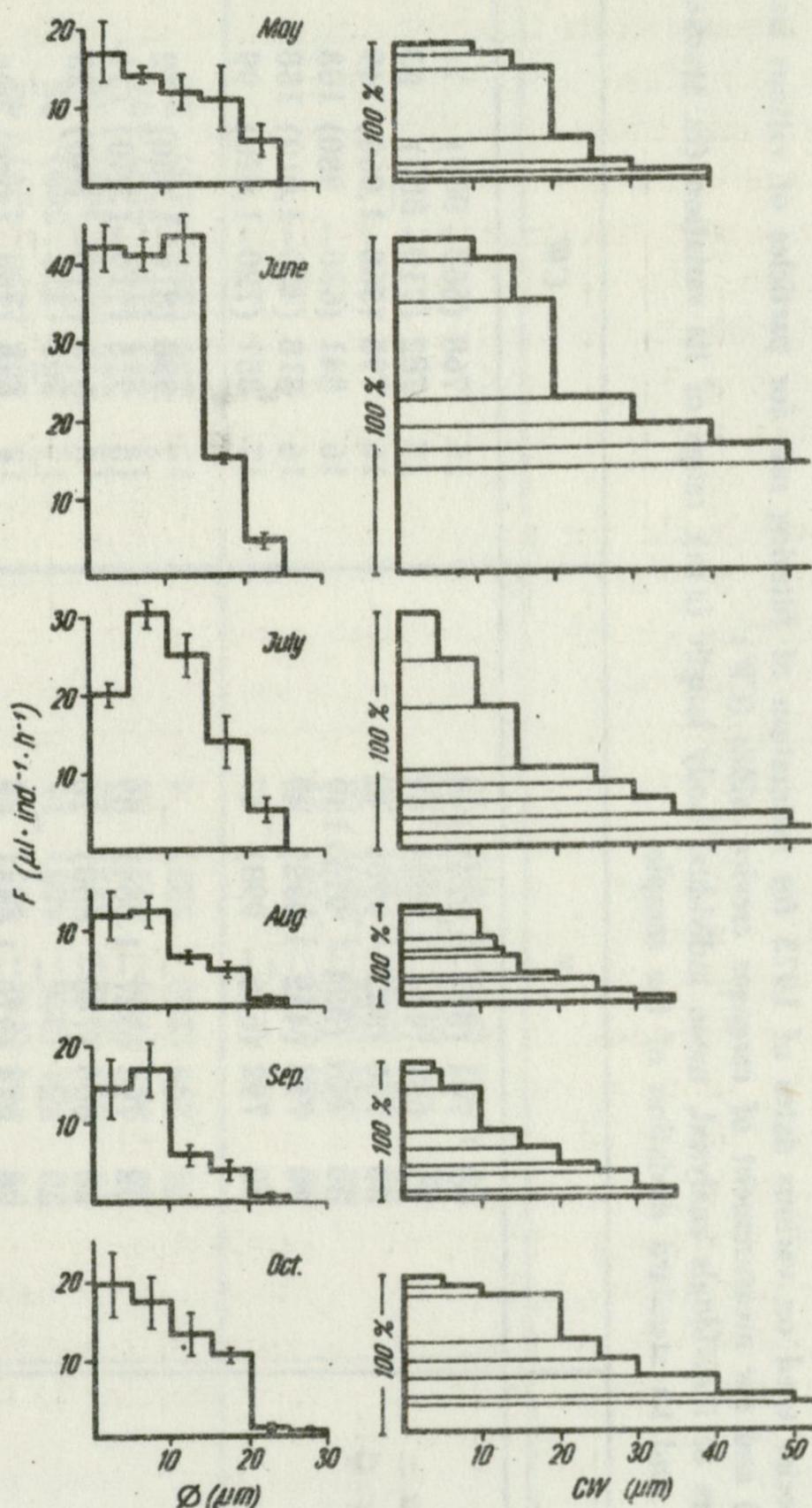
Fig. 1. Filtering rate (mean and standard deviation of the sample) of *Daphnia cucullata* (*F*) in respect of particles of various size ranges (ϕ) in different months of 1973 (left-hand side) and (on the right-hand side) percentage distribution of individuals according to carapace crevice width (CW) in the same months

hand side in Figs. 1—4) is the greatest in *Daphnia longispina* (Fig. 2) and in *Chydorus sphaericus* (Fig. 4). This suggests that in the case of these species the degree of carapace crevice opening is really responsible for the reduced filtering rate of larger particles as compared to smaller ones. Congruency, although less distinct, is also observed in *Daphnia cucullata* (Fig. 1). It is the least visible for *Bosmina coregoni* (Fig. 3) which, if this has not been a by-product of fixing animals, could be related to the fact that not all particles, which can theoretically pass through the carapace crevice, do in fact reach the filtering chamber. It may in turn be related to the narrower fissure between the edges of thoracic limbs in the abduction phase, not allowing the larger particles (e.g., 30 μm) to pass through (Fig. 3, *F*), which are small enough to pass through the wider carapace crevice (Fig. 3, *CW*).

Table II. Number and body length of various species used on various dates of 1973 for estimation of filtering rate for particles of various size ranges (F) and for measurement of carapace crevice width (CW)

Under both F and CW consecutively are: numbers of individuals analysed, mean individual body length (μm), range of its variation (in brackets) and its standard deviation of the sample

Species	Date	F				CW			
Daphnia cucullata	12 May	32	741	(544–1,024)	149	16	768	(660– 900)	74
	12 June	99	634	(416–1,082)	67	17	782	(710– 880)	63
	18 July	80	750	(582– 998)	42	16	795	(560–1,060)	149
	21 Aug.	80	651	(384– 915)	159	16	841	(630– 980)	103
	24 Sept.	80	715	(432–1,032)	49	16	818	(460–1,010)	150
	23 Oct.	80	792	(616– 998)	47	17	857	(720–1,020)	99
Daphnia longispina	12 May	—	—	—	—	7	928	(810–1,050)	72
	12 June	32	796	(527–1,054)	89	15	915	(710–1,040)	111
	18 July	20	800	(740– 850)	16	8	816	(770– 840)	23
	21 Aug.	—	—	—	—	—	—	—	—
	24 Sept.	20	974	(870–1,043)	68	7	949	(720–1,050)	105
	23 Oct.	20	1,013	(900–1,080)	50	16	1,003	(880–1,070)	72
Bosmina coregoni	12 May	100	527	(288– 704)	59	13	554	(460– 650)	65
	12 June	61	652	(240– 832)	146	13	630	(510– 800)	64
	18 July	42	531	(233– 865)	223	7	563	(480– 660)	57
	21 Aug.	39	565	(256– 882)	139	7	604	(490– 750)	71
	24 Sept.	105	562	(283– 965)	148	14	537	(420– 640)	65
	23 Oct.	162	603	(367– 945)	120	18	605	(490– 730)	65

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Diaphanosoma brachyurum	12 May	—	—	—	—					
	12 June	—	—	—	—					
	18 July	80	525	(322–	905)	91				
	21 Aug.	88	504	(310–	806)	52				
	24 Sept.	20	500	(403–	645)	50				
	23 Oct.	20	651	(484–	824)	139				
Chydorus sphaericus	12 May	—	—	—	—		13	310	(240–400)	40
	12 June	34	353	(248–	465)	44	13	368	(290–450)	43
	18 July	30	301	(226–	403)	15	14	303	(270–380)	35
	21 Aug.	30	318	(242–	372)	23	14	316	(250–390)	39
	24 Sept.	38	293	(186–	452)	33	13	291	(190–400)	101
	23 Oct.	20	299	(208–	322)	4	15	256	(240–310)	23
Eudiaptomus graciloides	12 May	—	—	—	—					
	12 June	80	986	(744–1,116)		99				
	18 July	80	964	(800–1,210)		85				
	21 Aug.	80	927	(768–1,120)		86				
	24 Sept.	80	766	(560–1,088)		154				
	23 Oct.	80	1,105	(944–1,280)		93				
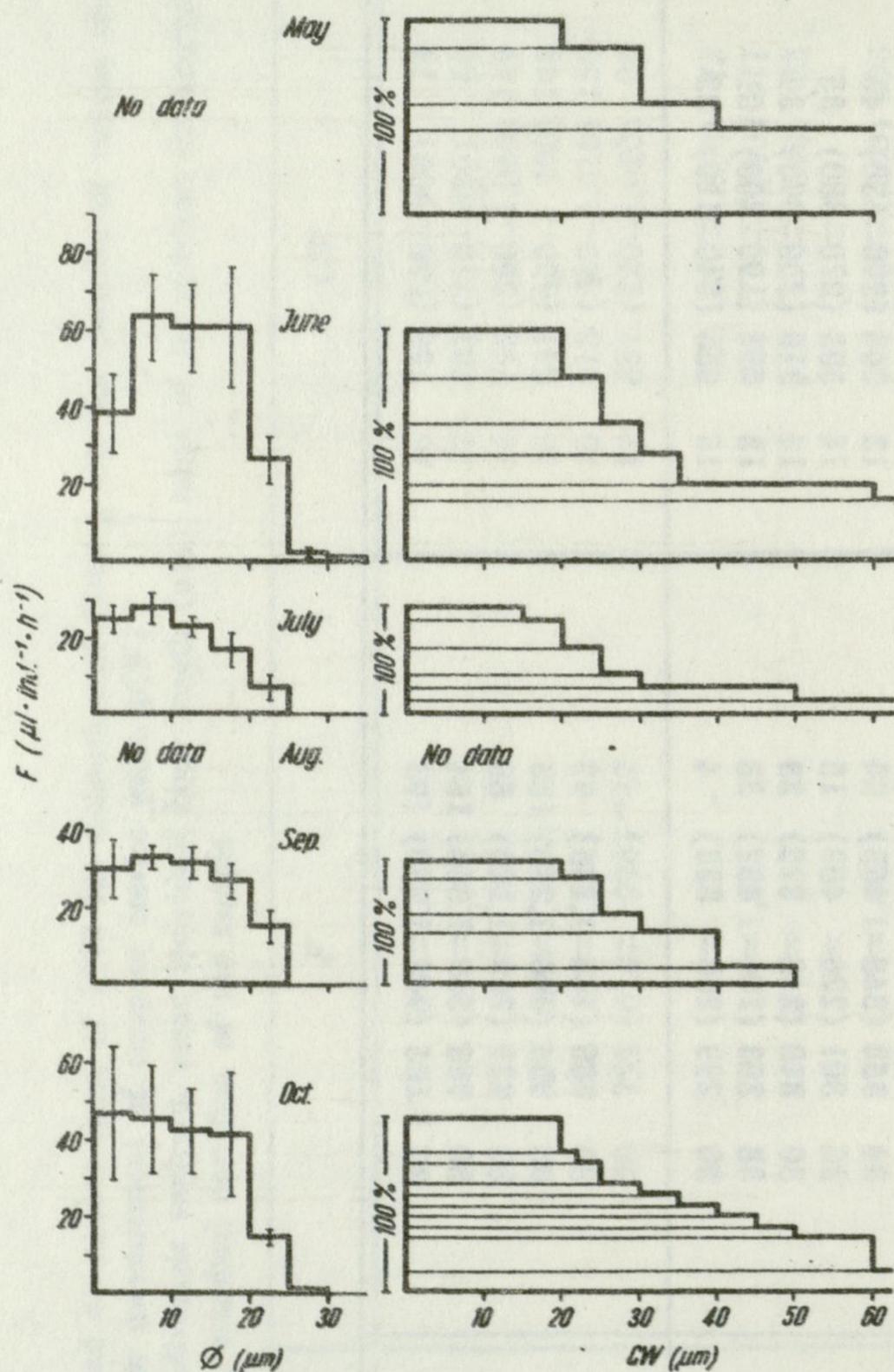
Fig. 2. Filtering rate (mean and standard deviation of the sample) of *Daphnia longispina* (*F*) in respect of particles of various size ranges (∅) in different months of 1973 (left-hand side) and (on the right-hand side) percentage distribution of individuals according to carapace crevice width (*CW*) in the same months

Due to the frailty of the carapace of *Diaphanosoma brachyurum*, rendering measurement of the crevice impossible, it is difficult to ascertain whether distance between the carapace margins or the distance between the edges of thoracic limbs is responsible for not allowing larger particles to enter the filtering chamber of animals of this species. In either case, particles larger than 10–15 µm have most certainly a very small chance of getting in (Fig. 4, *F*).

Noteworthy are also the lower *F* values for the smallest, 0–5 µm particles among both *Daphnia* species (Figs. 1, 2), which has been observed from June to September but significant only in July for *D. cucullata* (Fig. 1, *F*). This is rather unexpected as it is at this time that in a large proportion of individuals of this species the carapace crevice is set only ajar – up to 5 µm in width in 3 out of 15 measured individuals (Fig. 1, *CW*). So, the filtering rate of the smallest particles should be rather the highest. That it is not so (Fig. 1, *F*) may be related to the high numbers of several net phytoplankton species at this time (e g., highest abundance of *Peridinium* sp. of 40–50 µm diameter – see Section 3.5), the cells of which are sufficiently
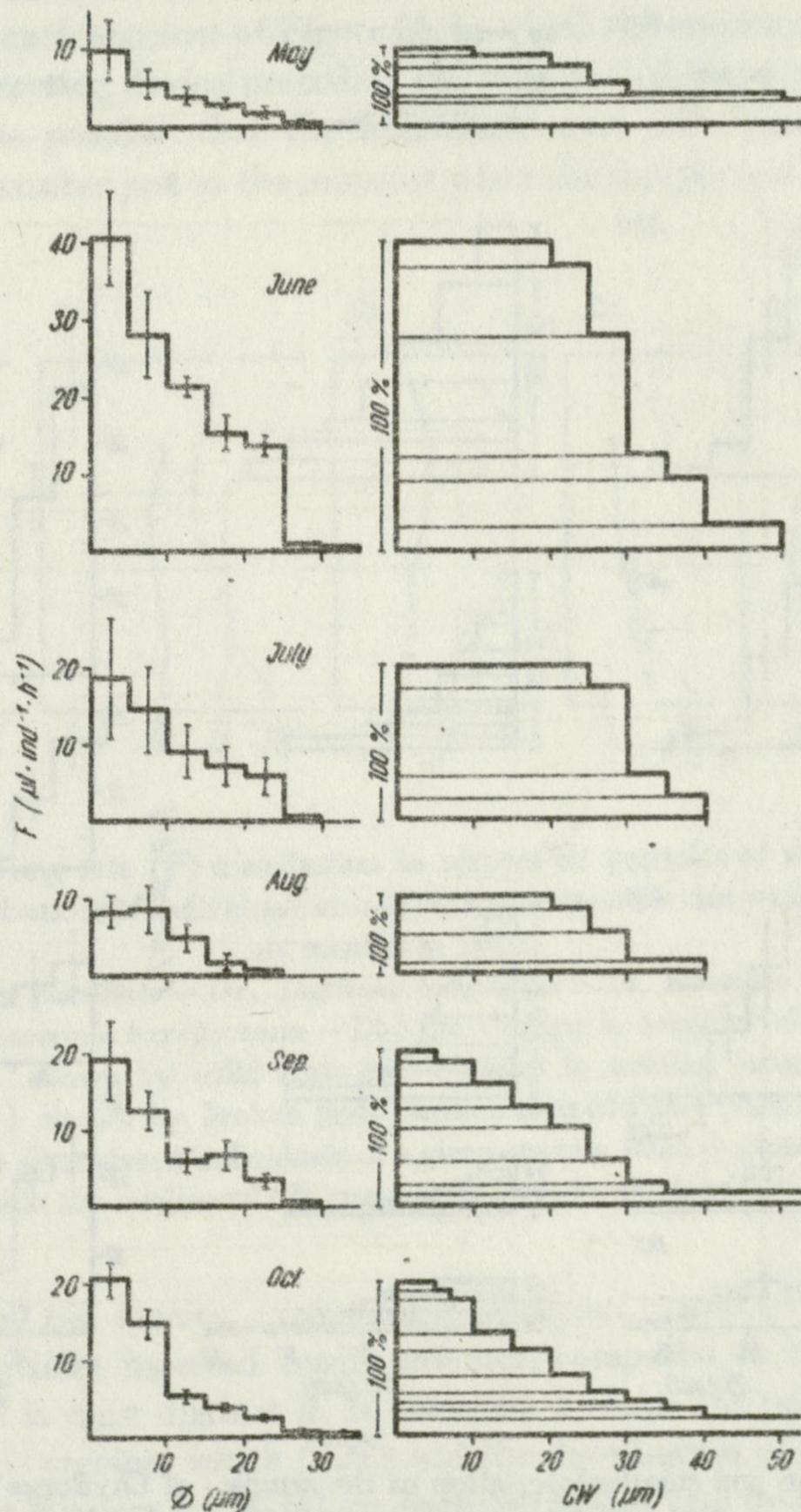
Fig. 3. Filtering rate (mean and standard deviation of the sample) of *Bosmina coregoni (F)* in respect of particles of various size ranges (ϕ) in different months of 1973 (left-hand side) and (on the right-hand side) percentage distribution of individuals according to carapace crevice width (*CW*) in the same months

small to get into the filtering chamber of some of the individuals (the crevice width in 13% of *D. cucullata* individuals is greater than $45 \, \mu m$ at this time – Fig. 1, *CW*), but large and solid enough to make tight closure of the filtering chamber difficult. As a result, particles smaller than $5 \, \mu m$ may escape from the chamber during the abduction-adduction phase, i.e., when the water is pressed out through the filters.

A comparison of the species analysed shows that the range of filtered particle sizes is the greatest (the upper particle size limit is the highest) for *Daphnia longispina* (Fig. 2), and the smallest for *Diaphanosoma brachyurum* and *Chydorus sphaericus* (Fig. 4). This is of course associated with the individual size of all five species (Table II) and ideally suits B u r n s ' (1968a) regression line, illustrating the relationship between the maximum size of particles
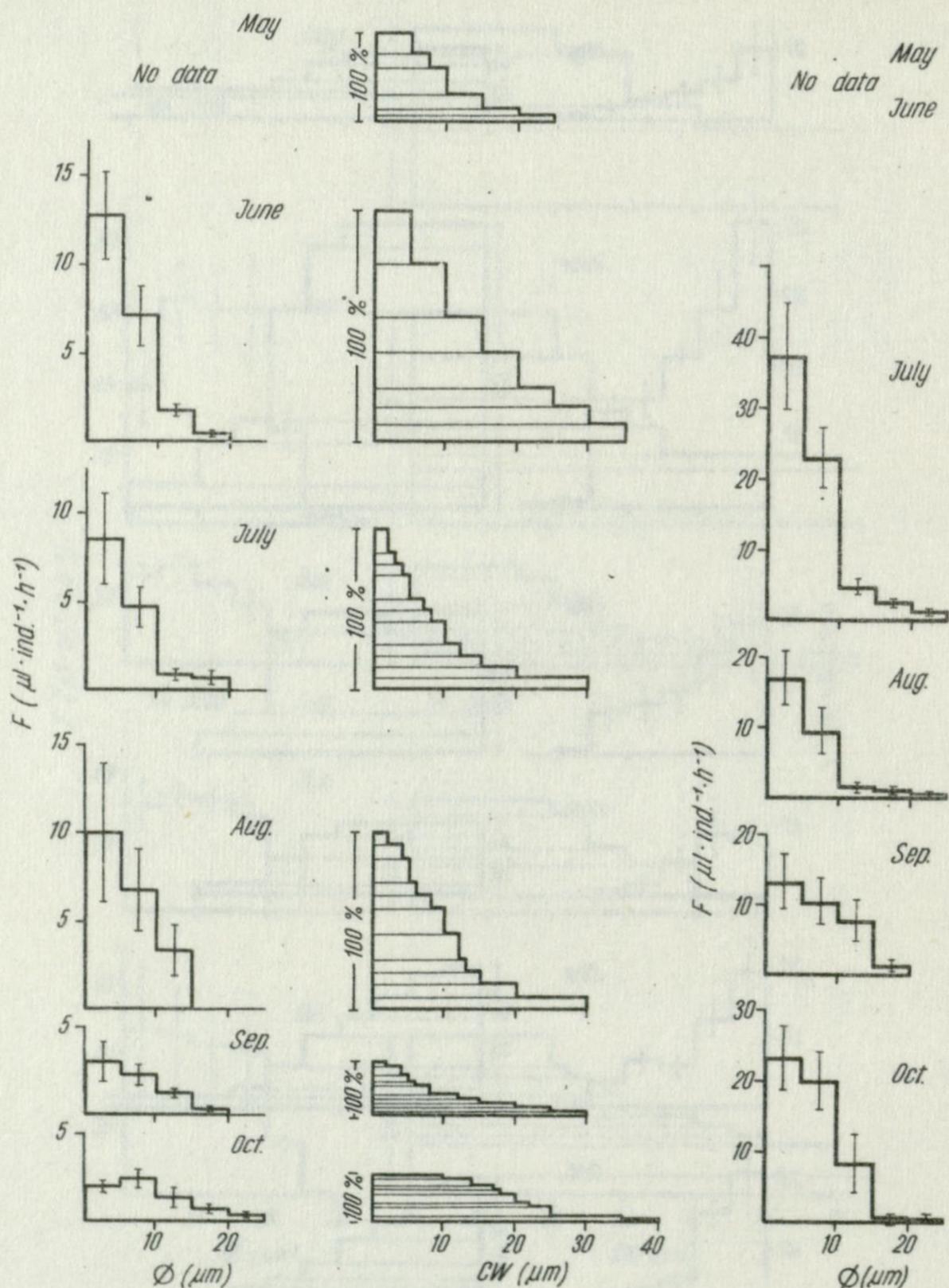
Fig. 4. Filtering rate (mean and standard deviation of the sample) of *Chydorus sphaericus* (*F*) in respect of particles of various size ranges (φ) in different months of 1973 (left-hand side), percentage distribution of individuals according to carapace crevice width (*CW*) in the same months (centre) and (on the right-hand side) filtering rate of *Diaphanosoma brachyurum* (*F*) in respect of particles of various size ranges (φ) in different months of 1973

ingested and carapace length in seven North American cladoceran species (all the points obtained from Mikołajskie Lake data would be in the 95% confidence limit of her line).

While the upper limit of filtered particle size seems to be in fact defined by individual size, so the shape of food size selection curves (Figs. 1–4, *F*) seems rather to be dependent on the degree of carapace crevice opening. This is confirmed by congruency of curve shapes on the left (*F*) and on the right (*CW*) hand sides of Figures 1–4, as well as by seasonal changes in the *F* values despite insignificant (Student's *t*-test) changes in average size of individuals (Table II).

The seasonal changes in the shape of food size selection curves (*F*) are similar to those in the shape of the curves of percentage distribution of individuals according to carapace crevice width (*CW*) as for all the species analysed. This is more easily noticed when comparing the seasonal

changes in median values of both F and CW curves (Fig. 5). This similarity becomes greater when from analysis excluded are individuals with crevice width of above 50 μm (broken lines on the left hand side of each segment of Figure 5), in which the crevice does not most probably act as an efficient preselecting device preceding the rejection of larger particles by the edges of thoracic limbs. It seems possible that the individuals with wide carapace crevice had been clearing their filtering chamber just at the moment when the sample was fixed.
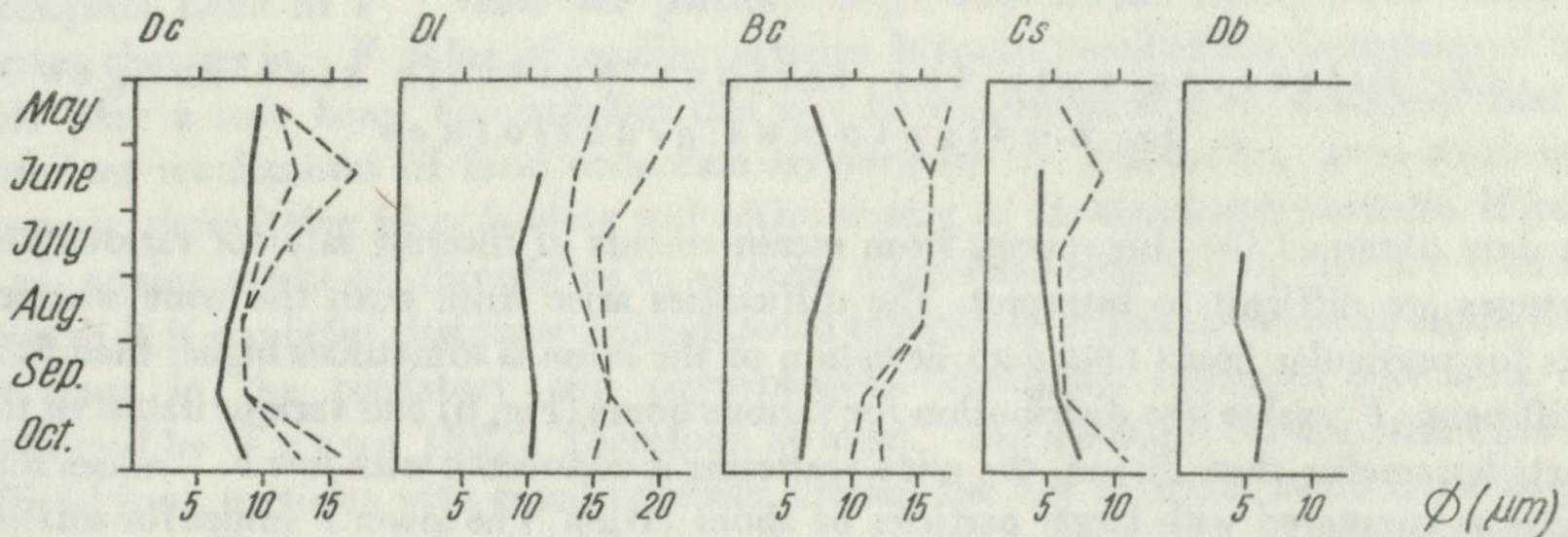

Fig. 5. Changes in the filtering rate (F) distribution in respect of particles of various size ranges (ϕ) and changes in percentage distribution of individuals according to carapace crevice width (CW) over the period of six months in 1973
For each species (*Daphnia cucullata* — Dc, *Daphnia longispina* — Dl, *Bosmina coregoni* — Bc, *Chydorus sphaericus* — Cs and *Diaphanosoma brychyurum* — Db) the changes in median value (in μm) of the F curves (Figs. 1—4, left-hand side) shown by solid lines and changes in median value (in um) of CW curves (Figs. 1—4, right-hand side) shown by broken lines. Broken lines of higher values (μm) show changes in the median of CW curve for all analysed individuals of a given species, while broken lines of lower values (μm) snow changes in the median of CW curve only for individuals of CW below 50 μm

A tendency among all the species, except for *B. coregoni*, could be observed to reduce the upper size limit of particles ingested during summer, compared to the spring and autumn situations (Fig. 5). This is most distinct in *D. cucullata* in both the percentage distribution of individuals according to crevice width (CW) and the distribution of filtering rate of various size particles (F): similar F values for 0—20 μm particles in May and 0—15 μm in June, followed by lower F values in July becoming significantly lower in August and September in respect of those particles above 10 μm, and again similar F values for all the 0—20 μm particles in October (Fig. 1, F). A similar but much less distinct tendency is seen in *D. longispina* (decrease in F values for particles above 10 μm in July — Fig. 2), although the August disappearance of this species population makes it impossible to ascertain whether this tendency becomes stronger in mid-summer. Also two other species follow a similar pattern. In *Diaphansoma brachyurum* lower F values are observed for particles above 5—10 μm in July and August when compared to September and October (Fig. 4, right hand side). In *Chydorus sphaericus*, a more gradual decrease in filtering rate (F) with particle size increase is in October accompanied by a raising in the upper size limit of particles ingested (Fig. 4, left hand side). This limit is 5—10 μm higher than in earlier months. In both species these changes are less distinct due to a much narrower size range of ingested particles. The tendency looks different in *B. coregoni*, in which decrease of F value for particles above 10 μm cannot be observed until autumn (Fig. 3, F).

In all species reduction of the filtering rate (F) for larger food particles is accompanied by a narrowing of the carapace crevice (CW). *D. cucullata* and *C. sphaericus* exhibit this most clearly (Figs. 1, 4). The share of individuals with their crevice just ajar in the total number of animals analysed is significantly higher in these species in July, August and September than in the spring months and October. The same, but of a smaller order, may be seen in *D. longispina* in July (Fig. 2) and in *B. coregoni* from August (Fig. 3).

3.2. Filtering rate for various particle size ranges in *Eudiaptomus graciloides*

The data obtained for this species from measurements of filtering rate for various particle size ranges are difficult to interpret. The difficulties arise from both the wide scattering of results for particular hours (standard deviation of the mean is sometimes higher than 50%) and the different F value size distribution for various hours (Fig. 6) and various dates. In the case of particles smaller than 20 μm, the wide scattering is connected with low F values for these particles as compared with larger particles of about 30 μm. The lower F values for smaller than for larger particles have already been observed in other calanoid copepod species as opposed to cladocerans (Haney 1973, Infante 1973, Bogdan and McNaught 1975). The high E values for larger, 30–40 μm particles, were only obtained for *E. graciloides* in June, September and October. In July and August, although individuals analysed were of similar size (Table II), no particle over 25 μm diameter was found, whereas the mean F value for all size ranges of particles between 0 and 25 μm was about 50% lower than in June and September and similar to F values observed in October.
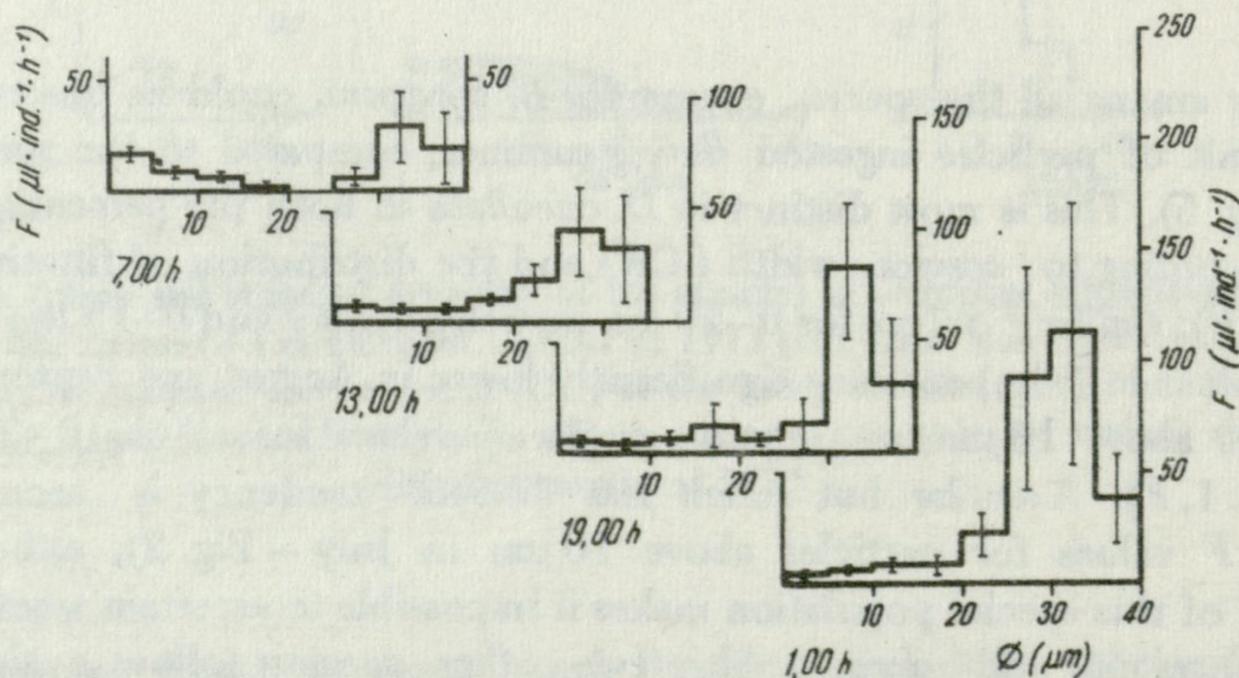

Fig. 6. Filtering rate (mean and standard deviation of the sample) of *Eudiaptomus graciloides* (F) in respect of particles of various size ranges (ϕ) in June, 1973, at various times of the day

Noteworthy are diurnal changes in F value distribution for various particle size ranges, which has not been observed in cladoceran species. They were similar in June (Fig. 6), September and October. While the F values for particles below 20 μm hardly changed diurnally,

so the F values of larger particles were significantly higher at night than during the day (lowest in the morning and at noon).

The phenomenon of higher F values for larger than for smaller food particles was noted for related calanoid species, both marine (H a r g r a v e and G e e n 1970, F r o s t 1972) and freshwater (Haney after R i g l e r 1972 and older papers listed in G l i w i c z 1974). The possible mechanism of changes in size of the most efficiently grazed particles was also being explained (W i l s o n 1973). Yet it seems difficult to find an explanation for the changes in Mikołajskie Lake of F value for particles larger than 20 μm taking place without simultaneous changes in F value of smaller particles. It seems possible that behaviour of copepods could play a role here. For instance, this can be explained if it is assumed that two independent mechanisms of food collection are used by $E.$ $graciloides$, as in some cyclopoid copepods, these being filter feeding and active seizing of chosen, larger particles. If indeed this is so, seizing might be thought of as working more selectively during the day than at night, although it is doubtful that these animals could effectively utilize the sense of sight (the role of this sense in the predatory and phytophagous cyclopoid copepods has been seriously questioned by F r y e r 1957). Therefore, at night $Eudiaptomus$ would seize algal cells and artificial food particles with equal intensity. During the day it would avoid artificial particles, although possibly the grazing intensity of natural larger food particles would remain unchanged, just as the filtering rate of smaller particles. This reasoning would be in accordance with the changes in F values for various particle sizes observed in June, September and October. It does not, however, explain the lack of larger particles in the alimentary tracts of animals in July and August.

If this is a correct explanation, it is difficult to accept as real the F values for $E.$ $graciloides$ obtained by the artificial food particle method. This is why the analysis of seasonal changes in the filtering rate of this species becomes impossible.

3.3. Filtering rate and its changes through the seasons

The highest filtering rate (F) for particles taken together from the 0—15 μm size ranges was observed in all (with the exception of $Diaphanosoma$ $brychyurum$ — no data) cladoceran species in June (Fig. 7). This could be stated despite a large standard deviation of the mean caused by both variation in size of individuals (body length) and diurnal changes of F values for average individual. June values of F resemble values of the filtering rate obtained by different methods in those experiments carried out in near natural conditions by other authors for the same ($Daphnia$ $longispina$ — N a u w e r c k 1959, 1963, $Diaphanosoma$ $bra-$ $chyurum$ and $Chydorus$ $sphaericus$ — H a n e y 1973) or closely related species (other species of $Daphnia,$ $Diaptomus$ and $Bosmina$ $longirostris$ (O. F. Müller) — B u r n s and R i g l e r 1967, H a n e y 1973, B o g d a n and M c N a u g h t 1975, H a n e y and H a l l 1975). But in general, they are much lower than results from the laboratory experiments, in which as a rule the same size, large individuals were used. Exceptions to this are the laboratory results of B u r n s and R i g l e r (1967), B u r n s (1969b) and E g l o f f and P a l m e r (1971), among which an exponential dependence can be found of filtering rate on body length for several American $Daphnia$ species. Corresponding to these are the June F values obtained for both $Daphnia$ species in Mikołajskie Lake at a temperature of 17°C. They are closest to the results of B u r n s (1969b) for a temperature of 15°C.

It can already be easily seen from the F curves for various particle size ranges (Figs. 1–4, F) that the filtering rate changes through the seasons significantly in all cladoceran species, even the filtering rate of smaller size particles which "are always ready to be grazed". Seasonal changes of F values for particles from the integrated 0–15 μm size range are shown on Figure 7 (solid lines) on the background of the theoretical changes in filtering rate F_c (broken lines) calculated on the basis of June F values for all species except of *Diaphanosoma brachyurum*. For the latter October F values were taken as the basis for F_c calculation in view of the lack of June data.
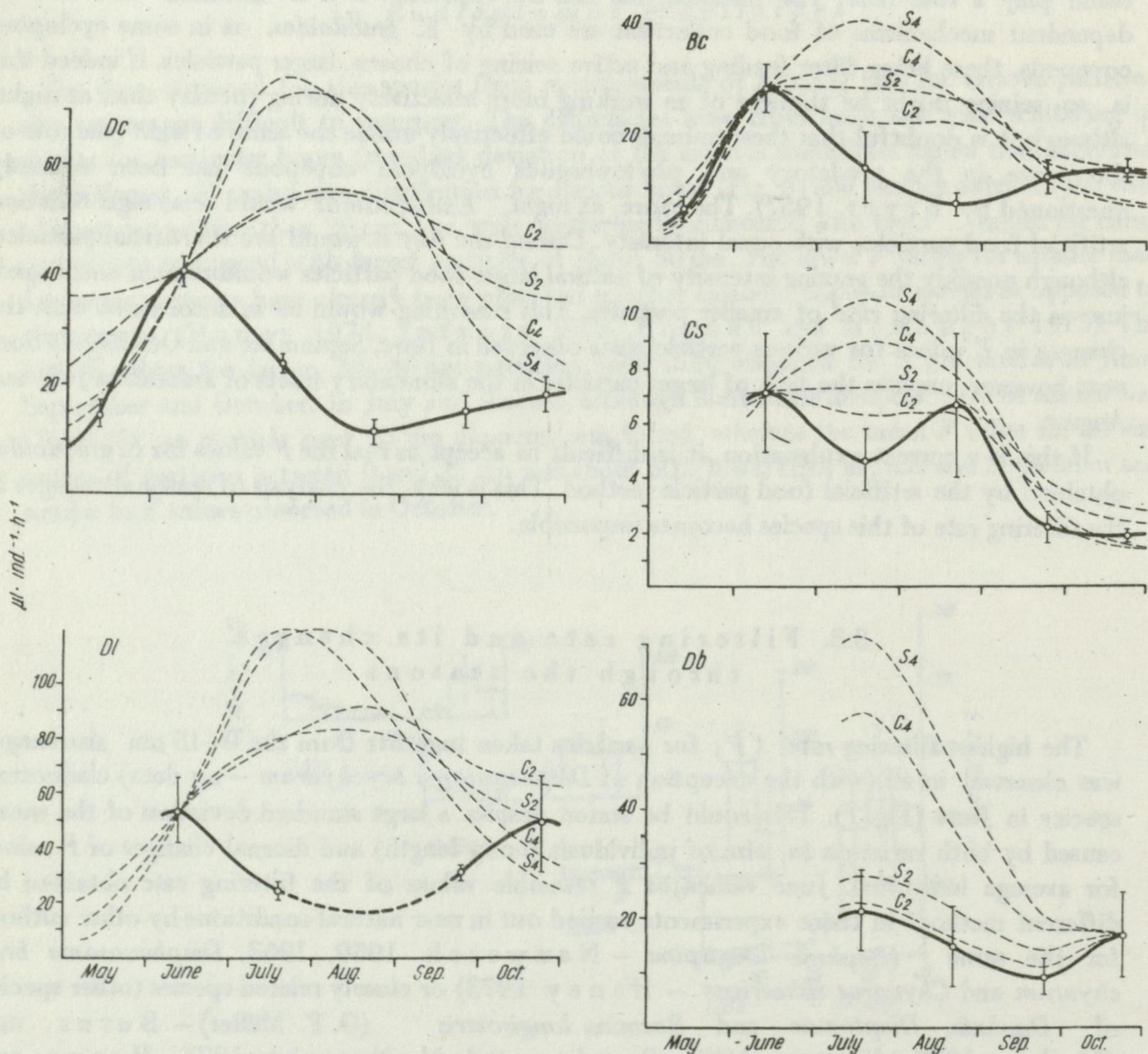

Fig. 7. Experimentally observed (F — solid line) and theoretical (F_c — broken lines) changes in filtering rate of five cladoceran species in 1973: *Daphnia cucullata (Dc)*, *Daphnia longispina (Dl)*, *Bosmina coregoni (Bc)*, *Chydorus sphaericus (Cs)* and *Diaphanosoma brachyurum (Db)*
The F_c values calculated assuming that filtering rate increases to the square of body length and $Q_{10} = 2 (S_2)$ or $Q_{10} = 4$ (S_4), or assuming that filtering increases to the cube of body length and $Q_{10} = 2 (C_2)$ or $Q_{10} = 4 (C_4)$. Explanation in the text. F values based on measurements carried out at 4 different times on every given date

When constructing the theoretical curves of F_c changes, it was assumed that June (October as for $Diaphanosoma$) F values are at their optima[2] for all the species in the actual temperature of $17^\circ C$ and that they are not limited by any other environmental factors (i.e., $F = F_c$). It was next assumed that in the range of observed temperatures the filtering rate doubles with a temperature (T) increase of $10^\circ C$ (in accordance with Krogh's curve) or it increases four-fold with T increase of $10^\circ C$ (according to M c M a h o n 's (1965) and B u r n s ' (1969b) Q_{10} exceeded 2.3 for $Daphnia$ $magna$ Straus and 2.8 for $D.$ $galeata$ Sars in a temperature range of $15-25^\circ C$, whereas according to a comparison of May and June F values for Mikołajskie Lake, having taken into account a correction for body length – see below, Q_{10} exceeded 3 for $D.$ $cucullata$ and approached 4 for $Bosmina$ $coregoni$). So both these assumptions take the values of Q_{10} to be at their extremes. Finally, it was assumed that filtering rate is a function of body length to the power of 2 or to the power of 3. This is in accordance with the results of M c M a h o n (1965), B u r n s and R i g l e r (1967) and B u r n s (1969b), who obtained this function for various $Daphnia$ species with powers ranging from 2.16 to 3.02 (e g., for $D.$ $magna$ $F = 0.153 \cdot L^{2.16}$, for $D.$ $rosea$ Sars $F = 0.31 \cdot L^{3.02}$, where: L is the body length).

When the all the above assumptions were taken into account, their various combinations produced four variants of theoretical changes in the filtering rate F_c for all the cladoceran species (Fig. 7), according to which the filtering rate would be expected to change, if no other factors, except for temperature and body length, would have a limiting effect:

variant I – $F_c = k_1 \cdot L^2,$ $\quad Q_{10} = 4$

variant II – $F_c = k_2 \cdot L^3,$ $\quad Q_{10} = 4$

variant III – $F_c = k_1 \cdot L^2,$ $\quad Q_{10} = 2$

variant IV – $F_c = k_2 \cdot L^3,$ $\quad Q_{10} = 2$

where L is the mean body length of individuals analysed for F on a given date (Table II), k_1 and k_2 are the coefficients calculated on the basis of June data (October for $Diaphanosoma$), by substituting the measured F and L values in the above formulae. The k_1 and k_2 values were, respectively, 0.10 and 0.16 for $D.$ $cucullata$, 0.085 and 0.107 for $D.$ $longispina$, 0.066 and 0.101 for $B.$ $coregoni$, 0.040 and 0.062 for $D.$ $brachyurum$, 0.056 and 0.160 for $C.$ $sphaericus$.

As can be seen (Fig. 7), $Chydorus$ $sphaericus$ and $Diaphanosoma$ $brachyurum$ are the only species in which the experimentally observed filtering rate (F) changes with reasonable accordance to the theoretical filtering rate (F_c) changes, although in July a certain reduction of F in respect of F_c is apparent in $Chydorus$. It is, however, negligible when compared to the summer reduction of F in other species, particularly in both $Daphnia$ species, in which even the values of the standard deviation of the sample do not approach the nearest values of F_c between July and September.

It is thus evident that while in spring (May to June) and autumn (October, September to October in $Bosmina$) the filtering rate of $Bosmina$ and both $Daphnia$ species remains as expected (at optimum in the actual temperature), so in summer it undergoes significant reduc-

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[2] Optimum, i.e., maximum within a given food concentration and in a given temperature. As the food concentration in Mikołajskie Lake is most probably lower than the incipient limiting concentration (see Section 3.6), at which filtering rate begins to drop while the food concentration increases (the feeding rate remaining at the same level), it should be accepted that the optimum filtering rate at a given temperature equals the maximum possible filtering rate at this temperature.

tion despite an increase in the temperature of the environment, this reduction being most dras-
tic in August, at least as far as *D. cucullata* and *B. coregoni* are concerned.

It is difficult to ascertain whether the filtering rate of *Eudiaptomus graciloides* also under-
goes such a drastic reduction, in view of the lack of representative data for the summer and
autumn months. Nevertheless, it may be supposed that in as far as larger food particles
(25—40 μm diamater) go, it is significantly lower in July and August than in June and
September, as it would not be reasonable to expect that only changes in animal behaviour were
responsible for a near total lack of these particles in the filter chambers and alimentary tracts of
these animals in these months.

The phenomenon of summer reduction in filtering rate of cladocerans and calanoid
copepods has already been observed in other eutrophic lakes and artificial reservoirs. It was
observed in the Queen Mary Reservoir near London among various *Daphnia* species by
N a d i n - H u r l e y and D u n c a n (1976) who noted a decrease in the degree of
alimentary tracts' filling during the summer bloom of filamentous blue-greens, *Anabaena* spp.
and *Tribonema* spp. It was also observed in Suzdalskie Lake near Leningrad by
G u t e l m a c h e r (1975) who had directly measured the filtering rate of *Daphnia longispina*,
Bosmina crassicornis (P. E. Müller) and *Eudiaptomus gracilis*, and in Heart Lake near Toronto,
for two different years, by B u r n s and R i g l e r (1967) and H a n e y (1973) who also
directly estimated the filtering rates of *Daphnia rosea* and *D. galeata*.   The spring filtering
rates of the Heart Lake species were ideally suited to the theoretical rates calculated on the
basis of data from laboratory experiments carried out on monospecific food. But from July to
October the filtering rate was observed as three times lower than the theoretically expected rate
determined by body length and temperature. However, it was not found out whether this
reduction had been caused by too great a food concentration in the lake, exceeding the
incipient limiting concentration (in accordance with S u š č e n i j a ' s (1958) and
R i g l e r ' s (1961) repeatedly confirmed regularity), or by a large presence of algae capable
of interfering with the filtering mechanism either chemically (as suggested by R y t h e r 1954)
or mechanically (as was shown in respect of filamentous blue-greens for *Daphnia rosea* by
B u r n s 1968b).

In order to check which of these factors was decisive for the summer reduction in filtering
rate of cladocerans in Mikołajskie Lake, fecundity for all the dominant species was ascertained
for each date of F estimation.

It was assumed that if the reduction in filtering rate was caused by increase in concentration
of food available above incipient limiting concentration, then fecundity would not drop as in
this case a decrease in the filtering rate would not bring about any decrease in the feeding rate
(a drop in the filtering rate would in such a case be caused by an excess of food, since animals
"purposely" reduce their filtering rate so as to avoid superfluous amounts of food ingested). If,
however, the reduction in the filtering rate was the result of chemical or mechanical inter-
ference by larger algae (e.g., filamentous blue-greens), then the fecundity would drop, as the
decrease in the filtering rate would in this case be equivalent to a drop in the feeding rate
(animals "want to but cannot" filter at a higher rate in order to gather more food).

3.4. Filtering rate and population fecundity and numbers

It is generally thought that the fecundity of planktonic crustaceans is most probably
co-determined by temperature and food concentration. This emerges from the results of
E d m o n d s o n (1962) and other authors (for review see W ę g l e ń s k a 1970). Therefore,

if the summer decrease in the filtering rate was caused by an excessive food concentration in the lake, then it should be expected not to adversely influence the feeding rate, thus, in its turn, the mean daily egg production per adult female (P_e) should increase along with the temperature from May to July-August, and then drop from August to October, in accordance with the T curve (Fig. 8, T).

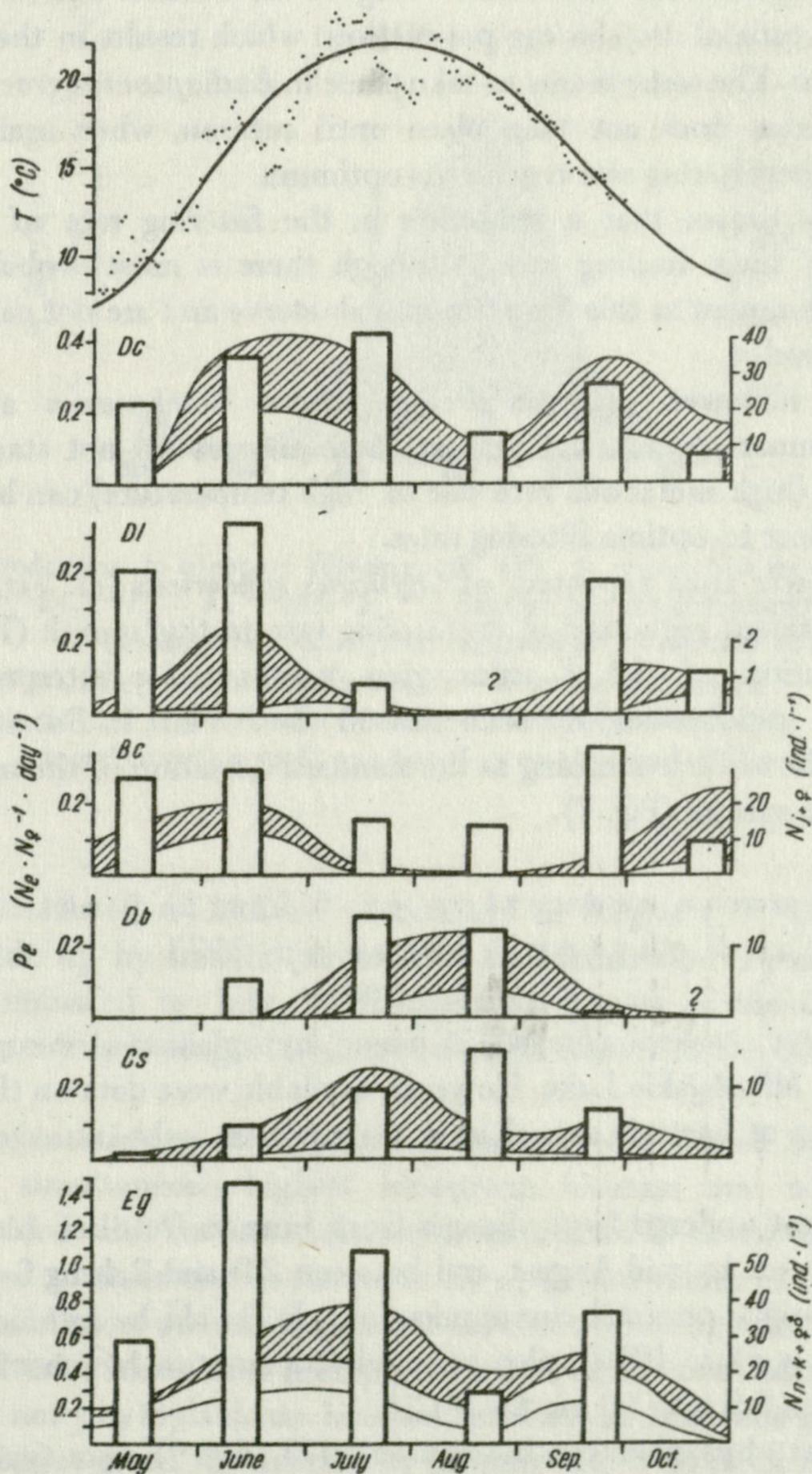However, this is true only of *Diaphanosoma brachyurum* (Fig. 8, Db) and *Chydorus*

Fig. 8. Temperature (T) on the surface of Mikołajskie Lake (dots) and mean for 0—6 m depth layer (solid line); daily egg production $(P_e$ — bars) and numbers $(N$ — lines) of six dominant in this lake filter feeding crustacean species in 1973
Daphnia cucullata (Dc), Daphnia longispina (Dl), Bosmina coregoni (Bc), Chydorus sphaericus (Cs), Diaphanosoma brychyurum (Db) and *Eudiaptomus graciloides (Eg)*. e — eggs, j — juvenile cladocerans, n — naupli, k — copepodites. Shaded areas — joint numbers of ♀♀ and ♂♂, unshaded areas — numbers of juveniles

sphaericus (Fig. 8, *Cs*), whereas in the remaining species the real egg production is several times lower in summer than expected. The most drastic reduction in egg production takes place in *Daphnia longispina* (Fig. 8, *Dl*). It seems to be no coincidence that it is this species which is most radically reduced in numbers, so as to render it impossible to determine its egg production in August (no egg-carrying female was found). Of similar magnitude is the decline in *Bosmina coregoni* numbers (Fig. 8, *Bc*), in which the reduction in egg production is by July already more drastic than in *Daphnia cucullata*. This may be why the population of the latter persists in large numbers during the summer (Fig. 8, *Dc*).

Thus, in both *Daphnia* species and in *Bosmina coregoni* the summer decrease in the filtering rate is accompanied by a radical drop in egg production, which results in the decrease in the populations of these species. The same seems to take place in *Eudiaptomus graciloides*. Renewal of these species' populations does not take place until autumn, when again the fecundity increases and when again the filtering rate reaches its optimum.

The conclusion can be drawn that a reduction in the filtering rate of these species is accompanied by a fall in their feeding rate. Although there is most probably a high food concentration in the environment at this time the animals starve and are not capable of keeping up reproduction at high level.

Fecundity does not, however, drop in *Diaphanosoma brachyurum* and *Chydorus sphaericus* during the summer, demonstrating that these animals do not starve at this time. Their high food demands (high metabolic rate due to high temperature) can be most probably satisfied because of their near to optima filtering rates.

The July fecundity, lower than expected, of *Chydorus sphaericus* (cf. Fig. 8, *T* and *Cs*) corresponds to the insignificant reduction in its filtering rate in this month (Fig. 7). However, the large standard deviation of the *F* value gives no basis for interpretation for this correspondence. Also the less drastic July reduction in the *F* value in *Bosmina* than in both *Daphnia* species seems to be of little meaning as the standard deviation of the mean of *F* is large compared to both *Daphnia* species (Fig. 7).

3.5. Summer reduction in filtering rate and phytoplankton in 1973

In 1973 no research on seasonal changes in nannophytoplankton or organic particulate matter was carried out in Mikołajskie Lake. However, available were data on the changes in the total numbers and biomass of bacteria as well as in the numbers and biomass of dominant taxa of net phytoplankton.

Bacterial biomass did not undergo large changes from June to October, oscillating between 1.4 and 2.0 mg f.w. $\cdot 1^{-1}$ up to mid-August and between 2.0 and 2.4 mg f.w. $\cdot 1^{-1}$ later on (Dr,W. A. Godlewska-Lipowa — personal communication). It should be assumed that just as in other years (S p o d n i e w s k a 1974), also nannophytoplankton biomass underwent small changes, oscillating between 0.5 and 3.0 mg f.w. $\cdot 1^{-1}$.

Seasonal changes in net phytoplankton biomass in 1973 (Fig. 9) were typical for this lake (compare with 1963, 1964 and 1966, in S p o d n i e w s k a 1967, 1974): a spring peak of diatoms, "remains" of which were still visible on May 12, the June minimum, and finally the summer peak dominated by peridinians in respect of biomass and by blue-greens in respect of numbers. Just as in other years, this peak must have reached its maximum soon before August 21, i.e., the date of August *F* estimation. The peridinian biomass was dominated by
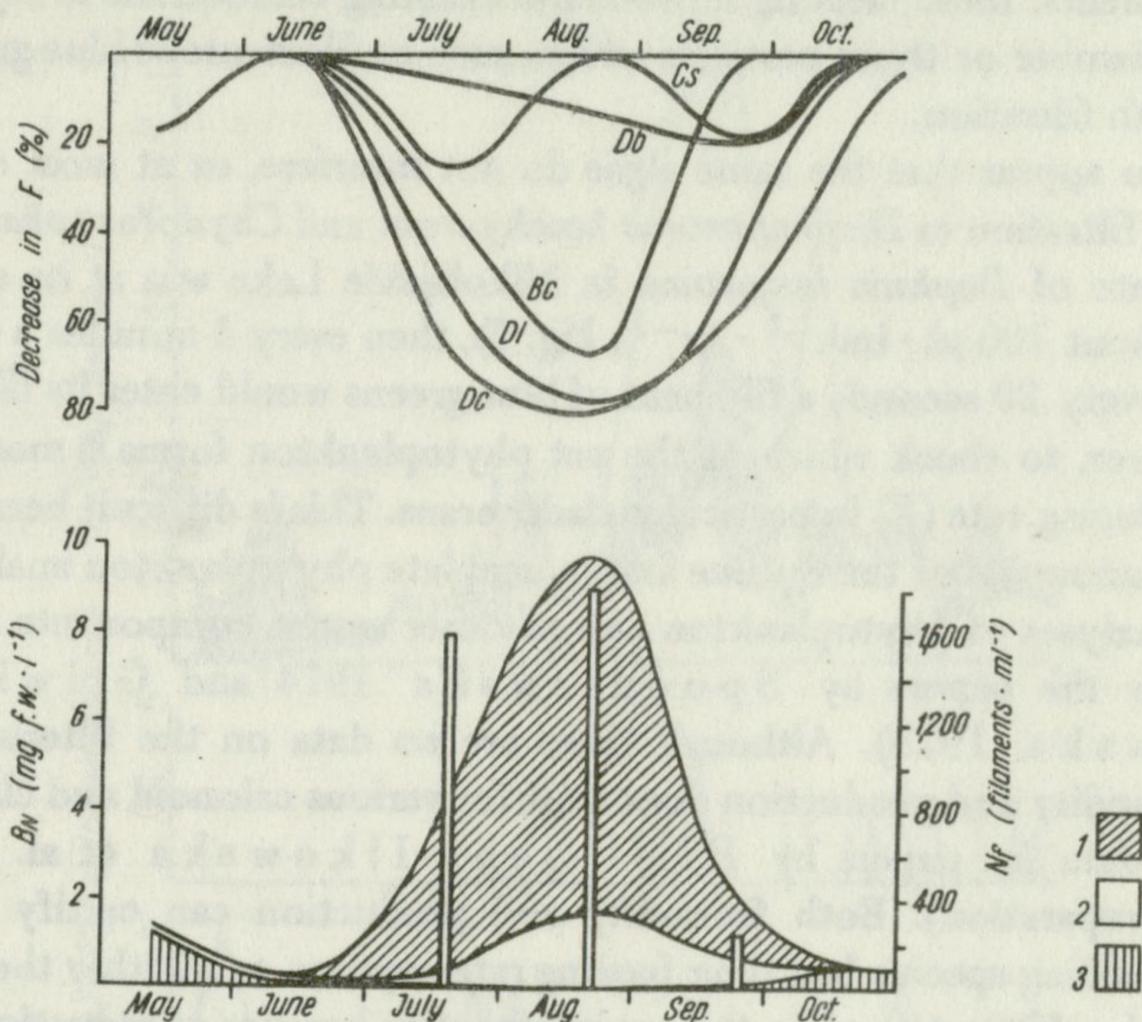
Fig. 9. Degree of reduction in observed filtering rate (F) in relation to its optimum values, taken as the lowest values of F_c, i.e., $(F_c - F) \cdot 100\% \cdot F_c^{-1}$; changes in net phytoplankton biomass $(B_N -$ curve) and in numbers of blue green filaments $(N_f -$ bars) in 1973

$Dc -$ *Daphnia cucullata*, $Dl -$ *Daphnia longispina*, $Bc -$ *Bosmina coregoni*, $Db -$ *Diaphanosoma brachyurum*, $Cs -$ *Chydorus sphaericus*, $1 -$ peridinians (mainly *Ceratium hirundinella*), $2 -$ blue-greens, $3 -$ diatoms together with a small number of green algae and of *Dinobryon* sp.

Ceratium hirundinella (O. F. Müller), particularly in August (95%), while in July 20% of this biomass was made up by smaller (about 50 μm diameter) *Peridinium* sp. The blue-green biomass was dominated in July by filamentous species of the *Oscillatoria*, *Lyngbya* and *Anabaena* genera, while in August by large colonies, mainly of the *Gloeotrichia* and *Microcystis* genera.

The period of maximum phytoplankton biomass, dominated by the peridinian *C. hirundinella*, of the simultaneous highest blue-green biomass and of filamentous blue-green abundance coincided with the most distinct reduction of *B. coregoni* and *D. cucullata* filtering rates, as compared to their closest theoretically optimum values at the temperature of 22.5°C (Fig. 9). This would most probably appear to be true of *D. longispina* as well, were August data available. The filtering rates of these species are reduced to a lesser degree in July, i.e., the period of lower net phytoplankton biomass, peridinians and blue-greens included, but not a lower number of blue-green filaments. The filtering rate is reduced to an even lesser degree in September, when the biomass and numbers of net algae are significantly lower. In *D. cucullata* a certain reduction in its filtering rate is also observed in May while there is still a fairly high biomass of diatoms.

Thus, it seems unquestionable that the summer decrease in filtering rates of these species is caused by an increase in the concentration of various net phytoplankton forms, which are sufficiently small or narrow to pass through the carapace crevice and into the filtering chamber,

but large or long enough to either interfere directly with filtration or cause an accelaration in postabdomen movements, these clearing movements enabling cladocerans to reject excess food from the filtering chamber or those particles which, such as filamentous blue-greens (B u r n s 1968b), interfere with filtration.

But, it would also appear that the same algae do not interfere, or at most do so to a much smaller degree, with filtration in *Diaphanosoma brachyurum* and *Chydorus sphaericus*.

If the filtering rate of *Daphnia longispina* in Mikołajskie Lake was at its optimum (maximum) in August (about $100 \mu l \cdot \text{ind.}^{-1} \cdot \text{hr}^{-1}$, Fig. 7), then every 4 minutes a cell of *Ceratium* or *Peridinium* and every 20 seconds a filament of blue-greens would enter its filtering chamber. It is difficult, however, to check which of the net phytoplankton forms is most significant for reduction of the filtering rate (F) in particular cladocerans. This is difficult because of both the time-dispersed measurements of the F value and incomplete phytoplankton analysis in 1973.

More detailed analyses of phytoplankton and of other seston components are available for 1966 (raw data for the papers by S p o d n i e w s k a 1974 and G l i w i c z and H i l - l b r i c h t - I l k o w s k a 1975). Although there are no data on the filtering rate, detailed information on fecundity and production does exist for various calonoid and cladoceran species for this year (raw data for papers by H i l l b r i c h t - I l k o w s k a et al. 1972 and W ę - g l e ń s k a − in preparation). Both fecundity and production can certify whether during summer the filter feeding species had their feeding rates optima or whether they starved, either because of a lack of sufficient food in the environment or because of reduction in the filtering rate due to interfering phytoplankton forms.

3.6. Fecundity and individual production of filter feeders against seasonal succession of phytoplankton in 1966

Reproduction intensity and growth rate of animals must not only be influenced by temperature but also by the concentration of both filtration inhibiting net phytoplankton forms and small nannoplanktonic algae, bacteria and particulate dead organic matter. The feeding rate, on which reproduction and body growth is strictly dependant, will drop both with a concentration increase in cells and colonies of inhibiting algae (filamentous blue-greens or other net algal forms), and with a decrease in nannophytoplankton, bacteria and detritus concentrations.

The seasonal changes in phytoplankton composition, biomass and numbers in 1966 were similar to those observed in other years at the same sampling offshore station in Mikołajskie Lake (S p o d n i e w s k a 1974). They were of larger magnitude in net phytoplankton than in nannoplankton (Fig. 10).

It seems that neither the six-fold changes in nannophytoplankton concentration $(0.5-3.0 \text{ mg f.w.} \cdot 1^{-1})$, particularly visible in the period of frequent sampling (second half in June), nor the concentration changes of other components of food source had any effect on the crustacean feeding rate, as it may be assumed that they remained below the level of incipient limiting food concentration. This may be certified by the simultaneously obtained results from Mikołajskie Lake by W ę g l e ń s k a (1971), which show that an increase in natural food concentration resulted in an increase in individual growth intensity and in egg production of all the species analysed here. So, it must be taken into account that nannophytoplankton concentration changes could have had an effect on fecundity and productivity of filter feeding crustaceans by conditioning their feeding rate at an unchanged, optimum filtering rate.
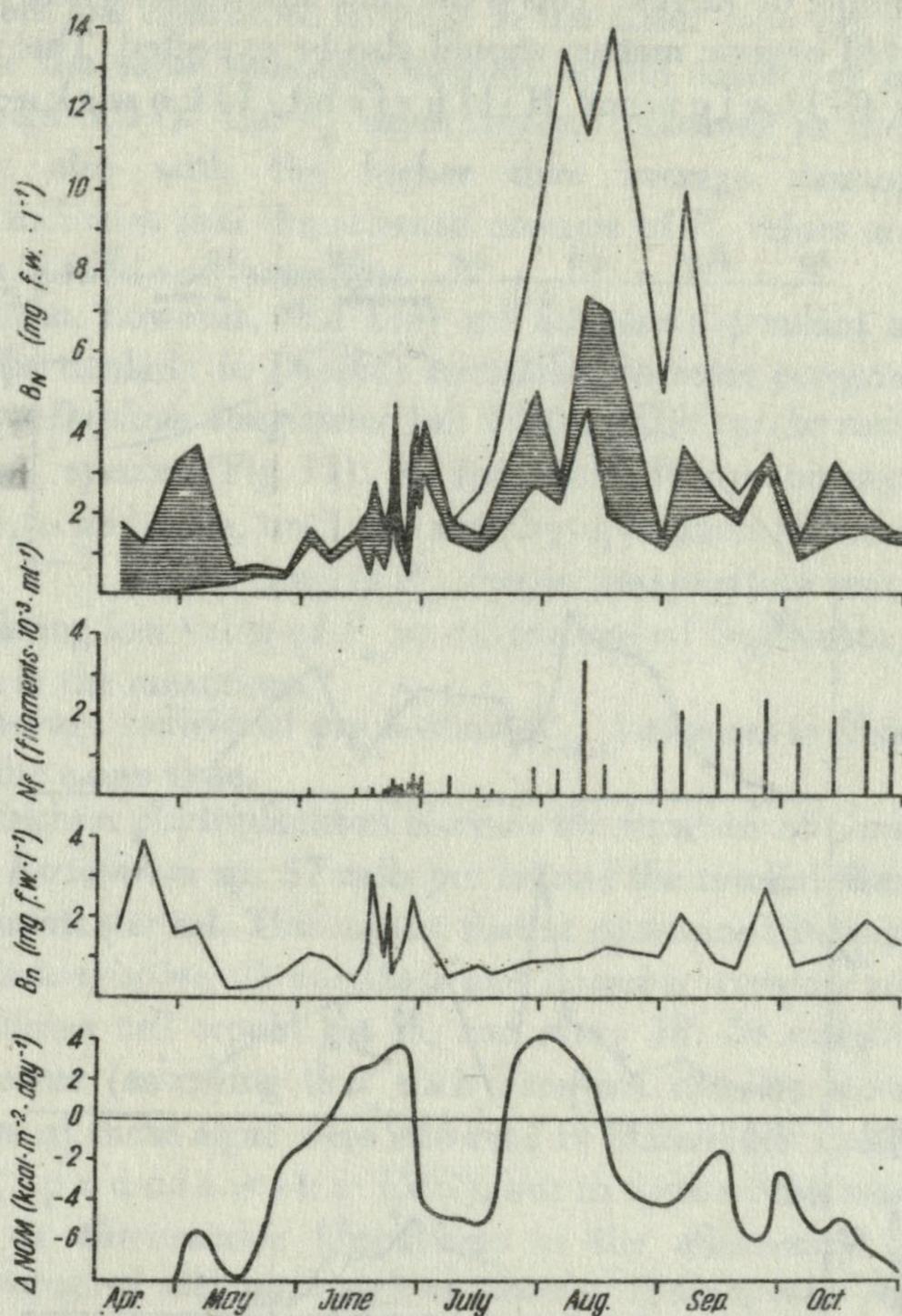
Fig. 10. Seasonal changes in net phytoplankton biomass (B_N) including *Ceratium hirundinella* (upper), blue greens (lower) and other forms (middle part of area under B_N — shaded), in numbers of blue-green filaments (N_f), in nannophytoplankton biomass (B_n) and in daily increase of non-algal organic matter (ΔNOM) in Mikołajskie Lake in 1966

B_N, B_f and B_n acc. to raw data for paper by S p o d n i e w s k a (1974), ΔNOM calculated acc. to G l i w i c z and H i l l b r i c h t - I l k o w s k a (1975)

Fecundity and productivity could have been effected in the same way by changes in the non-algal food concentration — bacteria and particulate dead organic matter, which in Mikołajskie Lake constitute the basic food source for filter feeding zooplankton (G l i w i c z 1969a, 1969b). Since 1966 data do not include this information, an indirectly calculated value for the same sampling station was used for this year to indicate the abundance of this material: increase in non-algal food concentration (cumulation rate of non-algal organic matter — ΔNOM).

The ΔNOM value has its two maxima — one towards the end of June and the other at the beginning of August (Fig. 10, ΔNOM). In other times there is a decrease in concentration of non-algal organic matter (NOM, negative values of ΔNOM) as a result of sedimentation or of high metabolic rate of heterotrophic organisms (G l i w i c z and H i l l b r i c h t - I l k o w s k a 1975). As a result of NOM cumulation in the surface layer its maximum

concentration in this layer should follow soon after the peak periods of ΔNOM, i.e., at the turn of June and at the beginning of August. This is the time when the highest numbers of bacteria, exploiting mainly dissolved organic matter, should also be expected. This is confirmed by the results of earlier analysis (G l i w i c z and H i l l b r i c h t - I l k o w s k a 1975).
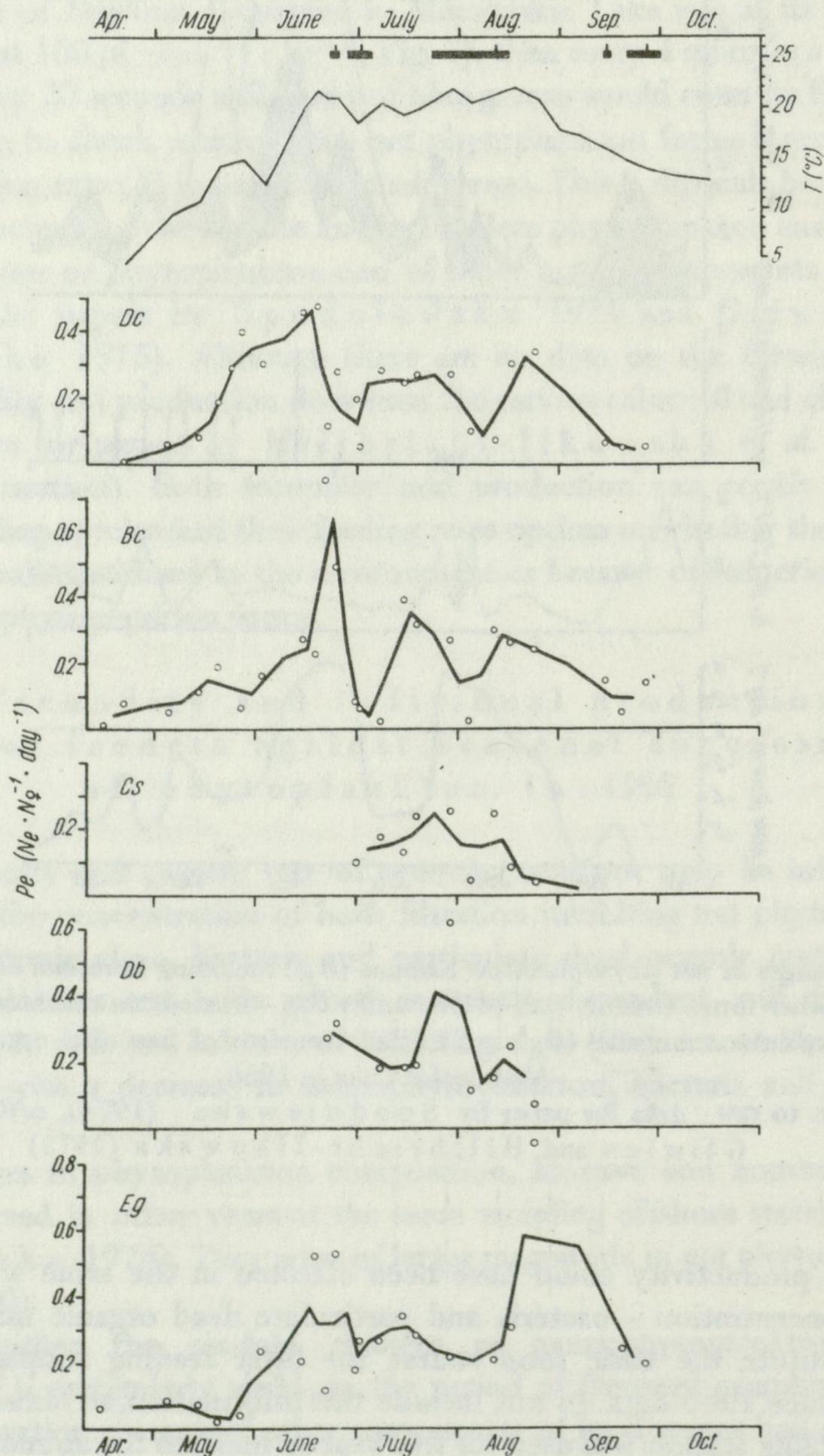

Fig. 11. Mean temperature in the 0—6 m depth layer (T), periods of blue-green biomass higher than 2 mg f.w. $\cdot$ 1^{-1} (horizontal bars with peak of biomass marked) and changes in daily egg production (P_e) of five dominant filter feeding crustacean species in Mikołajskie Lake in 1966
Daphnia cucullata (Dc), Bosmina coregoni (Bc), Chydorus sphaericus (Cs), Diaphanosoma brachyurum (Db) and *Eudiaptomus graciloides (Eg)*. P_e calculated on the basis of raw data for paper by W ę g l e ń s k a (in preparation)

And it is just at this time (the beginning of both July and August) that in nearly all the species analysed there is a significant increase in the mean daily egg production per adult (P_e) calculated (also for the same sampling station) in the same way as described for 1973 in Section 3.4. (cf. Figs. 8, 11). The P_e value increase observed in the very beginning of July (Fig. 11) coincides also with the higher than average nannophytoplankton biomass (Fig. 10, B_n). This indicates that the seasonal changes of P_e values are to some extent dependant on the changes in food concentration.

This does not mean, however, that they are not also dependant on changes in net phytoplankton biomass, particularly in *Daphnia cucullata*, *Bosmina coregoni* and *Eudiaptomus graciloides* (no data for *Daphnia longispina* for 1966). This can be seen from the overall curve shape of P_e for these species (Fig. 11): an increase in P_e accompanying the temperature (T) increase from April to mid-June, until the net phytoplankton biomass (Fig. 10, B_N) does not exceed 1.5 mg f.w. 1^{-1}, then a drop in P_e, despite temperature remaining at the same level, followed by a persisting low value of P_e up to the end of September, despite its two already mentioned increases in the meantime.

Also the daily average individual production (P_{ind}) changes in a similar pattern having its maxima at exactly the same time.

In the period of highest phytoplankton biomass the numbers of *Ceratium hirundinella* reach 216 cells per ml, of *Peridinium* sp. 57 cells per ml and the total of filamentous blue-greens approaches 3,300 filaments per ml. This means that at optimum filtering rates into the filtering chambers of *Daphnia longispina*, *D. cucullata* and *Bosmina coregoni* every 2, 4 and 5 minutes, respectively, a peridinian cell would get in, and every 18, 36 and 60 seconds a filament of blue-greens would enter (assuming that their carapace crevices would remain wide open). Similar high numbers of these algae were observed in Mikołajskie Lake in the summer months of 1963 and 1964 (S p o d n i e w s k a 1967), but in spite of this no trace was found of hard shelled peridinians or filamentous blue-greens in the alimentary tracts of *D. longispina*, *D. cucullata* and *B. coregoni*, although large numbers of these species' individuals were analysed in vivo (G l i w i c z 1969a). This indicates that either these algae do not get into the filtering chambers of the cladocerans analysed (probably true of *C. hirundinella*), or that they are removed from the chambers by postabdomen movements together with other valuable food particles, which reduces the effective filtering rate (collecting rate).

In spite of the fact that the concentration of valuable food is at the beginning of July (algal and non-algal food) and in the first decade of August (non-algal food) much higher than in mid-June, both the egg production (Fig. 11) and the individual production in *D. cucullata*, *B. coregoni* and *E. graciloides* is at this time lower, although the temperature remains at the same level. It seems that just as in 1973 both reproduction and growth are inhibited by the hunger food rations, i.e., low feeding rates due to the reduction in filtering rates resulting from interference by net algae, especially blue-greens. This is certified by time-overlap of blue-green biomas peaks[3] and of lowest egg production. The lowest P_e values of these three species are observed, besides spring, at the time when the blue-green biomass exceeds 2 mg f.w. $\cdot 1^{-1}$ (Fig. 11). The concurrence is not seen when comparing changes in blue-green biomass with changes in daily individual production (P_{ind}).

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[3] Another time-overlap is also noteworthy here, being in agreement with an earlier presented hypothesis on the role of zooplankton grazing in the modelling of phytoplankton composition (G l i w i c z 1975). The high values of nannophytoplankton biomass (B_n) are observed only (but not always) when zooplankton pressure is expected to be at its minimum — in April and at the beginning of May (low numbers of filter feeding zooplankton and low F resulting from low T), in the second half of June (blue-green filtration interference) and in September (also blue-greens, including high numbers of filamentous species).

Neither is it seen in *Chydorus sphaericus* and *Diaphanosoma brachyurum*. The P_e curves for these species follow the T curve patern much more closely.

In order to ascertain which of the analysed factors is to a greater and which to a smaller degree responsible for fecundity (i.e., egg production, P_e) and for individual production ($P_{ind.}$) of various filter feeding species, a stepwise multiple regression analysis was carried out. So as to eliminate the obvious effect of temperature on P_e and $P_{ind.}$, this analysis was limitet to 14 dates between 14 June and 23 August, which was a period of relatively constant mean epilimnetic temperature (Fig. 11, T).

P_e and $P_{ind.}$ were treated as variables dependent on a number of independent variables: *1* — cumulation rate of non-algal organic matter (ΔNOM), taken as the mean for a 20-day period preceding the date of P_e and $P_{ind.}$ estimations; *2* — nannoplanktonic algae concentration (B_n), taken as the mean for a 5-day period preceding the date of P_e and $P_{ind.}$ estimations; and, also taken as the means for the 5-day period preceding this date, *3* — blue-green biomass; *4* — filamentous blue-green numbers; *5* — *Ceratium hirundinella* numbers; *6* — total numbers in all *Peridinium* species; *7* — diatom biomass; *8* — green algae biomass. The independent variables (*1*–*8*) were correlated with P_e and $P_{ind.}$ also in other combinations (*1* taken as the mean for a 10-day period, *2*–*8* as the means for 5-day period preceding the date of P_e and $P_{ind.}$ estimations; *1*–*8* taken as the means for 5-day period; *1*–*8* for 20-day period), but the highest values of the multiple correlation coefficients were found in the first combination. The longer than for other variables period used for ΔNOM estimation was applied in view of the time-lag necessary for the already mentioned process of cumulation of *NOM* in the environment. In this only case the units of increase rate of mass were used, while in all other cases the standing crop values of (bio)mass were utilized.

Results of this analysis (Table III) indicate that P_e and $P_{ind.}$ in some species react more strongly to changes in food concentration (variables *1* and *2*), whereas in other species P_e and $P_{ind.}$ react more strongly to concentration changes in those phytoplankton forms which may be expected to interfere with their filtration (primarily variables *3* and *4*).

For example, egg production (P_e) in *Daphnia cucullata* (Fig. 12) seems to be most sensitive to the changes in blue-green biomass (mainly colonies of *Gloeotrichia* sp. and various species of *Microcystis*, *Gomphosphaeria*, *Anabaena*, *Aphanizomenon*, *Oscillatoria* and *Lyngbya* genera) mean for a 5-day period preceding P_e estimation. Significant (at $p = 0.05$) is already the individual correlation of P_e with the mean blue-green biomass (variable *3*). However, the algal food concentration (nannophytoplankton biomass — variable *2*) must also be important for the P_e of this species, as of all the pairs of independent variables the highest correlation with P_e is noted for the pair of variables *3* and *2* (multiple correlation coefficient significant at $p = 0.01$). The value of the multiple correlation coefficient climbs even higher with the next step in the regression (jointly for variables *3*, *2* and *1*) becoming significant at $p = 0.001$. The subsequent two steps in regression increase the correlation coefficient to a much smaller extent, and no effect is produced by the ramaining steps. It can then be thought that, beside variables *3* and *2*, variable *1* (non-algal food concentration) is also of significance for *D. cucullata* P_e, while variables *6* (*Peridinium* concentration) and *8* (green biomass) are of lesser importance. Both *Peridinium* and greens (mainly *Eudorina* sp. and *Pediastrum* sp.) can, in view of their size and solid cell walls, be regarded as forms interfering with filtration by preventing tight closure of the filtering chamber (see Subsection 3.1).

The results brought forth by such a detailed analysis can never, however, be sufficiently conclusive because of the scarcity of data for correlation and because of the statistically unverified values of the dependent (P_e and $P_{ind.}$) and independent (*1*–*8*) variables. This is why

Table III. Level of significance of the multiple correlation coefficient at subsequent steps of regression of various species' P_e and P_{ind} in relation to various independant variables (*1, 2, 3, 4, 5, 6, 7* and *8*) for the period 14 June-26 August, 1966

P_e (daily egg production per adult) and P_{ind} (daily mean individual somatic and generative production) treated as variables dependant on independant variables: *1* (mean daily increase in non-algal organic matter taken as an average for the 20-day period preceding the date of P_e and P_{ind} estimation), *2* (nannophytoplankton biomass taken as an average for the 5-day period preceding the date of P_e and P_{ind} estimation), *3* (blue-green biomass, also, like all the remaining variables, taken as the average for the 5-day period preceding the date of P_e and P_{ind} estimation), *4* (number of blue-green filaments), *5* (number of *Ceratium hirundinella* cells), *6* (number of *Peridinium* sp. cells), *7* (diatom biomass) and *8* (green algae biomass). All values calculated on the basis of raw data for papers by S p o d niewska (1974), Gliwicz and Hillbricht-Ilkowska (1974) and Węglenska (in preparation)

$\underline{1}$ and $\underline{2}$ — thought to be stimulating, $\bar{3}$ and $\bar{4}$ — thought to be most inhibiting for P_e and P_{ind}.

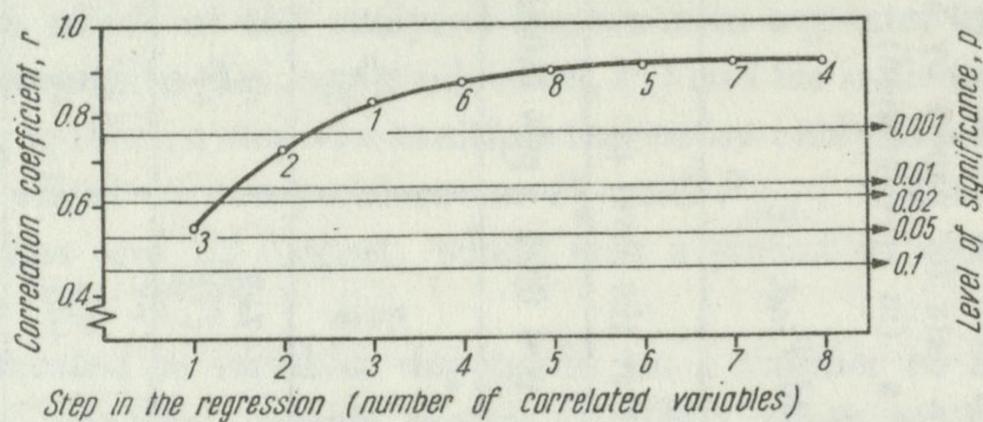| Depth layer (m)	Species	Dependant variables	Multiple correlation coefficient (r) significant at the level of:					
			p < 0.1	p = 0.1	p = 0.05	p = 0.02	p = 0.01	p = 0.001
0—6	*Daphnia cucullata*	P_e	—	—	$\bar{3}$		$+\underline{2}$	$+\underline{1}$
		P_{ind}	—	—	—	5	+8	$+\bar{3}$
	Bosmina coregoni	P_e	$\bar{3}$			$+\bar{4}$	$+7+\underline{2}$	$+\underline{1}$
		P_{ind}	—	$\bar{3}$	$+\bar{4}$		$+7+\underline{2}$	$+\underline{1}$
	Chydorus sphaericus	P_e	8+5					$+6+\underline{1}$
		P_{ind}	—	—	8		+7	+5
	Diaphanosoma brachyurum	P_e	—	—	—	—	7+2	+5
		P_{ind}	8	$+\underline{1}+\underline{2}$	$+\bar{3}$	+6	$+\bar{4}$ +7+5	
	Eudiaptomus graciloides	P_e	$\bar{3}$	$+\bar{4}$	+5+6+7	+8	$+\underline{2}$	
		P_{ind}	8	$+\bar{3}$			+4	+7
0—24	*Bosmina coregoni*	P_e	—	—	$\underline{2}$	—	$+\bar{4}$	$+\underline{1}$
		P_{ind}	—	—	—	—	$\underline{2}+\bar{4}$	$+\underline{1}$

Fig. 12. Dependence of daily egg production (P_e) of *Daphnia cucullata* on several independant variables (food concentration — variables *1* and *2* — and concentration of various net algal forms thought of as interfering in filtration — variables *3–8*) as an example of P_e and $P_{ind.}$ dependence on environmental conditions employing the stepwise multiple regression

Descriptions of variables *1—8* in Table III

the analysis was finally limited to finding out in which species food concentration (variables *1* and *2*) and in which phytoplankton forms regarded by many authors (for review see B u r n s 1968b) as inhibiting (*3* and *4*) has the greatest effect for egg production (P_e) and individual production ($P_{ind.}$).

When species are compared in this respect (Table III), it becomes evident that the concentration of inhibiting phytoplankton forms is of much greater significance than food concentration as far as *Bosmina coregoni* and *Eudiaptomus graciloides* are concerned. In the case of *Daphnia cucullata* food concentration seems to be of equal importance to that of inhibiting forms, for *Diaphanosoma brachyurum* food concentration is most probably of greater effect, while for *Chydorus sphaericus* neither concentration of food nor of inhibiting algae appears to play any important role. Of foremost importance for the last species seems rather to be abundance (biomass) of all, excepting blue-greens, net phytoplankton forms (peridinians, diatoms and greens). This would testify that other factors are involved here, such as abundance and availability of epiphytic food material covering the surface of algal cells and colonies, which according to F r y e r (1968) explains why *Chydorus sphaericus* is sometimes so widespread in the limnetic zone of lakes.

Another phenomenon should also be noticed here. The primary dependence of *Bosmina coregoni* P_e and $P_{ind.}$ on the inhibiting algae concentration is only true for the epi-metalimnetic part of its population (i.e., the part remaining in the 0–10 m depth layer). As a significantly large part of this, and only this, species population remains in the hypolimnion (10–24 m depth layer) up to the middle of July, the P_e and $P_{ind.}$ values were also calculated for the total population from the whole water column (0–24 m depth). The stepwise multiple regression analyses for these values revealed that inhibiting algae concentration (in epilimnion) was of much smaller and food (in epilimnion) was of much greater significance for the whole water column population than for its epi-metalimnetic part (Table III). This shows that the changes in epilimnetic food concentration are sooner reflected in the hypolimnion than are changes in epilimnetic inhibiting algae concentrations.

4. DISCUSSION

4.1. Phytoplankton, filtering rate and feeding rate

The summer reduction in fecundity and production observed among some of the filter feeding species in Mikołajskie Lake certifies that these species are not able to fully satisfy their

food demands at this time. This is so, as is well known, because the intensity of these processes is the combined effect of temperature and of food concentration. This is supported by many experimental studies, a review of which can be found in both H u t c h i n s o n (1967) and W ę g l e ń s k a (1970). The question does, however, arise, whether possibly the very temperature increase itself worsens these animals' trophic conditions. Indeed, a rise in temperature is tantamount to a higher metabolic rate and, therefore, an increase in food demands. This increased temperature influence may, however, be well compensated by a simultaneous increase in the filtering rate, which, in its turn, gives rise to a significantly higher feeding rate, although the food concentration remains at the same level. This compensation seems to be very efficient among filter feeding crustaceans. While their metabolic rate increases more or less in line with Krogh's curve ($Q_{10} = 2$), so the filtering rate generally seems to increase more decisively (according to B u r n s (1969b) Q_{10} reaches the value of 2.8 or even surpasses it[4]).

The incapability of satisfying the filter feeders' food requirements is neither the result of a decrease in food concentration, as it seems to be evident that there is rather a tendency for the food concentration to increase during the summer. If, however, the feeding rate does fall, there is no question that, despite the increase in temperature, the filtering rate must then be reduced.

The logic of this reasoning is only apparent now, when we are aware that a decrease in fecundity and production rate in Daphnia cucullata, D. longispina and Bosmina coregoni goes together with, or is probably preceded by a reduction in their filtering rates.

Another question does, however, come to mind: must a reduction in the filtering rate really mean a simultaneous drop in feeding rate? The F value experimentally measured for various size particles goes to show that the opposite could be true. Indeed, an increase in the filtering rate can coincide with a narrowing of the gap between the carapace margins. The water flow through the filtering chamber will then be faster, but each unit of water volume will bring in less food particles, since the larger particles, which could have earlier got throught the wider gap, will now be prevented from entering the filtering chamber. Together with, or independently of the changes in the carapace crevice width, changes may take place in the width of the fissure between the edges of thoracic limbs during the abduction phase (i.e., when the limbs are taken apart), which together with the crevice width must determine the upper size limit of particles grazed. Finally, account must be taken of the positioning of the first pair of thoracic limbs when water is being sucked into the filtering chamber. For instance, in Daphnia species, for which filter feeding behaviour is best described (C a n n o n 1933), the long setae of the first and second pair of thoracic limbs can probably withhold larger particles. In another paper (G l i w i c z — in preparation), cases of inverted correlation are shown for the filtering rate (treated as rate of water-flow through the filtering chamber) and the upper size limit of grazed particles. The correlation coefficient appeared to be the most significant in those cases when there was greatest probability of filtration interference by high densities of net algae. Accordingly, it may be deemed that the same feeding rate may be assured with different (e.g., lower) filtering rates, if only the carapace crevice width is simultaneously alternated (e.g., widened).

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[4]From the comparison of May (9°C) and June (17°C) filtering rates of Daphnia cucullata and of September (14°C) and October (9°C) filtering rates of D. longispina, Diaphanosoma brachyurum and Chydorus sphaericus Q_{10} values were obtained in the range 2.5–3.0, after taking into account a correction for the mean individual size (body length). Exceptionally high values of Q_{10} (4.0) obtained from a comparison of May and June filtering rates of Bosmina coregoni are most probably an artifact, and may rather reflect some inhibitory effect of the still high diatom concentration in May on this species' filtering rate, which seems to be at that time below its optimum value.

Results of F value measurements for various size particles demonstrate that large concentrations of net phytoplankton influence both the filtering rate itself as well as the degree of carapace crevice opening, and thus the upper size limit of grazed particles. It is seen from the analysis of the relationship between fecundity and individual production, on the one hand, and the presence of various algae, on the other, that filter feeding species react in different ways to various algal forms. Blue-greens appear to have the strongest inhibiting effect, but *Daphnia cucullata* and *Eudiaptomus graciloides* also seem to be affected by green algae (although this is rather doubtful in view of their low numbers) and by *Ceratium hirundinella*, while *Bosmina coregoni* by diatoms (Table III).

Narrowing[5] of the gap between the carapace margins may be considered as a defence measure, more or less effective, against"uninvited" algal forms. Among these are most certainly forms which render tight closure of the filtering chamber impossible, allowing smaller particles to escape when the water is pressed out, which consequently reduces the feeding rate while the filtering rate (in terms of water-flow through the chamber) remains the same. This is most probably what happened to *Daphnia cucullata* in Mikołajskie Lake[6] (July – Fig. 1), as well as to *Daphnia galeata* in some of the experiments of B o g d a n and M c N a u g h t (1975 and personal communication), who sometimes obtained a lower filtering rate of natural food particles of 0–20 μm size range than of those above 20 μm. Other phytoplankton forms clog the cladoceran filtering chambers or, although they reach the labral region, they are not ingested, as is the case of *Daphnia rosea* when *Anabaena* filaments enter its filtering chamber (B u r n s 1968b). In both cases the clearing movements of postabdomen are intensified to reject the unwanted particles from the filtering chamber, similarly as is observed when the animal is exposed to a high food concentration (M c M a h o n and R i g l e r 1963). This also results in a drop in feeding rate, while the filtering rate remains the same, as together with the rejected unwanted particles, other wanted particles must be accidentally removed from the filtering chamber too.

The results of these observations put in doubt the possibility of constructing permanent models of food size selectivity of filter feeding species (or even of their age stages), which could be useful for both determination of feeding rates of entire zooplankton communities as well as for gaining information on the extent and direction of zooplankton pressure on phytoplankton, as has been earlier proposed (G l i w i c z 1970).

4.2. Upper size limit of food particles and sensitivity to filtration interference

When in the environment the concentration of interfering particles becomes greater, but the amount of food remains below the incipient limiting concentration, the animal faces a

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[5] Whether this "narrowing" is passed from generation to generation (in the average individual of the next generation the carapace crevice would be more often narrowed to a greater degree than in the average individual of the preceding generation) is doubtful, as such a selection in a parthenogenetically reproducing population seems rather improbable.

[6] Possibility of an "interfering" action of the organic polimer beads used for F estimation must also be taken into account here. Filtering rates determined by this method (also when using other solid particles of artificial food) are much lower than those obtained through the use of marked natural food particles. The same was observed by Dr. Frank H. Rigler (personal communication). This is why such low concentrations of polimer particles, with a domination of those below 15 μm size, were used for F estimation in Mikołajskie Lake.

dilemma: either to narrow the carapace crevice (or not to take the edges of the thoracic limbs to much apart) to avoid interfering particles, or to leave it wide open so as not to give up larger food particles. In both cases the feeding rate must drop: either because of the smaller amount of food entering the filtering chamber in each unit of water, or as a result of a drop in the effective filtering rate (i.e., volume of water from which food particles were filtered and ingested). Neither solution is thus satisfactory. But if the filtering rate (in the sense of water through-flow) is already at the optimum (maximum possible) in the actual temperature, then there is no third solution.

Results of the fecundity and individual production analysis indicate that more "profitable" is rather the narrowing of the crevice and giving up of the larger food particles. *Daphnia cucullata* does so in the period of high net phytoplankton biomass to a greater degree than *D. longispina* and *Bosmina coregoni* do. It may be just this that is behind the only slight, as compared with the two others, decline in fecundity in *D. cucullata* and that allows the population of this species to persist in relatively high numbers throughout the algal bloom period.

These results also indicate that keeping to a lower upper size limit of food particles has its advantages, too. The populations of *Diaphanosoma brachyurum* and *Chydorus sphaericus* (in the latter the upper size limit is certainly determined by the small carapace crevice width) meet no obstacles in their summer increase. But this also has its disadvantages. The lower upper size limit of food particles is reflected in the smaller amount of food entering the filtering chamber in each unit of water volume. It seems, therefore, that both species need higher concentrations of particles available. This may be why their highest population numbers, resulting from the high fecundity and individual production, are observed in the summer period, when concentration of food, particularly of small non-algal particles (bacteria, detritus), is increased in the lake.

4.3. Algal blooms and "size-efficiency hypothesis"

It is difficult to say whether the summer increase in food concentration is connected exclusively with changes in the intensity of primary production and organic matter decomposition and sedimentation, or whether it has anything to do with the disappearance of *Daphnia longispina* and *Bosmina coregoni* populations and with the drop in *Daphnia cucullata* and *Eudiaptomus graciloides* population numbers, thus consequently with a decline in the exploitation of food sources[7]. If the latter were true, it would present an example of competition forces being at work.

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[7] In view of significantly lower numbers in the filter feeding species it should be doubted whether the food exploitation in Mikołajskie Lake was as intense as in H a n e y ' s (1973) Heart Lake, where the entire zooplankton community's filtering rate not infrequently exceeded 100% of the environment swept clear per day (1 litre of water filtered by animals found in 1 litre of lake water). In Mikołajskie Lake these values never exceeded 20%. In order to attain 100% the joint numbers of *D. longispina, D. cucullata* and *B. coregoni* would have to reach 500 ind. $\cdot$ l^{-1}. It can, however, be deemed that the generation time (renewal time) of the nannoplankton and bacteria biomass is in the eutrophic Mikołajskie Lake significantly longer than one day (according to R o d h e (1958) in Swedish eutrophic lakes it fluctuates between 2 and 5 days). If this were so, then the further summer increase of populations of these species would significantly limit the concentration of food available in the environment. What is more, only a slight alteration in food concentration might be thought of as a quite radical change for egg production of such a species as *Diaphanosoma brachyurum* or *Chydorus sphaericus*.

An analogy could here be drawn to the previously known phenomenon, which was later generalized by Brooks and Dodson (1965) and accepted as their "size-efficiency hypothesis". Those species with a more efficient filtering mechanism (higher filtering rate and higher upper size limit of particles grazed) dominate in an environment, until a selectively operating, negative factor appears, which will more strongly limit the "efficient" (competitively stronger) than the "inefficient" (competitively weaker) species. For Brooks and Dodson (1965) this factor is predation by planktivorous fish, which eliminate larger crustacean forms from the environment, thus enabling small forms to develop. In Mikołajskie Lake this factor would be the net algae interfering with filtration in the more efficient filter feeding species. The elimination of hitherto dominant species does take place by different means (there by increase in mortality, here by decrease in fecundity), but the final result is exactly the same: the populations of those species develop which are less sensitive to the introduced factor and which previously did not have a chance. Being constantly pushed out of the environment by the competitively stronger species, they could not reach higher numbers in spring and they had to retire in autumn.

That at work here was no selective predator but interfering algae is certified by the drop in egg production and individual growth rate, which preceded the reduction in numbers in the "efficient" species populations. An unselective predator could be more easily thought of as a factor responsible, which, in accordance to Gause's (1935 after Slobodkin 1963) model, modifies the end result of interspecific competition giving greater chances to those species which at that moment have a higher ecological reproduction rate (r), even when they are competitively weaker. In Mikołajskie Lake this could be the combined effect of an unselective predator and of filtration interfering net algae. This would be, on the one hand, the effect of interfering algae lowering the r value in competitively stronger (efficient) species ($D.$ $longispina$, $D.$ $cucullata$, $B.$ $coregoni$ and $E.$ $graciloides$) but not lowering the r value of competitively weaker (inefficient) species ($D.$ $brachyurum$ and $C.$ $sphaericus$), and on the other hand, of the unselective predation resulting in a faster disappearance of the populations of those species with a reduced r value.

Selective predation seems to be unlikely to be present here for other reasons, too. The predation by planktivorous fish (mostly vendace, $Coregonus$ $albula$ L., but also bleak, $Alburnus$ $alburnus$ (L.), and smelt, $Osmerus$ $eperlanus$ L.) on Mikołajskie Lake zooplankton does not seem to be strong enough to cause such a decrease in numbers of efficient cladoceran species (Gliwicz and Prejs — in press), while two planktonic invertebrate predators abundant in the limnetic zone — $Leptodora$ $kindtii$ Focke and $Chaoborus$ $flavicans$ (Meig.) — neither show any preference for the efficient species (Hillbricht-Ilkowska and Karabin 1970, Kajak and Ranke-Rybicka 1970, Kajak and Rybak — in preparation) nor do they have any distinct peaks in numbers during the periods of the efficient species' decline (Hillbricht-Ilkowska et al. 1972 and unpublished data, Kajak and Rybak — in preparation). For the same reasons the role of cyclopoid copepods seems unimportant.

4.4. The reasons for species withdrawal

$Diaphanosoma$ $brachyurum$ and $Chydorus$ $sphaericus$ are regarded as typical summer forms (Manujlova 1964), associated with algal blooms. Fryer (1968), who regards $C.$ $sphaericus$ as a typical littoral form, demonstrating this species' high level of specialization for feeding on bacterial films covering the solid substrates, believes, just like other authors cited

by him, that *C. sphaericus* cannot appear in the limnetic zone until the large phytoplankton forms (e.g., *Gloeotrichia*) are numerous, and to which it can attach itself and from the surface of which it can gather food. Results of analysis of *Chydorus'* filtering rate in Mikołajskie Lake, as do the results of investigations by B e l j a c k a j a - P o t a e n k o (1964) and by H a n e y (1973, p. 110), prove that it also intensively grazes on particles suspended in the water, the observed filtering rate not being lower than that of *Bosmina* species when body length is accounded for. It must, therefore, be recognized that despite of its unquestionable adaptations for grazing on epiphytic particles scraped from the surface (F r y e r 1968), *C. sphaericus* can also exploit the same food sources as other typically limnetic filter feeding cladocerans, although it is possibly to a lesser extent dependent on this type of food. This is confirmed by the results of the stepwise multiple regression analysis (Table III).

Diaphanosoma brachyurum is regarded as a typical warm water species (M a n u j l o v a 1964). There is nothing to support this opinion except for noticing its population peaks almost exclusively in summer time. Basing on the results of W ę g l e ń s k a ' s (1971) experiments it can be seen that this species is to no greater than other filter feeding species extent dependant on the environmental temperature, at least in the range applied by her, i.e., 17–22°C. In unlimiting, increased concentrations of natural food brought from the lake (above 3 mg f.w. $\cdot 1^{-1}$), with T increasing in the above range, the duration of postembryonic development in this species is shortened by only 43% (from 5.1 to 2.9 days), i.e., to a smaller degree than in *C. sphaericus* (by 54%) and in *D. longispina* (by 47%), and not to a much higher degree than in *D. cucullata* (by 39%) or *E. graciloides* (by 41%).

The same experiments (W ę g l e ń s k a 1971) do, however, clearly show that *D. brachyurum* is to a higher extent dependant on food concentration than are other species. With an increase in the natural food concentration from 0.5 to 4.0 mg f.w. $\cdot 1^{-1}$, duration of postembryonic development of this species is shortened by 54% (at the temperature of 17°C) or by 69% (at 22°C), while in other species these values are significantly lower: 39 and 53% for *D. longispina*, 40 and 53% for *D. cucullata* an 31 and 50% for *C. sphaericus*. This goes to show that it is not temperature but food which should be considered as the key factor responsible for limiting the numbers in the population of this species in Mikołajskie Lake. This is fully confirmed by the results of the stepwise multiple regression analysis for 1966 (Table III).

These results also confirm that significantly dependant on the concentration of food suspended in the water (small algae, bacteria and detritus) is *Chydorus sphaericus*. This is one further reason for acknowledging this species as a potential exploiter of the same food source which is used by other limnetic filter feeders.

The feeding rates of *Diaphanosoma brachyurum* and *Chydorus sphaericus* do not probably undergo large changes as a result of the appearance of large numbers of interfering algae. Both these species always keep to a fairly narrow range of food particle size, and so their filtering rates can remain close to the optimum. Thus, the feeding rate is rather determined by the food concentration and ultimately it is on this that egg production and individual production is dependant.

Too small a concentration of food in the environment can thus result in a reduction in numbers and consequently in a withdrawal of these species from the limnetic zone.

The opposite is the case both for *Daphnia* species and for *Bosmina coregoni* (most probably also for *Eudiaptomus graciloides*). These animals graze on food particles from a wider size range. Therefore, the same volume flow of water through their filtering chambers gives them the possibility of collecting larger amounts of food. So they grow and reproduce much faster than *Diaphanosoma* and *Chydorus* in the spring and autumn lower food concentrations. In

accordance with the results of Węgleńska's (1971) experiments presented above, they do not have any advantage over *Diaphanosoma* and *Chydorus* in respect of a lower temperature (e.g., 17°C in June 1973). Their advantage, therefore, comes rather from their wider size range of food particles grazed. However, when the net phytoplankton concentration increases in the lake this hitherto advantageous range becomes troublesome. Neither lowering the upper size limit of food particles grazed (as in *D. cucullata*) nor leaving it unchanged (as probably in *D. longispina*) can do anything to hold the feeding rate at the same level, and consequently to retain egg production and individual production at their previously high rates.

Too large a concentration of net algae in the environment can thus result in a breakdown of the populations of these species or even in their total, though temporary, withdrawal from the limnetic zone.

4.5. Mechanism of seasonal succession in filter feeding species

The mechanism of seasonal succession in filter feeding zooplankton observed over many years in Mikołajskie Lake can thus be seen as follows:

April-May. A high concentration of algal food — nannophytoplankton (Fig. 10, B_n), and most probably of non-algal food — particulate organic matter raised from the bottom by the April circulation. This is "take-off" for populations of all filter feeding species (Fig. 8). A high concentration of colonial diatoms (Fig. 10, B_N) must make food collecting difficult for both *Daphnia* species and for *B. coregoni* (probably also for *E. graciloides*). Diatoms, however, soon disappear from the surface layers, sinking and settling on the bottom of the lake (Gliwicz and Hillbricht-Ilkowska 1975). Simultaneously sedimenting are small particles of organic matter (negative values of ΔNOM — Fig. 10), not yet being stopped by a metalimnetic density gradient layer, which later on might have some significance for slowing down the sinking rate of particulate matter (Gliwicz 1976b). Together with a constantly increasing epilimnetic temperature, the growing in numbers filter feeding animals reduce the nannophytoplankton concentration (Fig. 10, B_n). Thus both non-algal and algal food concentrations decrease, remaining at a low level up to the middle of June. The populations of the efficient species continue in their intensive development (Fig. 8) due to their higher upper size limit of particles grazed, while those of inefficient species are limited, most probably as a result of the insufficient food concentration.

June-July-August. Both the algal and non-algal food concentration increases from mid-June (Fig. 10, B_n and ΔNOM). Increasing also are the fecundity and individual production of all the filter feeding species, bringing about an increase in numbers. The high density of filter feeding animals puts a limit on nannophytoplankton concentration (Fig. 10, B_n). However, the concentration of non-algal food, bacteria included, remains at its high level, as its increase is still observed (positive values of ΔNOM — Fig. 10). As a result of net phytoplankton becoming more abundant (Figs. 9, 10, B_N), the filtering rates of efficient species fall below their optimum for the temperature present (Fig. 7). The high F value reduction is for *D. longispina* (Fig. 9) most probably due to its persisting high upper size limit of particles grazed (Figs. 2, 5). This species, like *B. coregoni*, disappears from the limnetic zone (Fig. 8). Despite a significant drop in egg production (Figs. 8, 11) and individual production *E. graciloides* and *D. cucullata* populations remain in relatively high numbers, the latter most probably due to a lowering of its upper size limit of particles grazed (Figs. 1, 5). With a persisting high non-algal food concentra-

tion (and a decreased algal food concentration), populations of those species undergo intensive development, which are less (*Diaphanosoma brachyurum*) or probably not at all (*Chydorus sphaericus*) interfered with by net algal forms. This might be possible because of the disappearance or decline in numbers of those species, which otherwise would not have allowed such a high food concentration to remain.

September-October. The concentration of net algae declines (Figs. 9, 10). Fecundity and individual production rise in those filter feeding species, of which the feeding rate was hitherto below their food demands due to a reduced filtering rate and/or a lowered upper size limit of particles grazed. Their significant rise in numbers (Fig. 8) and some increase in their filtering rates (Fig. 7) must produce a decrease in the food concentration, although a significant drop in the amount of algal food is rather the result of a lowered primary production rate (S p o d - n i e w s k a 1974) and of an increased rate in organic matter decomposition, observed at the turn of August (G l i w i c z and H i l l b r i c h t - I l k o w s k a 1975). *D. brachyurum* and *C. sphaericus*, being species limited primarily by the food concentration, give up their place to the more efficient species. Despite a decreasing net algae concentration, which was especially radical in 1973 (Fig. 9), the *C. sphaericus* population holds its stand much longer than the *D. brachyurum* population (Fig. 8). This could possibly be due to a raising of its upper size limit of particles grazed (the maximum size of particles ingested increases decisively from August to October together with a gradual widening of the carapace crevice width – Fig. 4).

This picture of seasonal succession in filter feeding zooplankton leaves aside, of course, many significant factors. Of necessity it does not encompass either the role of predators or of other groups of animals, exploiting the same food sources, especially rotifers or protozoans. Neither does it take into account changes in organic matter inflow (and outflow) from (into) the littoral and drainage basin. Furthermore, it reflects observations made in one particular lake. Might similar mechanisms be at work also in other eutrophic lakes?

4.6. Seasonal succession in other eutrophic lakes

Seasonal succession of planktonic crustaceans often follows a similar pattern in other, particularly eutrophic lakes: spring development of the population of a *Daphnia* species, its summer recession accompanied by abundant appearance of *Diaphanosoma*, *Chydorus* and *Ceriodaphnia* species, and finally its temporary return in autumn. Many such cases are described in H u t c h i n s o n (1967), who also considers the possibility of blooms of inedible algae as being responsible for the summer decline in numbers of certain cladoceran species (H u t - c h i n s o n 1967, p. 623).

Unfortunately, it is rare for such detailed descriptions of seasonal changes in zooplankton populations to go hand in hand with equally detailed, if any, descriptions of changes in phytoplankton species composition, numbers and biomass, as those to be found in N a u w e r c k 's (1963) study of Lake Erken. In many ways Lake Erken is similar to Mikołajskie Lake. In both lakes there is a resemblance as to zooplankton and phytoplankton species compositions and patterns of their seasonal succession. Similar in Lake Erken is also the nannophytoplankton biomass throughout the seasons ($0.3-2.5$ mg f.w. $\cdot 1^{-1}$), almost as high a peak biomass of net phytoplankton in August (nearly 10 mg f.w. 1^{-1} in the surface layer) dominated, as in Mikołajskie Lake, by *Ceratium hirundinella* and including an equally high blue-green biomass in July (nearly 2 mg f.w. $\cdot 1^{-1}$ in the surface layer), of which a large share is also made up by *Anabaena* and *Aphanizomenon* filaments. There is also a similar pattern in the seasonal changes of filter feeding species fecundity (number of eggs per adult and percentage of

egg-carrying females). From July (peak of blue-green biomass) both the fecundity indices for *Eudiaptomus graciloides*, *Daphnia longispina* and *Bosmina coregoni* begin to decrease and consequently the populations of all three species are reduced in numbers almost to zero. During July and August *Diaphanosoma brachyurum* and *Chydorus sphaericus* appear, building up their populations, their numbers reaching almost those of the hitherto abundant cladoceran species. Later on, in September, when the net algal blooms subside, the *Diaphanosoma* and *Chydorus* populations decline, the former disappearing more quickly. Simultaneously, there is a distinct increase in the *Daphnia* and *Bosmina* populations, which persist in fairly high numbers right up to November.

The pattern observed in Lake Erken might be successfully explained by the action of the same mechanisms that are at work in Mikołajskie Lake although N a u w e r c k (1963) did not find even the slightest summer reduction in the filtering rate of the species disappearing from limnetic zone during net algae blooms. It seems, however, that the high filtering rates of these species, persisting throughout the summer, should be considered as an artifact resulting from the method he used, in which the animals were exposed in lake water (with natural nannophytoplankton pre-experimentally marked with ^{14}C) deprived of net phytoplankton.

Besides the changes in the surface layers of Lake Erken, an abundant appearance of *Ceriodaphnia quadrangula* was observed. Just as in Mikołajskie Lake in 1973 (R a c z k o w s k a 1974), *Ceriodaphnia* remains in small numbers in the surface layer up to June, only to, after moving down to the upper layer of the hypolimnion (in Mikołajskie Lake) or to the near-bottom layer (in Lake Erken), build up a numerous population by July which persists up to September.

The possibility should not be counted out, that this could be another solution for a species faced by a hunger threat in consequence of the too large a net, interfering algae concentration[8]. It seems possible that other, so called "cold-water" (H u t c h i n s o n 1967, p. 608) cladoceran species descend to the hypolimnion not because of the lower temperature but because of the absence of interfering algae there. If indeed these species are well adapted to lower temperature, it could be that this evolved secondarily as a result of their summer refuge in the cooler hypolimnetic waters (or in cold Arctic and alpine lakes), where algal blooms are not heard of.

Similarly, a diacmic pattern of seasonal population changes in various *Daphnia*, *Bosmina* and *Eudiaptomus* species is often interpreted not as a result of changes in fecundity, but rather as a result of mortality changes resulting either from the varying pressure of planktivorous fish (e.g., P a t a l a s 1963, L i m p a d a n a i 1974) or of invertebrate predators (e.g., C o m i t a 1972), or from other, unknown reasons (e.g., W i k t o r 1961). However, it would appear that in most cases we might be concerned with factors of the same nature as in Mikołajskie Lake. For instance, in several eutrophic (and so, rich in net phytoplankton) lakes investigated by P a t a l a s (1963) a July population decline of *Daphnia*, *Bosmina* and *Eudiaptomus* is coincided with an increase in *Diaphanosoma brachyurum*, *Ceriodaphnia quadrangula* and *Chydorus sphaericus* populations. Similarly, in the net phytoplankton rich (in July over 50 mg f.w. $\cdot 1^{-1}$ of biomass, dominated by blue-greens) Severson Lake, investigated by C o m i t a (1972), a July population decline in *Daphnia parvula* Fordyce and *Diaptomus siciloides* Lill. again coincides with an increase in *Diaphanosoma leuchtenbergianum* Fischer. It is quite difficult to envisage such a selective effect of either planktonivorous fish or predaceous larvae of *Chaoborus punctipennis* (Say) onto species of so similar sizes. It seems that the observed filter feeding species replacements could be more easily caused by such a selectively working factor as interference by large or filamentous algal forms,

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[8] In view of the fact that the filtering rate measurements were made only on animals from the surface, epilimnetic layer, no data on *Ceriodaphnia*'s upper size limit of particles grazed is available. But occasionally taken measurements of the carapace crevice width (most individuals 25–40 μm) indicate that this species might be susceptible to interference by large phytoplankton forms.

if *Daphnia* and *Diaphanosoma* species from Lake Severson are similar to those from Mikołajskie Lake.

4.7. Eutrophication – the success of species resistant to algal blooms

The species of the *Daphnia, Bosmina* or *Diaptomus* and *Eudiaptomus* genera, usually diacmic in eutrophic lakes, are often monacmic in less eutrophicated lakes, having their maximum in mid-summer. Several such examples are given by Hutchinson (1967, pp. 609–620). In this context, a tendency, observed by Patalas (1954) in August in 28 lakes in northern Poland, seems noteworthy here:

1. In lakes with a diversed, rich in species filter feeding community, dominated in summer by *Daphnia cucullata, Eudiaptomus graciloides* (or *E. gracilis*) and *Eurytemora lacustris* (Poppe), never found are *Diaphanosoma brychyurum* and *Chydorus sphaericus*. These are deep lakes, with high Secchi disc readings (5–6 m in August) and a well oxygen saturated hypolimnion (i.e., lakes of a low trophy, and so with a low net phytoplankton biomass);

2. In those lakes, where in summer there is a smaller abundance of *D. cucullata* and *E. graciloides* and where there is no more *E. lacustris* present, *D. brachyurum* appears as a co-dominating species. These lakes are fairly deep, with lower Secchi disc readings (2–5 m in August) and a less oxygen saturated hypolimnion (i.e., eutrophic lakes, and so with a significant net phytoplankton biomass);

3. In those lakes, where in summer *D. cucullata* and *E. graciloides* are much less abundant, *Diaphanosoma brachyurum* is joined by *C. sphaericus* as decisively dominating species. There are shallower lakes (up to 10 m in depth), with low Sacchi disc readings (0.7–3.5 m in August) and an oxygen deficiency in the hypolimnion (i.e., strongly eutrophicated lakes, and so with summer blooms of net phytoplankton).

These distinctive changes in filter feeding species composition along the trophy spectrum of lakes are just about identical to the seasonal changes observed yearly in the eutrophic Mikołajskie Lake from spring to the mid-summer. It should not be excluded that similar or even the same factors are responsible for both seasonal and long-term succession.

There should also be a similar pattern of long-term filter species succession observed in any one lake undergoing eutrophication. Since such a succession must take place over a long time-span, it can only be reconstructed by means of laborious paleolimnological methods. Unfortunately, little information can be found on this subject from the results of paleolimnological research. Noteworthy are, however, the investigation results of Kerfoot (1974), who was successful in reconstructing the changes in the relative numbers of three cladoceran genera in what is now the strongly eutrophicated Frains Lake, Michigan, over the past 10 thousand years (core from 11 m of sediment depth). These changes were most distinct about 140 years ago, following the forest clearing in the drainage basin, which resulted in a massive silt inflow into the lake and, in its turn, a lake eutrophication certified by a complete oxygen depletion in the hypolimnion (proved by the presence of dark sapropel). Together with eutrophication, the disappearance of an unidentified large *Daphnia* species, the decline in numbers of smaller *Daphnia* species, which are currently present in the lake (*D. ambigua* Scourfield and *D. parvula*), and the increase in numbers of *Bosmina longirostris* and of *Chydorus sphaericus* were all found to have simultaneously occurred.

When interpreting these changes Kerfoot (1974) sticks to the lines of Brooks and Dodson's (1965) size-efficiency hypothesis, explaining them as the result of increased

planktonivorous fish pressure on zooplankton, which is, according to him, strictly connected with the simultaneous development of the littoral zone with its macrophytes 140 years ago, ensuring fish with more hiding and feeding places.

Equally acceptable, however, could well be another explanation – the elimination or summer depression of the populations of those species which were more susceptible to interference by net algae, dominated by blue-greens, and the resulting increase in populations of smaller filter feeding species, both requiring higher available food concentrations and being more resistant to algal blooms due to their lower, upper size limit of particles grazed. While the decisive changes in the net algae concentration of 140 years ago is proved by K e r f o o t (1974) himself, so his reasoning on the increase in pressure of fish on zooplankton is based exclusively on unconvincing, indirect evidence. In order to make a judgement as to which of these two explanations makes a better guess, it would be necessary to get information on, besides the pressure of planktivorous fish, the filtering rates and food-size selection of cladoceran species currently residing in Frains Lake.

Similar long-term changes in cladoceran species composition were described on the basis of paleolimnological data by G o u l d e n (1964) for Esthwaite Water in England and were interpreted as the result of this lake's eutrophication. Again in this case it would seem that the replacement of *Bosmina coregoni* by *B. longirostris*, as well as a domination switch of a larger *Daphnia* by a smaller *Daphnia* species, could have been caused by an increase in numbers of large algae rather than by the increase in pressure of planktivorous fish selecting the large crustacean forms.

The same explanation might also be thought as applicable to the shift in domination from the larger to smaller filter feeding species during the eutrophication of lakes observed during the last decades, especially of those lakes in which these shifts cannot be explained exclusively by the increase in pressure of planktivorous fish, e.g., in Lake Michigan (G a n n o n 1972).

It is beyond doubt that in most cases lake eutrophication is accompanied by decrease, not increase in the pressure of planktivorous fish on zooplankton due to the withdrawal of salmonid species. In European lakes these are primarily vendace (*Coregonus albula*) and other whitefish species, regarded as the only planktivorous fish feeding in the limnetic zone. This is also confirmed by P a t a l a s (1954, p. 80) for 28 lakes in northern Poland – vendace occurs in all the lakes of his first group, in some lakes of his second group, and in none of the most strongly eutrophicated lakes of his third group. Therefore, if according to B r o o k s and D o d s o n 's (1965) hypothesis, this factor is to be of significance, then, rather than cause, it would counteract the observed changes in filter feeding species domination.

Bosmina longirostris seems to be more susceptible than *B. coregoni* to net algae and other large particles, which could interfere in filtration. It occurs in high numbers in the shallow littoral waters (also in Mikołajskie Lake – G l i w i c z and R y b a k – in press), where large concentrations can be found of detrital suspension raised from the bottom, and of filamentous algae ripped off the periphyton by wave action. This species is also observed in summer in the limnetic zone of eutrophic lakes (including those in the third group of P a t a l a s (1954) and Mikołajskie Lake) and dystrophic lakes. In the dystrophic Drowned Bog Lake, Ontario, this species appears as decisively dominating, its numbers reaching 3,000 ind. $\cdot l^{-1}$ (H a n e y 1973). Its filtering rate in this lake, similarly to the filtering rate of the also abundant *Diaphanosoma brychyurum*, remains at the same level as in the eutrophic Heart Lake, while the filtering rate of *Daphnia parvula* in Drowned Bog Lake is several times lower than in Heart Lake (cf. results of ·H a n e y 1973, pp. 110 and 118). The higher resistance of *B. longirostris* to interfering particles may well be due not to a low upper grazed particle size limit but to a

distinctive shape of modified II antennae, which form two stiff adventrally directed excrescences, being possibly of some use as a protective morphological adaptation to environments containing high concentrations of interfering particles. These antennae, although usually shorter than those of *B. coregoni*, are more distinctively bent towards the carapace margins (cf. e.g., Figs. 148 and 149 with Figs. 151 and 152 in M a n u j l o v a 1964), forming a sort of natural pre-crevice barrier, on which larger, particularly elongated, particles can be withhold when approaching in the animal induced current. It would be worth-while to check in this species the seasonal changes in II antennae positioning in respect of the carapace margins in the eutrophic, "algal blooming" Frains Lake, where K e r f o o t (1975) did observe their significant shortening during the summer.

4.8. Inhibition of filtration and zooplankton species diversity

According to older conceptions of L i t y ń s k i (1925) and B o w k i e w i c z (1938), as to recent ideas of M a r g a l e f (1968), the number of species as well as the species diversity of the zooplankton should progress from the eutrophic to the oligotrophic end of the trophy spectrum, since it is also in this direction that all other indices of planktonic community maturity progress (M a r g a l e f 1968). It seems that in accordance with the mentioned (Subsection 4.3) model of Gause (1935 after S l o b o d k i n 1963), this is the same direction of the increasing pressure of planktivorous fish, allowing an ever increasing number of competitively weaker species, the more so if like in B r o o k s and D o d s o n 's (1965) hypothesis they are less susceptible to predation. However, analyses of species diversity (Shannon-Weaver formula) of either entire zooplankton crustacean communities (G i l a r o v 1972) or restricted to filter feeding crustacean communities (S t e r z y ń s k a 1976) do not show any significant trend to increase from the eu- to the oligotrophic end of spectrum.

It should, therefore, be deemed that such a trend must be counteracted by some other tendency. It seems plausible to suggest that this counteracting tendency, modifying the final picture, could be the very increase in net phytoplankton biomass in the reverse direction, i.e., towards the eutrophic end of the spectrum. An increase in net interfering algae concentrations does, it is true, inhibit and eventually eliminate many filter feeding species, but, on the other hand, it allows the appearance of other species (e.g., *Diaphanosoma brachyurum* or *Chydorus sphaericus*), which would otherwise remain competitively weaker in view of their less efficient food collection and would have no chance to build up numerous and persisting populations.

The effect of this factor can, therefore, be in principle the same as of selective predation modifying the final result of interspecific competition. It is also possible that this factor is co-responsible for the characteristic size distribution of all contemporary cladoceran planktonic species (higher frequency of smaller forms), which according to A l l a n 's (1974) model analysis seemed to be the result of the combined effect of species' competitive strength (higher in larger forms) and of species' ability to avoid predation (higher in smaller forms). It might be so as overall the smaller forms are also less susceptible than the larger forms to the inhibiting interference by net phytoplankton.

5. CONCLUSION

The influence of phytoplankton upon the demography and productivity of planktonic animal populations ought to be not only considered in terms of the positive effect of phytoplankton as the animals' food source, but also in terms of its negative effect on animals.

The first aspect is primarily associated with nannophytoplankton and the trophic structure of the system, the second with net phytoplankton and the paratrophic[9] structure of the system.

In both aspects (through both structures) various filter feeding species are affected in various degree by phytoplankton. The selective inhibitory effect of large concentrations of net phytoplankton can act as an important factor modifying the result of competition between the more and less efficient filter feeding species. None the less, however, just as the effect of selective predation, this may also in the future turn out to be just one of many biotic factors which together combined produce the final result of competition between zooplankton species.

6. SUMMARY

For many years in Mikołajskie Lake the same sequence has been observed of seasonal succession in filter feeding zooplankton species: spring increase in populations of *Daphnia cucullata* (*Dc*), *D. longispina* (*Dl*), *Bosmina coregoni* (*Bc*) and *Eudiaptomus graciloides* (*Eg*), reaching their peaks in June; summer decline of this populations coinciding with an increase in the populations of *Diaphanosoma brachyurum* (*Db*) and *Chydorus sphaericus* (*Cs*); and autumn return of abundant populations of the former species accompanied by the disappearance of the latter species.

Measurements of the filtering rates (F) of various size particles by all these species, carried out from May to October, 1973, show that *Dc*, *Dl*, *Bc* and *Eg* have a significantly higher upper size limit of particles grazed than *Db* and *Cs* have (cf. Figs. 1—4, left-hand side, and Fig. 5). This is partly conditioned by the different, for various cladoceran species, carapace crevice width in its anterior part through which water with food particles is sucked into the filtering chamber (Figs. 1—4, right-hand side). Since the filtering rate of *Db* and *Cs* is not higher than that of other species (even when individuals of the same size are compared), it can be expected that *Db* and *Cs* need higher concentrations of available food, in order to attain, with their lower upper size limit of particles grazed, the same feeding rate as other species, for which also larger food particles are available. This is probably the reason why, with a lower food concentration in spring and autumn, the species with a more effective filtration dominate (larger amount of food filtered from each volume unit of water pumped through the filtering chamber), i.e., *Dc*, *Dl*, *Bc* and *Eg*.

The filtering rates, averaged for particles of the 0—15 μm range (F), are for the "efficient" cladoceran species (*Dc*, *Dl*, *Bc*) close to their optima in spring and autumn, but they fall significantly below their optima is summer (Fig. 7), when there is a high concentration of net phytoplankton forms (Fig. 9), primarily blue-greens and peridinians, capable of interfering mechanically with these cladocerans' filtration. The summer F reduction is accompanied by a drop in daily egg production (P_e) in the efficient species, consequently leading to the decline in their populations (Fig. 8). A summer F reduction is, however, not observed in the

"inefficient" species, i.e., Db and Cs (Fig. 7), which most probably is connected with a narrow gap between their carapace margins not letting the interfering algae in. Their daily egg production (P_e) does not decrease, on the contrary it is highest in summer allowing for successful population growth in this time (Fig. 8).

Thus, while the efficient (because of their higher upper size limit of particles grazed) species are more susceptible to interference by net algae and less sensitive to low available food concentrations, so the inefficient (due to their lower upper size of particles grazed) species are limited rather by low available food concentrations than by high net algae concentrations.

The same results from an analysis of the dependence of daily egg production (P_e) and individual production ($P_{ind.}$) on changes in the concentrations of algal and non-algal food and in numbers and biomass of various forms of net phytoplankton, taken for 1966 (cf. Figs. 10, 11). This is supported by a stepwise multiple regression analysis, where P_e and $P_{ind.}$ of various species in a period of fairly constant mean epilimnetic temperature (14 June-23 August, Fig. 11) were treated as variables dependent on several independent variables, these being nannophytoplankton biomass (B_n), increase in non-algal organic matter (ΔNOM), blue-green biomass, filamentous blue-green concentration, and biomass or numbers of other net phytoplankton forms (Fig. 12, Table III).

In view of all these facts the net phytoplankton concentration seems to be a selectively working factor, modifying the final result of competition between the more and less efficient filter feeding species. Similarly to selective predation, it seems to have a greater limiting influence on competitively stronger species, enabling the appearance and persistence of the competitively weaker species. In the eutrophic Mikołajskie Lake this takes place during the summer algal blooms.

The same mechanism appears to be responsible for the changes in zooplankton species composition in the lake trophy spectrum from its oligo- to its eutrophic end. The domination of inefficient filter feeding species. such as *Diaphanosoma brachyurum* or *Chydorus sphaericus*, seems to be possible only in eutrophic lakes, from where the more efficient *Daphnia* and *Eudiaptomus* species withdraw due to the blooms of interfering net phytoplankton forms.

7. POLISH SUMMARY (STRESZCZENIE)

W Jeziorze Mikołajskim obserwuje się co roku tę samą, typową dla jezior eutroficznych, sekwencję sezonowych zmian dominacji gatunków filtrujących zooplanktonu: wiosenny rozwój populacji *Daphnia cucullata* (*Dc*), *D. longispina* (*Dl*), *Bosmina coregoni* (*Bc*) i *Eudiaptomus graciloides* (*Eg*), osiągających szczyt liczebności w czerwcu, letnią redukcję liczebności tych populacji i rozwój liczebnych populacji *Diaphanosoma brachyurum* (*Db*) i *Chydorus sphaericus* (*Cs*), wreszcie jesienny ponowny rozwój populacji tych pierwszych gatunków, któremu towarzyszy zanik populacji tych ostatnich.

Z pomiarów tempa filtracji (*F*) cząstek różnych wielkości przez wymienione gatunki, przeprowadzonych od maja do października 1973 roku, wynika, że *Dc*, *Dl*, *Bc* i *Eg* mają znacznie szersze spektrum wielkości odfiltrowywanych cząstek (większe wymiary maksymalnych cząstek dostępnych jako pokarm) niż *Db* i *Cs* (por. lewą stronę fig. 1–4 i fig. 5). Wiąże się to m. in. z różną u różnych gatunków wioślarek szerokością brzusznej szczeliny karapaksu w jej przedniej części, przez którą zasysana jest do komory filtracyjnej woda wraz z cząstkami pokarmu (prawa strona fig. 1–4). Ponieważ tempo filtracji *Db* i *Cs* nie jest większe niż tempo filtracji innych gatunków (nawet gdy porówna się osobniki o tych samych rozmiarach), można sądzić, że *Db* i *Cs* potrzebują większych koncentracji dostępnego pokarmu, by przy węższym spektrum wielkości odfiltrowywanych cząstek uzyskać tę samą rację pokarmową, co inne gatunki, dla których dostępne są również większe cząstki pokarmu. Dlatego też przy mniejszej koncentracji pokarmu wiosną i jesienią dominują gatunki o bardziej efektywnej filtracji (większa masa pokarmu odfiltrowana z jednostki objętości przepompowanej przez komorę filtracyjną wody) – *Dc*, *Dl*, *Bc* i *Eg*.

Z tych samych pomiarów tempa filtracji (*F*) wynika również, że wartości *F* gatunków „efektywnych" są bliskie optimum wiosną i jesienią, natomiast stają się znacznie niższe od optymalnych latem (fig. 7), gdy w środowisku pojawiają się licznie duże formy fitoplanktonu (fig. 9), przede wszystkim sinice i bruzdnice, które mechanicznie zakłócać mogą proces filtracji. Tej letniej redukcji *F* towarzyszy spadek intensywności rozrodu (*P_e*) u gatunków „efektywnych" a – w konsekwencji – redukcja liczebności ich populacji (fig. 8). Letniej redukcji *F* nie obserwuje się natomiast u gatunków „nieefektywnych" – *Db* i *Cs* (fig. 7). Nie spada też intensywność rozrodu tych gatunków, wręcz przeciwnie – jest ona największa latem, co sprzyja letniemu wzrostowi liczebności ich populacji (fig. 8).

O ile więc gatunki „efektywne" (ze względu na swe szerokie spektrum wielkości dostępnych cząstek

pokarmu) są bardziej wrażliwe na zbyt duże koncentracje fitoplanktonu sieciowego i mniej wrażliwe na niskie koncentracje pokarmu, o tyle gatunki „nieefektywne" (ze względu na wąskie spektrum wielkości dostępnych cząstek pokarmu) są ograniczane raczej przez niskie koncentracje pokarmu niż przez wysokie koncentracje fitoplanktonu sieciowego.

Wynika to również z analizy zależności sezonowych zmian intensywności rozrodu (P_e) i tempa wzrostu osobników ($P_{ind.}$) od zmian koncentracji zielonego i niezielonego pokarmu oraz koncentracji różnych form dużych glonów sieciowych w 1966 roku (por. fig. 10, 11). Świadczą o tym wyniki regresji wielokrotnej, w której P_e i $P_{ind.}$ różnych gatunków, z okresu dość stabilnej temperatury średniej epilimnionu (14 VI–23 VIII, patrz fig. 11), potraktowano jako zmienne zależne od szeregu zmiennych niezależnych – biomasy nannofitoplanktonu, produkcji pokarmu niezielonego, biomasy sinic, liczebności sinic nitkowatych, oraz biomasy lub liczebności innych sieciowych form fitoplanktonu (fig. 12, tab. III).

W świetle przedstawionych powyżej faktów koncentracja fitoplanktonu sieciowego wydaje się wybiórczo działającym czynnikiem modyfikującym wynik konkurencji pomiędzy bardziej i mniej efektywnymi gatunkami filtratorów. Podobnie jak wyspecjalizowany drapieżca działa on ograniczająco mocniej na silniejsze konkurencyjnie gatunki umożliwiając wystąpienie gatunkom konkurencyjnie słabszym. W eutroficznym Jeziorze Mikołajskim występuje to w czasie letnich zakwitów glonów.

Ten sam mechanizm wydaje się również odpowiedzialny za zmianę składu gatunkowego zooplanktonu w szeregu jezior od oligo- do eutrofii. Dominacja takich form „nieefektywnych" filtratorów, jak *Diaphanosoma brachyurum* lub *Chydorus sphaericus* w jeziorach eutroficznych jest prawdopodobnie możliwa dzięki eliminowaniu z tych środowisk różnych gatunków rodzajów *Daphnia* i *Eudiaptomus* przez „zakwity" glonów sieciowych.

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