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STUDIES ON THE FEEDING OF PELAGIC ZOOPLANKTON
IN LAKES WITH VARYING TROPHY

In field and laboratory experiments a decided dominance of bacteria has been found in the zooplankton food in eutrophic lakes while in lakes near to oligotrophy — nanoplanktonic algae prevail, although the share of bacteria is also quite considerable. The food composition of zooplankton depends on one hand on the species composition of communities: dominance of macrofiltrators (lakes near to oligotrophy) or microfiltrators and sedimentators (eutrophic lakes), and on the other hand — on the share of nanoplankton in the total primary production of pelagial (it is greater in lakes of lower trophy). The efficiency of using the primary production by planktonic consumers in pelagial of lakes with varying trophy is discussed.

The aim of the work is to characterize the food composition of pelagic zooplankton in some lakes of various trophic type. The role of phytoplankton, bacteria and organic tripton have been analyzed in the feeding of plankton communities of primary consumers (filtrators and sedimentators).

A survey of literature on the feeding of zooplankton (Gliwicz 1969b) shows that zooplankton food ordinarily has a complex character and that phytoplankton does not have to be at all its main, dominant component. The more so, that large phytoplankton forms (the so-called net phytoplankton) are not accessible as food for the majority of plankton species of crustaceans and

rotifers. As there is no active food selectivity (preference) not only small algae (nannophytoplankton) are intensively grazed out of the environment but also bacteria and organic tripton – dead organic matter in the form of particulate remains of animals, plant, bacteria (detritus) or coagulums of dissolved organic matter. However there is no direct information available in literature about the share of alive planktonic algae, bacteria and tripton in the food of zooplankton. Information on this subject has been mostly obtained indirectly and therefore it does not have a quantitative character (investigations on the number dynamics of zooplankton and its potential food) or concerns only single species (analysis of gut contents, observations on the feeding mechanism) and is in general difficult to explain because of the simplified food conditions, in which they have been obtained (cultures on chosen kinds of food, experimental determining of the filtering rate, feeding rate and assimilation). Such information seems to be essential from the standpoint of efficiency in using the primary production by planktonic consumers. Thus it is not meaningless, which part of primary production is directly used by planktonic consumers in the form of alive algae, and which part comes to these animals indirectly through bacteria and tripton, what in connection with the energy losses on numerous destruction levels must lower considerably this efficiency in using the primary production by consumers.

The results presented in this paper were obtained during investigations carried out in the years 1963–1966, in six lakes representing various trophic types. They based on: 1) analysis of the food of dominant crustacean and rotifer species (examining the gut contents) and estimations of their food selectivity (laboratory experiments), 2) analysis of food selectivity and food composition of natural zooplankton communities of several lakes (field experiments). A report of the most important results of this research has been already published (Gliwicz 1969c).

I. CHARACTERISTIC OF THE INVESTIGATED LAKES

Investigations were carried out on six lakes of the Mazurian Lake District. Characteristic of the investigated lakes is presented in Table I and Figure 1.

The chosen lakes were similar in size and morphometry but at the same time differential to maximum with regard to trophy in the classical meaning of the word (Thienemann 1918, 1925, Naumann 1931, Findenegg 1955) i.e. lakes greatly differentiated as far as the resources of mineral salts were concerned. The definition of the trophic type of lakes according to Stangenberg's (1936) classification is based on the materials of Thienemann

Some morphometric and typological features of investigated lakes

Tab. I

Lake	Trophic type* acc. to Stangen- berg's classifi- cation (1936)	Eleva- tion above sea le- vel** (m)	Area** (ha)	Maxi- mum depth** (m)	Depth of epili- mion (m)	Area of the active bottom in % of total bottom area	Secchi disc reading (m)		Gross primary production of pelagial*** (in mg O ₂ /l/day)		
							July 1966	August 1966	July 1966	August 1966	Ave- rage
Mikołajskie	eutrophy	116	470.0	27.8	8	34.6	3.0	3.0	0.76	0.72	0.74
Tały	eutrophy	116	762.0	51.0	10	32.3	3.5	3.5	0.65	0.51	0.58
Tałtowisko	β-mesotrophy	116	326.9	39.5	8	38.7	4.5	4.5	0.67	0.34	0.50
Piłakno	α-mesotrophy	143	278.7	52.0	7	30.6	8.0	8.0	0.21	0.13	0.17
Mamry-Przystań	α-mesotrophy	116	500.4	43.8	10	36.4	7.5		0.07	0.32	0.19
Wukśniki	α-mesotrophy- -oligotrophy	118	125.0	66.5	8	21.3	8.5				

*acc. to data of Thienemann (1925), Goldbeck (1937), Olszewski (1951), Olszewski and Paschalski (1959), and Paschalski and Szczepański (unpublished data).

**acc. to The Catalogue of Polish Lakes (1954).

***acc. to Gliwicz (1967b), material obtained by the oxygen method of dark and light bottles in situ; the mean of 10 repetitions on 10 levels from the surface to the depth equal to the Secchi disc reading.

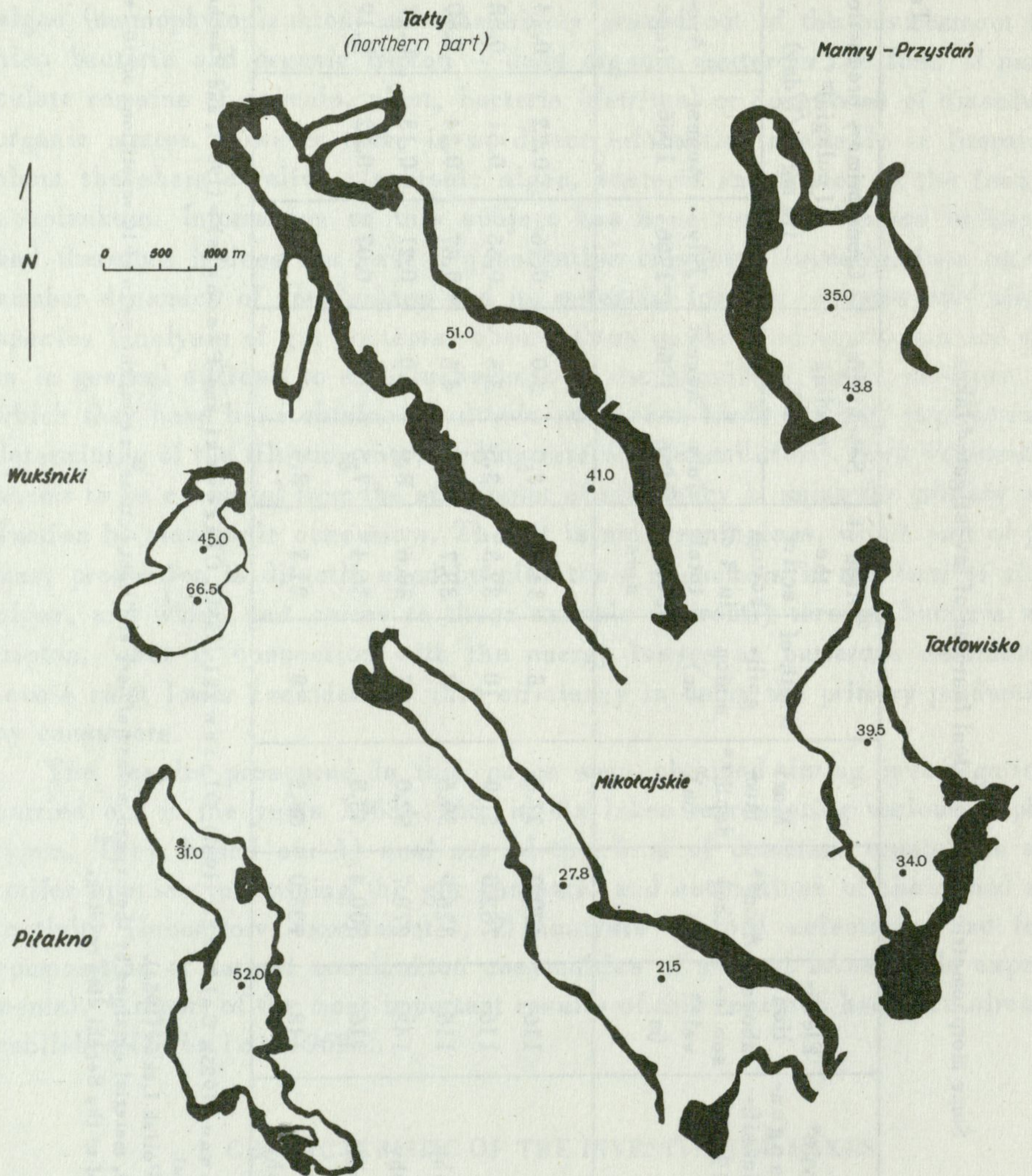


Fig. 1. Bathymetry of investigated lakes and the area of "active bottom" in these reservoirs (darkened)

(1925), Goldbeck (1937), Olszewski (1951), Olszewski and Paschalski (1959), Paschalski and Szczepański (unpublished data) and also on own author's observations of oxygen stratification (Fig. 2).

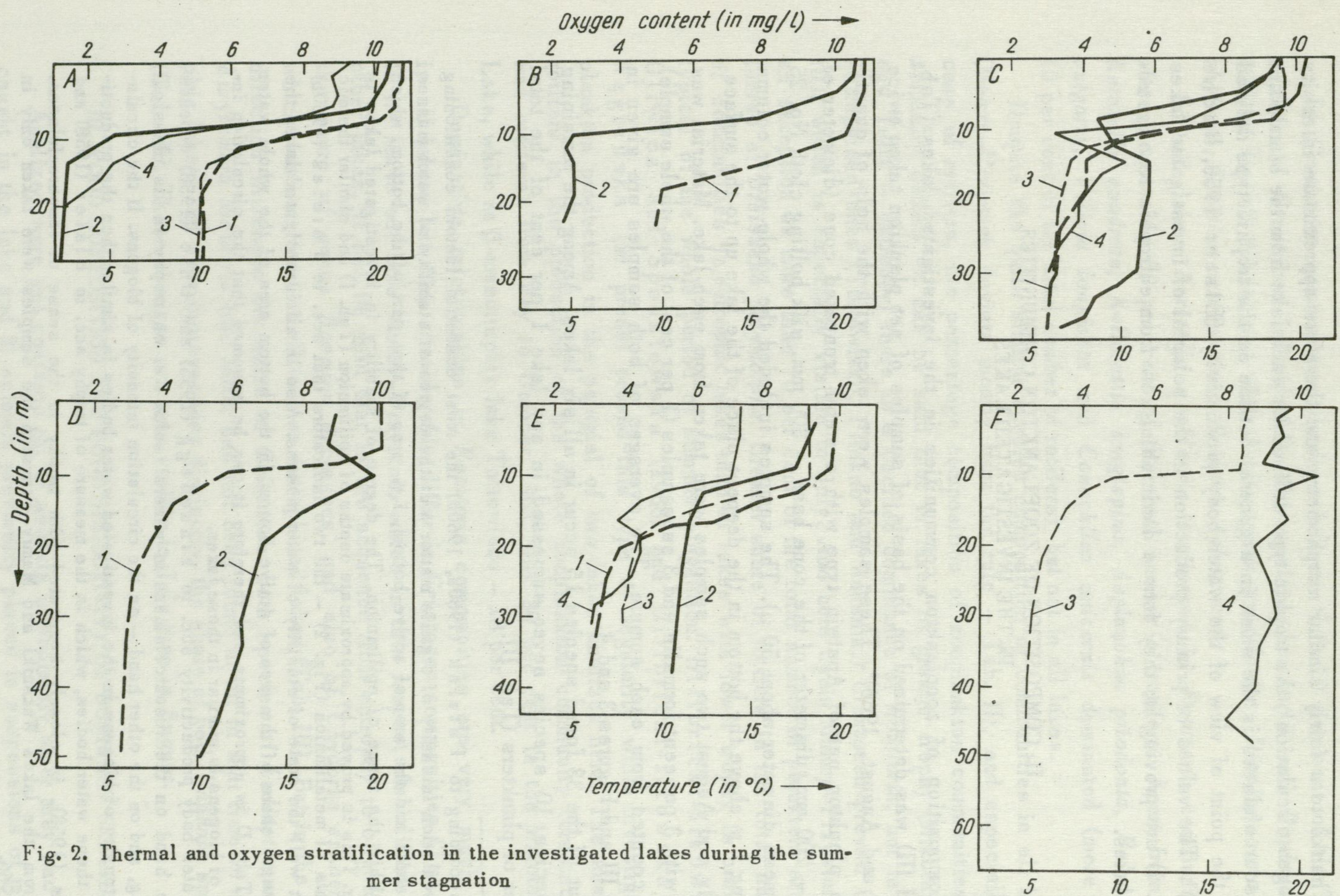


Fig. 2. Thermal and oxygen stratification in the investigated lakes during the summer stagnation

1 — thermal stratification acc. to the author's own measurements, 2 — oxygen stratification acc. to the author's own measurements, 3 — thermal stratification acc. to Paschalski's measurements (unpublished data), 4 — oxygen stratification acc. to Paschalski's measurements (unpublished data)
 A — Mikołajskie, 30 VIII 1966 (1, 2) and 5 VIII 1958 (3, 4), B — Tały, 1 VIII 1966, C — Taktowisko, 3 VIII 1966 (1, 2) and 9 VIII 1958 (3, 4), D — Piłakno, 6 VIII 1966, E — Mamry-Przystań, 10 VIII 1966 (1, 2) and 5 VIII 1957 (3, 4), F — Wukśniki, 28 VIII 1957

Thanks to a fairly similar morphometry and therefore approximate intensity of biogen circulation¹, the trophic type defined for each lake from the standpoint of resourcefulness is the same in a general outline as the trophic type defined from the point of view of the water body productivity (Elster 1958, Rodhe 1958)². The values of primary production in the pelagial of investigated lakes (Tab. I) are proving it; they form a diminishing row from eutrophic to oligotrophic lakes.

II. COMPOSITION OF ZOOPLANKTON COMMUNITIES IN THE INVESTIGATED LAKES

Composition of zooplankton communities in the investigated lakes (Tab. II and III) was determined on the basis of samples of net plankton taken twice (July and August, 1966)³. These samples were taken with the help of quantitative plankton net of Apstein type with a metal truncated cone (diameter of inlet – 200 mm, diameter of the cone base – 300 mm, silk bolting cloth No. 25 with mesh diameter about 50 μ). The samples included the whole water column starting 1 m above the bottom in the deepest place of the lake up to the surface. In July and August two such samples were taken from each lake. Material was fixed with 3 per cent formalin and 3 subsamples (1 per cent of the whole sample) were counted from each sample. The averages of both samples are given in Table III and Figures 3 and 4.

Out of the 33 found species 15 occur in all six lakes. Among the remaining 18 species 10 species never surpassed in any lake 1 per cent of the total number of plankters (Tab. II).

¹According to Patalas (1960a, 1960b) the most essential factors conditioning the circulation intensity of organic matter are: the degree of stability of water masses in the lake and the area of active bottom, i.e. area of that part (of the bottom, which lies within the range of epilimnion. The degree of stability in investigated lakes is similar. This is proved by approximate depths of epilimnion (Tab. I) and similar thermic gradients of metalimnion (Fig. 2) – the two indicators that acc. to Patalas (1960b) present well the state of stability of water masses. Also in all investigated lakes the percentage share of the area of active bottom in the bottom area of the whole water body (Tab. I) is approximate and therefore it can be assumed that the circulation intensity of biogens is similar in these lakes.

²Water body productivity acc. to Findenegg (1955) and Ohle (1958) depends on one hand on the resourcefulness in mineral salts i.e. on trophy in its classical meaning, and on the other hand – on the circulation intensity of biogens. If the circulation intensity of biogens in the investigated water bodies is similar then the productivity of these water bodies, which is the measure of trophy acc. to Elster (1958) and Rodhe (1958), is closely connected with trophy in the sense of resourcefulness.

³From the lakes Wukśniki and Mamry-Przystań the samples were taken only in July, 1966.

In *Crustacea* communities dominated (more than 10 per cent of the total number of *Crustacea* individuals): *Mesocyclops leuckartii* and *Daphnia cucullata* (in all lakes) and also *Eudiaptomus graciloides*, *Diaphanosoma brachyurum*, *Bosmina coregoni* and *Chydorus sphaericus*.

In all lakes *Keratella cochlearis* dominated in *Rotatoria* communities, often surpassing 50 per cent of the total number of rotifers. Apart from that *Keratella quadrata*, *Kellicottia longispina*, *Asplanchna priodonta*, *Polyarthra vulgaris*, *Filinia longiseta* and *Conochilus unicornis* dominated (more than 10 per cent of the total number of rotifers), but not in all lakes.

Despite the quite similar species composition of communities in all lakes (Mamry–Przystań deviate mostly from the rule – Tab. II), and especially in case of rotifers, the percentage composition of zooplankton communities essentially differs. It can be said that in lakes of greater trophy (Mikołajskie and Tałty – eutrophy) there is a decided dominance of *Rotatoria*, but in less eutrophized ones (Tałtowisko, Piłakno and Wukśniki) *Crustacea* prevail (Tab. III), which is especially visible in July. And here again Mamry–Przystań are an exception as more than 70 per cent of the total number of plankters are the larvae of *Dreissena polymorpha*. Greater share of rotifers in the total number of communities in eutrophic lakes than in lakes with lower trophy is probably typical of the whole period of summer stagnation. Hillbricht-Ilkowska, Gliwicz and Spodniewska (1966) and Hillbricht-Ilkowska and Węgleńska (in press) proved this type of regularity while investigating plankton production in the pelagial of two lakes analyzed here. The share of rotifers in the production of the whole zooplankton community (crustaceans and rotifers) from May to October 1963, was 30 per cent in the Mikołajskie Lake, while in β -mesotrophic lake Tałtowisko – 18 per cent.

Dominative relationships in *Rotatoria* communities are very much alike in all lakes, but they considerably differ in *Crustacea* communities (Tab. III). If we leave out lake Mamry–Przystań, which in this respect also differs from other lakes, it can be said that in the sequence from eutrophy to oligotrophy the share of genus *Bosmina* decreases, and also of *Chydorus sphaericus*, which was not found at all in less eutrophized lakes (Tab. III). But in the same direction increases the share of *Calanoida*: both species of *Eudiaptomus* and *Eurytemora lacustris* (the latter has not been found at all in that time in eutrophic lakes) and also, however less distinctly, the share of both *Daphnia* species (Tab. III). These changes are less visible in July than in August.

III. FOOD COMPOSITION AND FOOD SELECTIVITY OF DOMINANT SPECIES

Analyzed were gut contents of: 1) animals immediately after they had been caught in the lake and 2) animals previously placed in suspensions of mineral

List of species found in the net zooplankton of the investigated lakes

+++ greater share, + smaller than 1% of the total number of individuals

Tab. II

Group and species			Lake					
			Mikołaj- skie	Tały	Tałow- wisko	Piżakno	Wuk- śniki	Mamry- -Przy- stań
Copepoda	Diaptomidae	<i>Eudiaptomus gracilis</i> (Sars)	+++	+++	+++	+	+++	
		<i>E. graciloides</i> (Lilljeborg)	+++	+++	+++	+++	+++	+
	Temoridae	<i>Eurytemora lacustris</i> (Poppe)		+	+	+++	+++	
	Cyclopidae	<i>Eucyclops serrulatus</i> (Fischer)	+	+		+		
		<i>Cyclops strenuus</i> s. lato Fischer	+	+	+		+	
<i>Acanthocyclops viridis</i> (Jurine)		+	+					
<i>Mesocyclops leuckarti</i> (Claus)		+++	+++	+++	+++	+++	+++	
		<i>M. oithonoides</i> (Sars)	+++	+++	+++	+++	+++	
Cladocera	Sididae	<i>Sida crystalina</i> (O.F. Müller)	+		+			
		<i>Diaphanosoma brachyurum</i> Lièvin	+++	+++	+++	+++		+
	Daphnidae	<i>Daphnia longispina</i> O.F. Müller	+++	+	+	+	+	
		<i>D. cucullata</i> Sars	+++	+++	+++	+++	+++	+++
		<i>Ceriodaphnia quadrangula</i> (O.F. Müller)	+		+	+		
	Bosminidae	<i>Bosmina longirostris</i> (O.F. Müller)	+++	+++	+++	+	+++	+
<i>B. coregoni</i> Baird		+++	+++	+++	+++	+++	+	
Chydoridae	<i>Chydorus sphaericus</i> (O.F. Müller)	+++	+++	+				
Leptodoridae	<i>Leptodora kindtii</i> Focke	+++	+	+	+	+	+	

Rotatoria	Brachionidae	<i>Brachionus angularis</i> Gosse	+				+	
		<i>Keratella cochlearis</i> (Gosse)	+++	+++	+++	+++	+++	+++
		<i>K. quadrata</i> (Müller)	+++	+++	+++	+++	+++	+++
		<i>Kellicottia longispina</i> (Kellicott)	+++	+++	+++	+++	+++	+++
	Trichocercidae	<i>Trichocerca tigris</i> (Müller)	+	+		+	+	
		<i>T. capucina</i> (Wierzejski et Zacharias)	+					
	Gastropodidae	<i>Gastropus stylifer</i> Imhof	+	+		+		
		<i>Chromogaster testudo</i> Lauterborn	+	+		+		
Asplanchnidae	<i>Asplanchna priodonta</i> Gosse	+++	+++	+++	+++	+++	+++	
Synchaetidae	<i>Synchaeta pectinata</i> Ehrenberg			+				
	<i>Polyarthra vulgaris</i> Carlin	+++	+++	+++	+++	+++	+++	
Testudinellidae	<i>Pompholyx sulcata</i> Hudson	+		+				
Filinidae	<i>Filinia longiseta</i> (Ehrenberg)	+++	+++	+++	+++	+++	+++	
Conochilidae	<i>Conochilus unicornis</i> Rousselet	+++	+++	+++	+++	+++	+++	
<i>Dreissena polymorpha</i> Pall. larvae				+	+++	+++	+++	+++
<i>Chaoborus</i> sp. larvae			+	+				

Composition and number of zooplankton communities in the investigated lakes in July and August 1966

In frames — date of experiment

Tab. III

Elements compared		July 1966					August 1966				
		Mikołajskie eutrophy (9 VII)	Tały eutrophy (10 VII)	Tałtowski β -mesotrophy (11 VII)	Piłakno α -mesotrophy (5 VII)	Wukśniki α -mesotrophy-oligotrophy (8 VII)	Mamry—Przystań α -mesotrophy (12 VII)	Mikołajskie eutrophy (2 VIII)	Tały eutrophy (3 VIII)	Tałtowski β -mesotrophy (4 VIII)	Piłakno α -mesotrophy (7 VIII)
Number of plankters under 1 dcm ² of area		72,000	114,000	16,000	24,000	22,000	75,000	26,000	99,000	18,000	16,000
Mean number of plankters in 1 l of water in the lake		268	224	42	47	40	172	94	195	46	31
Mean number of plankters in 1 l of lake water isolated in experimental chambers		433	450	148	181	150	398	260	203	178	142
Share of sedimentators (<i>Rotatoria</i>) in zooplankton communities (in % of the total number of plankters)		70.7	61.3	26.0	42.0	37.7	21.1	58.5	36.9	29.9	32.6
Share of <i>Dreissena polymorpha</i> larvae in zooplankton communities (in % of the total number of plankters)		0	6.3	7.8	11.6	14.1	72.7	0	0	37.3	2.6
Share of dominating filtrator species (<i>Cladocera</i> and <i>Calanoida</i>) in communities of plankton crustaceans (in % of total number of plankton crustaceans)	<i>Chydorus sphaericus</i>	11.8	5.6	0	0	0	0	8.9	18.3	0	0
	<i>Bosmina coregoni</i> and <i>B. longirostris</i>	21.2	18.4	11.9	8.1	11.3	2.8	7.3	22.5	9.5	7.3
	<i>Daphnia cucullata</i> and <i>D. longispina</i>	7.8	17.2	31.1	25.6	23.5	29.5	19.3	12.5	19.5	21.8
	<i>Diaphanosoma brachyurum</i>	1.4	0.9	3.5	0	0	2.8	3.9	0.9	24.8	0.8
	<i>Eudiaptomus gracilis</i> and <i>E. graciloides</i>	11.2	9.4	15.0	15.7	32.8	9.8	19.7	2.5	29.0	27.4
	<i>Eurytemora lacustris</i>	0	0	4.0	4.2	6.9	0	0	0	5.3	4.0

particles having a considerable concentration. First of all the gut contents were analyzed to find out, which seston elements dominate in the gut contents of dominant species. Next — to find out the size of seston particles most intensively caught by these species and the size limits of particles filtrated (sedimentated) out of water.

1. Methods

a. Analyses of gut contents

Systematic analyses of gut contents of rotifers and crustaceans were made on the material from Mikołajskie Lake and lake Tałtowisko in the period from July 15, 1963, to September 1, 1964. During the both periods of summer stagnations the analyses were made 13 times on the material from Mikołajskie Lake, and 10 times — on the material from the lake Tałtowisko; during the winter stagnation — 7 times on the material from Mikołajskie Lake. The gut contents of 10 individuals of each of the momentarily dominating species were examined. These analyses included 7 *Rotatoria* species and 14 *Crustacea* species (Tab. IV). All together the gut contents of 1,560 individuals were examined.

Gut analyses were made under the microscope shortly after the collection in the lake either in the boat or in the laboratory, where the material was transferred in vacuum flasks of 10 litres capacity (lake water with 2–3 times concentrated net plankton).

The gut contents of *Copepoda* and *Rotatoria* (excl. *Asplanchna priodonta*) were analyzed after being exuded by careful pressure exerted on the cover slip acc. to the method described among others by Fryer (1957) for *Copepoda* and Erman (1962) for *Rotatoria*. The gut contents of *Cladocera* were not exuded as the size and shape of food particles is seen at its best in case of these animals in the front gut section of the living animal placed in between the cover and microscopic slide. Regular movements of this gut section cause constant shifting in both directions of food particles loosely distributed between the gutlet and further gut sections, where the food is more compact. Therefore each food particle can be thoroughly looked at from different sides and measured. Similarly in case of *Asplanchna priodonta* the stomach contents were not exuded because of the transparency of its body tissues and mobility of stomach musculature and therefore were observed at their best on living individuals.

Gut analyses of alive animals allowed sometimes to observe directly the swallowing and ingestion.

b. Experimental determination of filtration intensity
of seston particles of various size

In order to determine the size of the most intensively filtrated food particles by the given species, the number of particles different size in environment and in the food of individuals (in gut contents) should be known. In case of natural food it seems to be impossible as the bacteria and algal cells are deformed and stuck together.

Therefore a suspension of hard mineral particles – small grains of siliceous sand and fragments of diatom frustules (ground sand and diatomite) was used. First it has been experimentally found that these particles were consumed by all analyzed species with the same intensity as other organic seston particles. While increasing the concentration of the suspension of mineral particles in lake water, in which the animals were exposed, the percentage of share of these particles in the gut contents increased to almost 100 per cent.

To determine the filtration intensity of particles of different size two experiments (on 26 and 28 October 1965) were carried out on the material from Mikołajskie Lake and are described below.

The sand and diatomite were thoroughly brayed in the mortar, then roasted in muffle furnace at a temperature 600°C (to prevent the sticking together of grains and frustules), and after all that, a concentrated suspension of these grains was prepared in water (in 1 ml about $1 \cdot 10^7$ grains and frustules smaller than 16μ)⁴. When mixed it was added to lake water with natural zooplankton communities in glass vessels of 3 litres capacity (about 3 ml of initial suspension per 1 litre of water). Sedimentation of the suspension was prevented by constant mixing of water in the vessels. After a period of 3–10 hours zooplankton was separated and microscopic analyses of gut contents⁵ were made taking 10 individuals of each species momentarily dominating. Estimates were made of the number of particles of various size found in the guts in classes of size with a difference of 1μ ($< 1 \mu$, $2-3 \mu$ and so on up to $15-16 \mu$; bigger particles were not found in the guts of all 8 analyzed species). Sharp and distinct edges of sand grains and fragments of diatom frustules enabled a precise measurement. During a 10-hour exposure 20 millilitre water samples were taken (after 30 min., and then after 2, 3, 5 and 10 hrs), in which after 24-hour sedimentation the suspension particles were counted in the same classes of size. Knowing the number of particles of various size in the environment during the experiment, and the number of these particles in the

⁴Only smaller grains or equal 16μ were counted; apart from those relatively few bigger grains were present in the suspension.

⁵Time necessary for complete filling of the alimentary canal does not exceed 30 min. in case of *Cladocera* (Šrámek-Hušek 1962); it seems to be not much longer for *Calanoida* and *Rotatoria*.

alimentary canals after a determined time of exposure of animals in the water with the suspension, the size limits of filtrated (sedimentated) particles can be determined for each species, and also it would be known, which of them are most intensively grazed.

Apart from that, on 24 October 1965, an experiment was made with various concentrations of this suspension. In this experiment, also on the material from Mikołajskie Lake, the lake water containing natural zooplankton communities, to which various volumes of initial suspension were added, was exposed. The exposure was identical as that in experiments where the consumption intensity of particles of different sizes was determined. After 3–10 hours of exposure the gut contents were analyzed of 10 individuals of each dominant species, estimating the percentage share of mineral particles in the volume of the whole food.

2. Gut contents of animals sampled directly from the lake

Out of the total number of 1,560 analyzed individuals, representing 21 crustacean and rotifer species, only 132 individuals contained in their alimentary canals remains possible to identify. This is hardly 8.5 per cent of all analyzed individuals.

This per cent is exceptionally high in case of *Asplanchna priodonta* (42.5), which can be explained by the kind of food of this macrophagous species (Tab. IV) and also by the mechanism of feeding on bites of food that despite their large size are swallowed entirely. Out of 34 individuals, which comprised remains possible for identification, 10 contained in their stomachs animal remains or whole cuticles of animals, and as many as 27 individuals – plant cells and colonies (and also faecal pellets of *Copepoda*), which is adequately 29 and 79 per cent. This points to the fact that the species is undoubtedly polyphagous and it contradicts the opinion of Erman (1962), Pourriot (1965) and Sorokin and Morduchaj-Boltovskaja (1962), who consider *A. priodonta* as a typical, however facultative predator, while confirms the opinion of Tribun (1960) and Nauwerck (1963).

Gut contents of other rotifer species most frequently contain a greenish-brownish mush of minute particles, the diameter of which in most cases does not exceed 2 μ , and they are partly brayed or macerated cells of algae or bacteria, or detritus fragments (tripton).

Gut contents of non-predacious *Cladocera* species look similar. Alimentary canals of these species are filled with a mush of minute particles, diameter of which does not exceed 2–3 μ in the majority of cases. Among these particles a small per cent of mineral particles (up to 15 per cent of the whole food) can

Remains of plankton organisms in alimentary canals of various zooplankton species on the basis of microscopic analysis of the material from Mikołajskie and Tałtowisko lakes (July 15, 1963 – September 1, 1964)

Tab. IV

Species	Number of analyzed individuals	Number of individuals in which the found remains could be identified	Identified remains and their greatest linear measures (in μ)
<i>Eucyclops serrulatus</i>	20	—	
<i>Cyclops strenuus</i> s. lato	20	1	fragments of the <i>Cladocera</i> (14)
<i>Acanthocyclops viridis</i>	20	2	fragments of the <i>Cladocera</i> (12, 16)
<i>Mesocyclops leuckartii</i> and <i>M. oithonoides</i>	280	27	fragments of <i>Chlorophyta</i> colonies (3–10), <i>Phacotus</i> sp. (12), fragments of the <i>Dinophlagellatae</i> (4–8), other plant cells (3–5), fragments of the <i>Cladocera</i> (8–14)
<i>Eudiaptomus graciloides</i> and <i>E. gracilis</i>	280	30	fragments of <i>Chlorophyta</i> colonies (4–9), fragment of <i>Eudorina</i> sp. colony (10), <i>Bacillariophyceae-Pennatae</i> (10), fragment of <i>Bacillariophyceae-Centricae</i> colony (16), other plant cells (4–7)
<i>Diaphanosoma brachyurum</i>	150	5	<i>Chlorophyta</i> (7, 13, 15), <i>Bacillariophyceae-Centricae</i> (12), other plant cells (5)
<i>Daphnia cucullata</i> and <i>D. longispina</i>	220	21	<i>Chlorophyta</i> (8, 10, 12), fragment of <i>Eudorina</i> sp. colony (12), fragments of <i>Cyanophyceae</i> colonies (8, 10), <i>Phacotus</i> sp. (11), <i>Bacillariophyceae-Centricae</i> (16), <i>Amphora</i> sp. (14), other plant cells (3, 5)

<i>Ceriodaphnia quadrangula</i>	20	—	
<i>Bosmina coregoni</i> and <i>B. longirostris</i>	210	8	<i>Chlorophyta</i> (7, 13, 14), fragments of <i>Eudorina</i> sp. colonies (12), fragments of <i>Cyanophyceae</i> colonies (6, 8), other plant cells (3, 4)
<i>Chydorus sphaericus</i>	60	1	unidentified plant cells (3)
<i>Leptodora kindtii</i>	20	—	
<i>Brachionus angularis</i>	20	1	fragment of <i>Cyanophyceae</i> colony (5)
<i>Keratella cochlearis</i>	40	—	
<i>K. quadrata</i>	40	—	
<i>Kellicottia longispina</i>	20	—	
<i>Asplanchna priodonta</i>	80	34	<i>Bacillariophyceae-Centricae</i> (10), fragments of <i>Melosira</i> sp. colonies (16–300), <i>Ceratium hirundinella</i> (250), fragments of <i>Anabaena</i> sp. colonies (80–200), fragments of <i>Lingblya</i> sp. colonies (15–120), <i>Bosmina</i> sp. (160–270), <i>Cladocera</i> embryos (140–180), <i>Keratella cochlearis</i> (110–120), <i>Copepoda</i> faeces (105–140)
<i>Polyarthra vulgaris</i>	20	—	
<i>Conochilus unicornis</i>	40	2	<i>Chlorophyta</i> (2, 3)

be distinguished because of their distinct, sharp edges. In the alimentary canals of predacious *Leptodora kindtii*, in connection with the feeding mechanism of individuals from this species (sucking out liquids from the body cavity of the prey – Morduchaj-Boltovskaja 1958), no food particles with a determined shape were found.

In alimentary canals of *Eudiaptomus graciloides* and *E. gracilis* usually a similar, compact mush of minute particles is found, but it does not fill the whole gut and concentrates in its two sections taking the shape of evacuated faecal pellets. Scarcely 11 per cent of analyzed individuals of this species had in their alimentary canals fragments of plant colonies or single algal cells (Tab. IV) possible for identification.

The gut contents of *Cyclopoida* are both from the structural and distribution point of view similar to the gut contents of both *Eudiaptomus* species. Frequently in *Cyclopoida* are found chitin fragments, majority of which can be determined as remains of *Cladocera* cuticles. In both *Mesocyclops* species in guts were also found fragments of plant colonies and single algal cells. Out of the total number of 27 individuals of this species, containing in their guts remains possible for identification, 14 contained remains of plant origin, and 18 – remains of animal origin. This is respectively 52 and 67 per cent and confirms the results of Fryer's investigations (1957), out of which it can be concluded that *M. leuckartii* is a predacious species replenishing its meat diet to a great extent with plants.

The comparable data presented at the beginning of this chapter prove that of 90 per cent of analyzed individuals nothing more can be said about the composition of animals' gut contents than that they are composed of minute seston particles. Therefore it is not possible to determine the role of algae, bacteria and tripton in that way. It seems however, that the kind of food is to some extent determined by the size of particles found in the alimentary canals. If a distinct domination of minute, not exceeding 1–2 μ , particles is found in the gut, a large share of bacteria can be expected in the food, in case of bigger particles – greater share of algae.

3. Maximum size of food particles

The analyzed individuals of dominant species were divided into groups according to the size of the largest food particles found in their alimentary canals (Tab. V). Figure 3 presents the percentage share of these groups in the total number of individuals of the given species.

As the majority of natural food components is destroyed during their filtration (sedimentation) out of water and also when being ingested, these com-

parisons are not perfectly true of the real relationships. They present however, the distinct differences between each species from the point of view of top size limit of grazed particles.

Maximum size of food particles (in μ) in the alimentary canals of crustaceans and rotifers sampled straight from the lake (a) and from lake water with the addition of suspension of sand grains and diatomite (b)

Tab. V

Species	a	b
<i>Eudiaptomus graciloides</i>	16	15
<i>Diaphanosoma brachyurum</i>	15	16
<i>Daphnia cucullata</i>	16	16
<i>Bosmina coregoni</i>	14	14
<i>Chydorus sphaericus</i>	4	5
<i>Conochilus unicornis</i>	4	5
<i>Keratella quadrata</i>	2	3
<i>K. cochlearis</i>	2	3

The following restriction can be placed: individuals of all species do not destroy to the same extent the filtrated (sedimentated) food particles and therefore the maximum sizes of particles found in the gut are not fully comparable. This is especially essential when comparing *Rotatoria* and *Crustacea* as the former grind food in mastaxes and therefore the probability of finding big food particles in their stomachs lessens. However, it should be added, that similar results were obtained also in the experiment where animals were exposed in the suspension of sand grains and diatomite of various dimensions, although the sand grains were swallowed in their entirety. In Table V compared are the maximum sizes of particles found in alimentary canals of crustaceans and rotifers caught directly from the lake, and those exposed in lake water with the addition of above mentioned suspension. In both cases the sizes of the largest particles in guts do not practically differ among themselves.

It has been found that in alimentary canals of crustaceans bigger food particles are more frequently occurring than in the alimentary canals of rotifers (excl. *Asplanchna priodonta*), and that the maximum sizes of particles in rotifers are considerably lower (Fig. 3, Tab. V). This is in conformity with the observations of Remane (acc. to Edmondson 1957), who said that the size of food particles accessible for rotifers depends on the mastax structure, and that rotifers with a malleate type of mastax (also *Keratella*) feed on particles, the size of which does not exceed several microns.

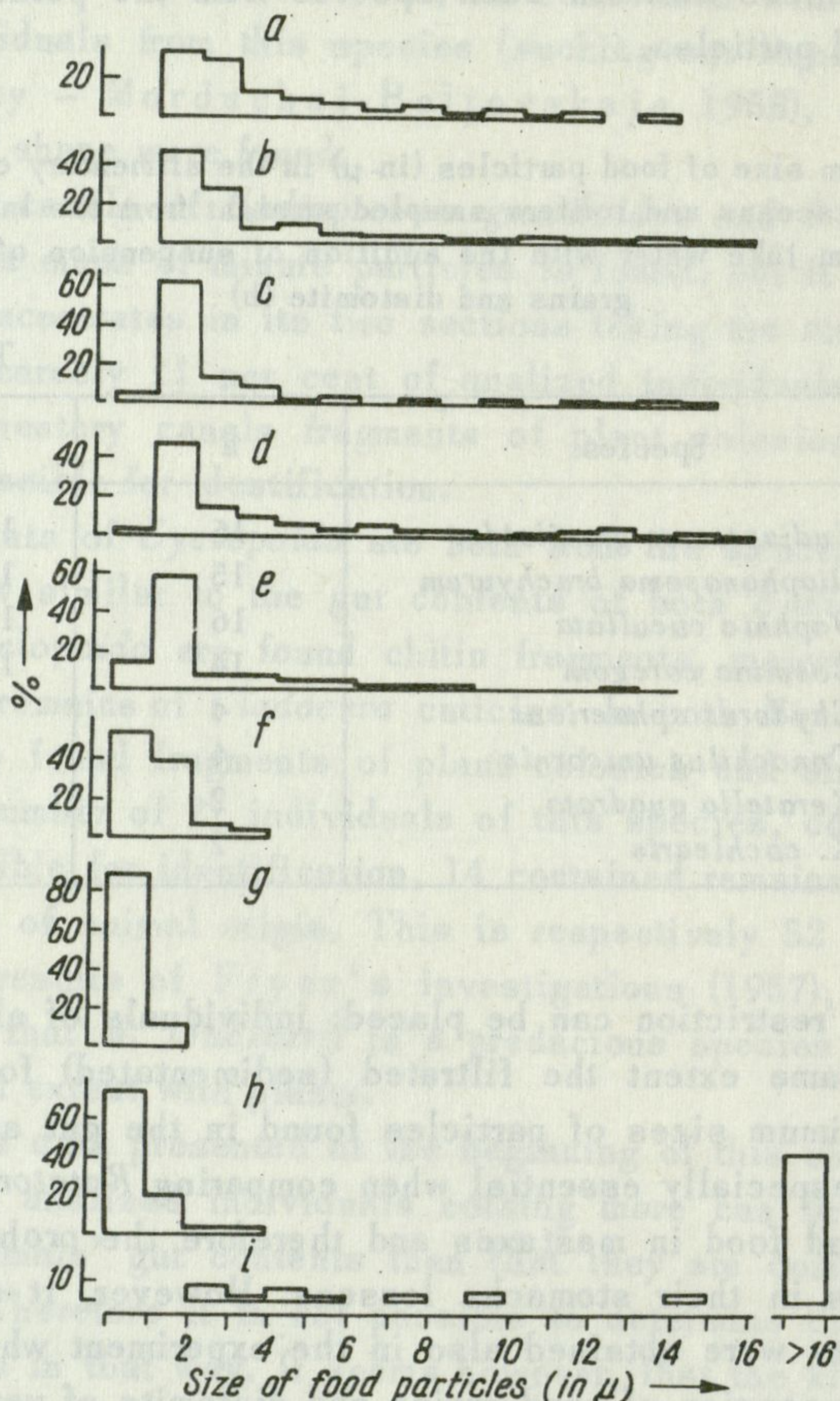


Fig. 3. Maximum size of food particles found in the gut contents of dominating crustacean and rotifer species

Vertical axis: Per cent of individuals with a given size of the biggest particles in the alimentary canals out of the total number of examined individuals of the given species

The greatest linear measure of particles was accepted

a — *Mesocyclops leuckarti* and *M. oithonoides*, b — *Eudiaptomus graciloides* and *E. gracilis*, c — *Diaphanosoma brachyurum*, d — *Daphnia cucullata* and *D. longispina*, e — *Bosmina coregoni* and *B. longirostris*, f — *Chydorus sphaericus*, g — *Keratella cochlearis*, h — *Conochilus unicornis*, i — *Asplanchna priodonta*

Also among crustaceans the size of the biggest, grazed food particles is really different in case of each species. Among the filtrators *Eudiaptomus* is on the first place in this respect (Fig. 3), which corresponds with the common opinion that all species of that genus are considered as macrofiltrators (Malovickaja and Sorokin 1961a, 1961b and others) with a restriction that in

comparison with other species (e.g. *Asplanchna* genus) they are microphags. Further places in respect of the maximum size of food particles have: *Diaphanosoma brachyurum* and *Daphnia* genus, then *Bosmina* genus, and the last one – *Chydorus sphaericus*, in the alimentary canals of which no particles exceeding the linear measure of 5μ were found, and as much as 55 per cent of analyzed individuals did not have in their guts particles exceeding 1μ . It is worth pointing out that *Chydorus sphaericus* is the smallest one of analyzed *Cladocera* species, whereas *Diaphanosoma brachyurum* and both species of *Daphnia* genus – the largest.

4. Food selectivity of dominant species

Results of experiment with an exposure of plankters in various concentrations of the suspension of sand and diatomite (Tab. VI) seem to confirm the common belief about the mechanical, passive character of food selectivity of

Average share of mineral particles in the gut contents of crustaceans and rotifers depending on the number of these particles in the environment

Results for each species on the basis of the estimation of the percentage share of mineral particles in the gut contents volume of 10 individuals; October 24, 1966

Tab. VI

Species	Per cent of mineral particles in the alimentary canals of individuals exposed for 3 hours:							Degree of filling the alimentary canals together with the increase of the concentration of mineral particles:
	in lake water	in lake water with an addition of suspension of sand grains and diatomite (ml/l of water)*						
		0.2	1	3	5	10	20	
<i>Eudiaptomus graciloides</i>	10	40	60	80	85	90	90	decreases
<i>Diaphanosoma brachyurum</i>	15	50	75	85	90	95	95	increases
<i>Daphnia cucullata</i>	15	55	75	90	95	95	95	increases
<i>Bosmina coregoni</i>	10	50	75	85	90	95	95	increases
<i>Chydorus sphaericus</i>	15	50	80	85	90	95	95	increases
<i>Conochilus unicornis</i>		50	70	85	90	95	95	does not change
<i>Keratella quadrata</i>		40	70	85	95	95	95	does not change
<i>K. cochlearis</i>		40	60	80	90	95	90	does not change

*1 ml of suspension contained about $1 \cdot 10^7$ sand grains and fragments of diatom frustules of a size $< 16 \mu$.

filtrators and sedimentators. With an increase of the concentration of mineral particles in the environment, the share of these particles in gut contents in-

Comparison of the number of sand grains and fragments of diatom frustules in the environ
Mean values from the experiments carried out on the 26 and 28 of October 1966,

Elements compared	Classes of size of the sand grains and						
	< 1	1-2	2-3	3-4	4-5	5-6	6-7
Environment*	18,619	7,547	4,450	1,887	587	267	98
Alimentary canals**							
<i>Eudiaptomus graciloides</i>	30	23	20	19	17	18	29
<i>Diaphanosoma brachyurum</i>	1,450	4,300	4,750	1,030	380	80	27
<i>Daphnia cucullata</i>	1,400	3,950	3,550	590	134	35	18
<i>Bosmina coregoni</i>	1,470	810	76	13	3	2	—
<i>Chydorus sphaericus</i>	980	114	28	8	2	—	—
<i>Conochilus unicornis</i>	149	35	9	1	1	—	—
<i>Keratella quadrata</i>	158	37	5	—	—	—	—
<i>K. cochlearis</i>	123	7	1	—	—	—	—

*Mean number in 1 ml of water for the 10 hours of experiment.

**Total number in the alimentary canals of 10 individuals.

creases, while in case of *Cladocera* the degree of filling the alimentary canals also increases. This proves that the filtering rate of *Cladocera* does not decrease when there is a large amount of valueless food in environment, which the animals can not avoid nor get rid of selectively as it is done by *Daphnia rosea* (acc. to observations of Burns 1966) with filamentous colonies of blue-green algae. An addition of minute grains of sand to the water with algal cultures, with which sea cladocerans were fed, can even increase the filtering rate of these animals (Reeve 1963 acc. to Rigler in press). There are no similar observations to be found in literature with respect of *Calanoida* and *Rotatoria*. Out of the experiment described in this paper (Tab. IV) it results that *Eudiaptomus graciloides* reacts to an increase of the concentration of mineral particles in environment rather by lowering the filtering rate (the degree of filling the guts decreases), although on the other hand a higher concentrations an increased faeces production was observed, which may prove that the rate of getting through the guts of food increased.

Food selectivity of animals has usually a quite complex character. According to Ivlev (1955) there are two decisive factors: 1) the animal's preference for a determined kind of food and 2) the availability of food. On the basis of the discussed above results of experiments it can be assumed that in case of the analyzed species of filtrators and sedimentators the food selectivity — as

ment and alimentary canals of crustaceans and rotifers caught in the same environment in which the same concentrations of the grain suspension were applied

Tab. VII

the fragments of diatom frustules (in μ)								
7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16
71	62	62	49	44	40	31	27	22
19	16	10	4	2	1	—	1	—
13	10	4	4	3	1	3	4	1
9	1	1	2	1	1	—	2	1
1	—	1	—	—	—	1	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—

a result of a lack of food preference — depends chiefly on the food availability, not in the meaning of its distribution in the environment but in the sense of the possibility of catching and swallowing the food particles by animals.

In order to determine the intensity of filtration of particles of various dimensions from the environment, in an analysis of the results of experiments with the suspension of sand grains and diatomite (Tab. VII) Ivlev's (1955) coefficient of food selectivity was applied:

$$S = \frac{g - e}{g + e},$$

where: g — share (in %) of the given class of size of grains in the total number of grains found in the alimentary canals of 10 individuals of a given species,

e — share (in %) of the given class of size of grains in the total number of grains $< 16 \mu$ found in the environment (bigger grains were not found in any of the alimentary canals of the analyzed species).

The coefficient value (calculated for each species) is for each class of size of grains an indicator of intensity, with which it is filtrated by the specific species. Comparison of the coefficient values obtained for various classes

of size, gives information, which class of size of grains is most intensively (rapidly) filtrated by the given species. Because of the passive, mechanical character of food selectivity of analyzed species the obtained results can be applied with some restrictions to natural food.

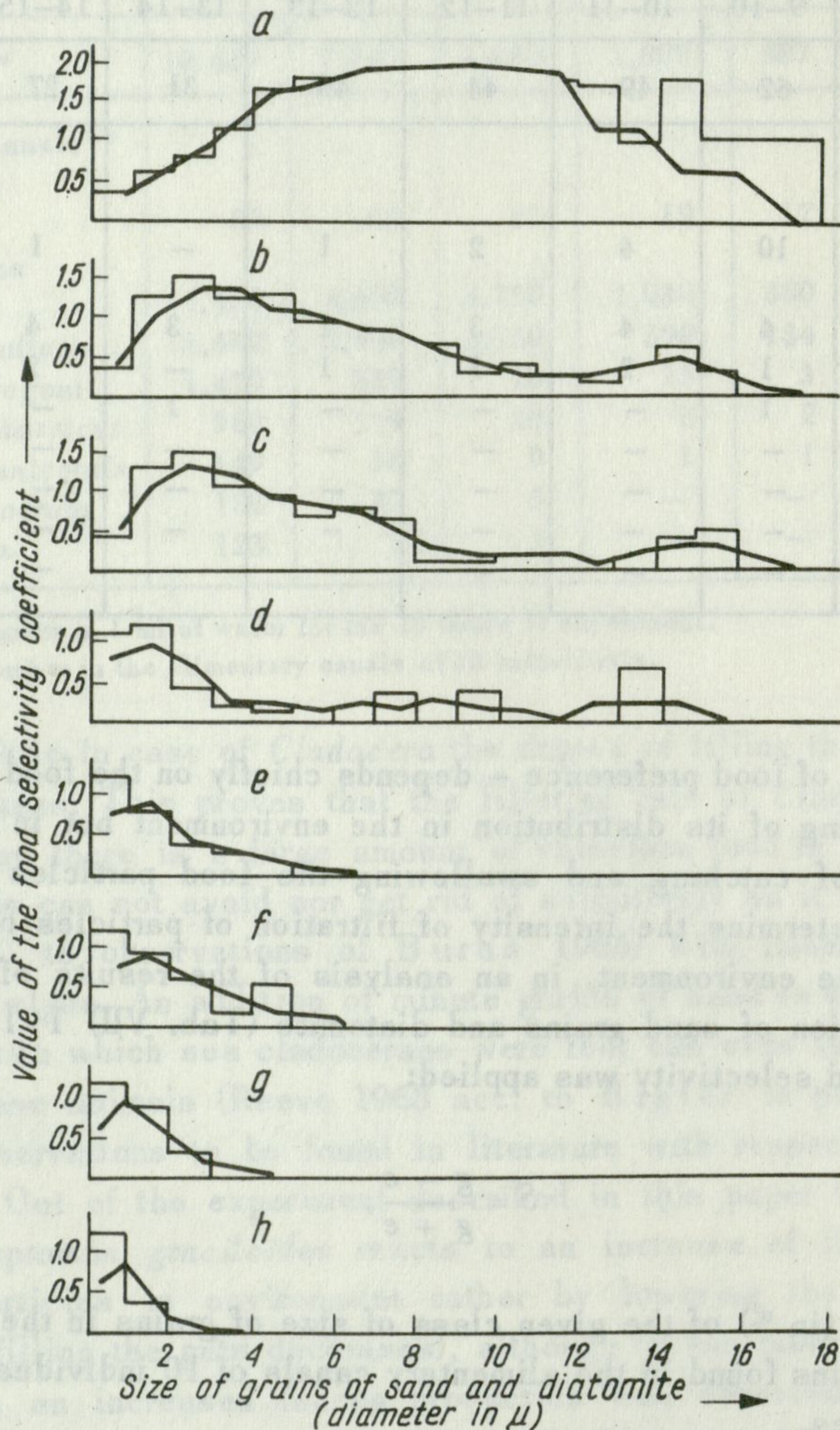


Fig. 4. Intensity of grazing the food particles of various size by dominating filtrator and sedimentator species

Intensity of grazing expressed in (increased with 1) values of Ivlev's (1955) food selectivity coefficient for various classes of size of grains of sand and diatomite (curves on the basis of mobile mean from three successive points)

a - *Eudiaptomus graciloides*, b - *Diaphanosoma brachyurum*, c - *Daphnia cucullata*, d - *Bosmina coregoni*, e - *Chydorus sphaericus*, f - *Conochilus unicornis*, g - *Keratella quadrata*, h - *K. cochlearis*

For each of the analyzed species the values of the selectivity coefficient obtained for various classes of size of food particles were plotted. For the sake of graphical simplification these values were presented differently by moving them from the range -1 to $+2$ to the range 0 to 2 (Fig. 4). These values form characteristic curves informing about the food selectivity of species. They show that:

1) In case of crustaceans the filtration intensity of food particles in dependence on their dimensions decreases from their certain size, not only together with the decrease of the size of particles (with the exception of *Chydorus sphaericus*), which has been already proved for various species of macrofiltrators (e.g. Marshall and Orr 1955, Malovickaja and Sorokin 1961a, 1961b), but also with an increase of the particles' dimensions. This confirms the results of experiments of Suščenija (1959), who found this dependence for 11 cladoceran and calanoid copepods species, using the food consisting of mixed cultures of several algae species with various size of cells.

The decrease of the filtration intensity of particles together with a decrease of their dimensions is, as it seems, conditioned by the compactness of the net formed of the setae of filtering appendages. The decrease of the filtration intensity of particles together with an increase of their dimensions (which has been observed above all in case of *Cladocera*) may be caused by a limited width of crevice, by which the food particles enter the filtration chamber (in case of *Cladocera* – by the spacing width of right and left thoracic appendages in the abduction phase).

Eudiaptomus graciloides displays a tendency of filtering most intensively particles of greater dimensions ($> 6 \mu$), which confirms the opinion that this species is a macrofiltrator.

Daphnia cucullata and *Diaphanosoma brachyurum* have a tendency to graze bigger particles than the remaining *Cladocera* species. *Bosmina coregoni* has a tendency to graze finer particles, and *Chydorus sphaericus* – the finest ones ($< 1 \mu$). Particles smaller than 1μ are not very intensively grazed in case of *D. cucullata* and *D. brachyurum*, which is probably connected with the width of crevices between the setae of filtering appendages, which is in case of these species about 1μ (Coker and Hayes 1940).

2) Rotifers (*Keratella quadrata*, *K. cochlearis* and *Conochilus unicornis*) collect most intensively particles smaller than 1μ . The intensity of collecting bigger particles is considerably lower in all three species. Perhaps while grazing natural food the intensity of collecting bigger particles is slightly higher, because the soft algal cells or detritus particles may get into the stomachs after being ground in the mastax, which in case of hard grains seems impossible.

Knowing that the food selectivity of species varies essentially and that the composition of zooplankton communities is different in lakes with varying trophic level, differences in food selectivity of whole zooplankton communities can be expected and what more different food composition of communities in various trophic water bodies.

IV. FOOD SELECTIVITY AND FOOD COMPOSITION OF ZOOPLANKTON COMMUNITIES

This chapter discusses the results of experiments carried out on several lakes, in situ, in conditions resembling to maximum the natural ones. The experiments present the effect of feeding of whole zooplankton communities, typical for various lakes.

1. The method

The principle of the method, described in detail previously (Gliwicz 1968), is a comparison of the number of particles of the potential zooplankton food (cells of minute algae, bacteria and tripton particles): 1) in lake water with active, grazing zooplankton and 2) in lake water with anaesthetized zooplankton, after a determined time of exposure. Exposure is carried out in situ (in the sense of lake and depth), in transparent, of 3 litres capacity experimental chambers made of organic glass. These chambers function on the principle of plankton sampler of Bernatowicz (1960) type. Lake water with an active, food consuming zooplankton plays the part of control; water with anaesthetized zooplankton, which does not take food is the experimental variant. The difference between the number of food particles in the control and experimental variant informs how many particles from various classes of size were consumed during the period of exposure by the whole zooplankton isolated in the chamber.

The zooplankton in the experimental variant is anaesthetized at the beginning of experiment (in the moment of closing the chamber on a determined depth) by adding automatically to the water closed in chamber anaesthetizing substance – physostigminum salycilicum (15 ml of solution with an initial concentration $1 \cdot 10^{-2}$ g/ml, which in the exposed water gives a concentration $5 \cdot 10^{-5}$ g/ml).

It has been previously said (Gliwicz 1968) that this substance: 1) does not act on algae and bacteria (result of a comparison of the intensity of photosynthesis and respiration of nanoplankton in water with physostigminum and water without physostigminum, by the oxygen method of dark and light bottles)

and 2) in a concentration $5 \cdot 10^{-5}$ g/ml causes a complete paralysis of crustaceans' appendages (in case of *Cladocera* after 3–5 min., in case of *Copepoda* after 10–20 min.) and disturbance in functioning of the ciliated systems of the trochal discs of rotifers (after 15–20 min.), as a result of which the animals sink to the bottom of the chamber.

Each time both variants were exposed for 4 hours in two repetitions. Such time of exposure has been accepted on the basis of the results of methodical experiments as the shortest possible, after which the differences in number of algae and bacteria in the control and experimental variants are sufficiently visible. The same experimental chambers (samplers) were used in control sampling (initial), when starting the exposure. Algae cells and tripton particles were counted (after sedimentation) in 5 classes of size: < 3, 3–6, 6–9, 9–12 and 12–30 μ . Bacteria were counted by the modified Razumov's method on membrane filters Coli 5 in two classes of size: < 0.5 and > 0.5 μ . The preservation and elaboration of material is described in an earlier paper (Gliwicz 1968).

Differences in the number of a given class of size of algae or bacteria after the exposure time in the experimental and control variants (Tab. VIII) were treated as the number of grazed cells of this class during the time of experiment. The per cent of grazed cells from the given class of size was counted as a ratio of this difference to the number in the experimental variant, multiplied by 100.

In case of tripton the difference ~~between~~ the number of particles of a concrete class of size in the experimental and control variants could not be treated as the number of grazed particles. It was therefore not only the result of grazing dead organic matter but also the defecation of unassimilated food, which only in case of *Copepoda* takes the form of enveloped small pellets, whereas in other animals it reaches the water in the form of small particles. Bearing in mind the mechanical character of food selectivity it was assumed that the same percentage of tripton particles was grazed as that of the algae cells in the respective classes of size (Tab. VIII). Taking the number of particles in the given class of size in the initial control sample as 100 per cent, the number of grazed tripton particles from the given class of size was calculated. The final number in the experimental variant was not accepted as 100 per cent, as the number of tripton particles after the exposure was also a result of some other factors e.g. cutting off the inflow of sedimentating tripton, or the settlement process of dead organic matter particles on the walls of experimental chambers, what decreased the number of each class of size in favour of bigger ones (coagulation of small particles into big ones).

Next summing up the volume of cells (particles) grazed from different

Results of one of the experiments with active and anaesthetized zooplankton communities*

Experiment carried out on the 9th of July 1966, in the Mikołajskie Lake on the depth of 4 m
 Number of cells (particles) of each class of size of algae, bacteria and tripton given as means from 2 repetitions,
 in number of cells (particles) in 1 ml of water

Tab. VIII

Kind of food (fraction of nanoseston) and class of size of cells or particles (diameter in μ)	Control number in the lake (initial state)	Number in control variant (active zooplankton) after 4 hrs of exposure	Number in experimental variant (anaesthetized zooplankton) after 4 hrs of exposure	Number of cells (particles) grazed during the 4 hrs of exposition out of 1 ml of water	Per cent of grazed cells (particles) during the 4 hrs of exposition	Volume of grazed cells (particles) in μ^3	
Algae	< 3	2,243	704	1,166	462	39.6	1,940
	3-6	1,994	650	970	320	33.0	15,264
	6-9	872	498	641	143	22.3	31,546
	9-12	347	320	365	45	12.3	23,548
	> 12	258	311	338	27	8.0	27,580
Bacteria	< 0,5	$115 \cdot 10^4$	$83 \cdot 10^4$	$88 \cdot 10^4$	$5 \cdot 10^4$	5.7	700
	> 0.5	$509 \cdot 10^4$	$339 \cdot 10^4$	$507 \cdot 10^4$	$168 \cdot 10^4$	33.1	453,600
Tripton	< 3	19,518			7,729		32,462
	3-6	453			149		7,107
	6-9	392			87		19,192
	9-12	383			47		24,595
	> 12	383			31		31,666

*Composition of zooplankton isolated in chambers (mean number of dominating species, in individuals/l): *Cyclopoida* (females, males and copepodits) - 46, *Cyclopoida* (naupli) - 51, *Eudiaptomus* (females, males and copepodits) - 8, *Eudiaptomus* (naupli) - 13, *Daphnia cucullata* and *D. longispina* - 15, *Diaphanosoma brachyurum* - 2, *Bosmina coregoni* and *B. longirostris* - 1, *Chydorus sphaericus* - 34, *Keratella cochlearis* - 131, other *Rotatoria* - 135.

classes of size of algae, bacteria and tripton (the number of grazed cells or particles multiplied by the mean volume of cells or particles of the given class of size), the volume of food grazed during the time of exposure was obtained. Knowing the consumed volume of phytoplankton, bacteria and detritus, calculation was made of the percentage of these elements in the food of zooplankton community isolated in the experimental chambers.

Size of cells of nanoplankton algae and bacteria from various classes of size and their mean volumes in three investigated lakes

Measurements were taken with a tolerance of 0.5 μ in case of algae and 0.2 μ in case of bacteria

Tab. IX

Class of size of cells (in μ)	Diameter (in μ)*				Volume (in μ^3)**	
	Mikołajskie	Tałowisko	Piśakno	Mean		
Algae	< 3	1.95	1.85	2.15	1.95	4.2
	3-6	4.20	4.70	4.40	4.43	47.7
	6-9	7.60	7.55	7.30	7.48	220.6
	9-12	9.50	10.45	10.20	10.05	523.3
	> 12	12.95	12.75	12.20	12.63	1,021.5
Bacteria	< 0.5	0.3			0.32	0.014
	> 0.5	0.8			0.81	0.27

*The mean of measurements of 20 algae cells and 60 bacteria cells.

**Calculated on the basis of globe formula. In case of bacteria the rod-forms were not taken into account because of the decided dominance of coccoidal forms. In case of algal cells having the shape of rotary ellipse (e.g. *Chlamydomonas* sp., *Cryptomonas* sp.) the mean of the length and width of the cell was accepted as the diameter.

The mean volume of algae and bacteria cells (Tab. IX) was calculated on the basis of microscopic measurements carried out in July and August on the material from Mikołajskie Lake (bacteria and algae) and lakes Tałowisko and Piśakno (algae). On the whole 60 cells from each class of size were measured. Mean volumes of tripton particles were accepted as equal to mean volumes of algae cells from corresponding classes of size. Together in July and August 1966, 10 experiments with anaesthetising the zooplankton were carried out: twice in Mikołajskie Lake and the lakes Tały, Tałowisko and Piśakno, and once (July) in the lakes Wukśniki and Mamry-Przystań.

The depth, on which the exposure was made was chosen directly before each experiment on the basis of the analysis of the vertical zooplankton distribution. Experiments were carried out on the depth, on which the maxima of the majority of dominant species were found. Thanks to it very big differences were obtained in the number of particles of the potential zooplankton

food in experimental and control variants, and the zooplankton isolated in experimental chambers fully represented the zooplankton community of the given water body.

A comparison of the composition of zooplankton community isolated during the exposure in experimental chambers and the composition of zooplankton community in lake showed that the percentage of species in the total number of plankters was on the whole in both cases very similar. The similarity of zooplankton composition in experimental chambers and in the whole water column can be explained by the fact that the majority of pelagic species form maxima during summer stagnation on the same depth; Warda (1968) found it also in Mikołajskie Lake.

Table VIII presents an exemplary results of experiment carried out in July, in Mikołajskie Lake: the number of algae and bacteria cells and tripton particles from various classes of size in the initial control sample, control sample, and experimental sample, number of grazed cells (particles), their grazing percentage and the volume of grazed cells and particles.

2. Food selectivity of zooplankton communities

Comparison of the grazing percentages of algae and bacteria cells from various classes of size by whole zooplankton communities from different lakes points to some differences in the food selectivity of these communities (Fig. 5).

Both in experiments carried out in July and August, the intensity of grazing minute food particles (algae cells of a diameter smaller than $6\ \mu$ and bacteria cells) is greater in eutrophic lakes than in lakes with lower trophy. In the latter the intensity of grazing relatively big nannophytoplankton cells is greater.

Lake Mamry-Przystań (poorly eutrophized) is an exception, in which high intensity of grazing smaller food particles was observed. In the β -mesotrophic lake Tałtowisko the size of most intensively grazed cells varies in July and August. It is similar in those months in the eutrophic lakes Mikołajskie and Tałty; most intensively grazed are the particles smaller than $3\ \mu$. It is also similar, in the same period of time, in the α -mesotrophic lake Piłakno; most intensively grazed are the particles from the class of size $6-9\ \mu$.

The tendency to graze smaller food particles in eutrophic lakes and bigger particles in lakes of a lower trophy has been also observed with the help of another modification of the described here method (Fig. 6). Unfiltered water (control variant) and water deprived of zooplankton (experimental variant) were parallely exposed (2-hour exposure in the same experimental chambers of organic glass, in situ, on similarly chosen depth). The water was filtered automatically when the chambers were lowered with the help of cones of silk

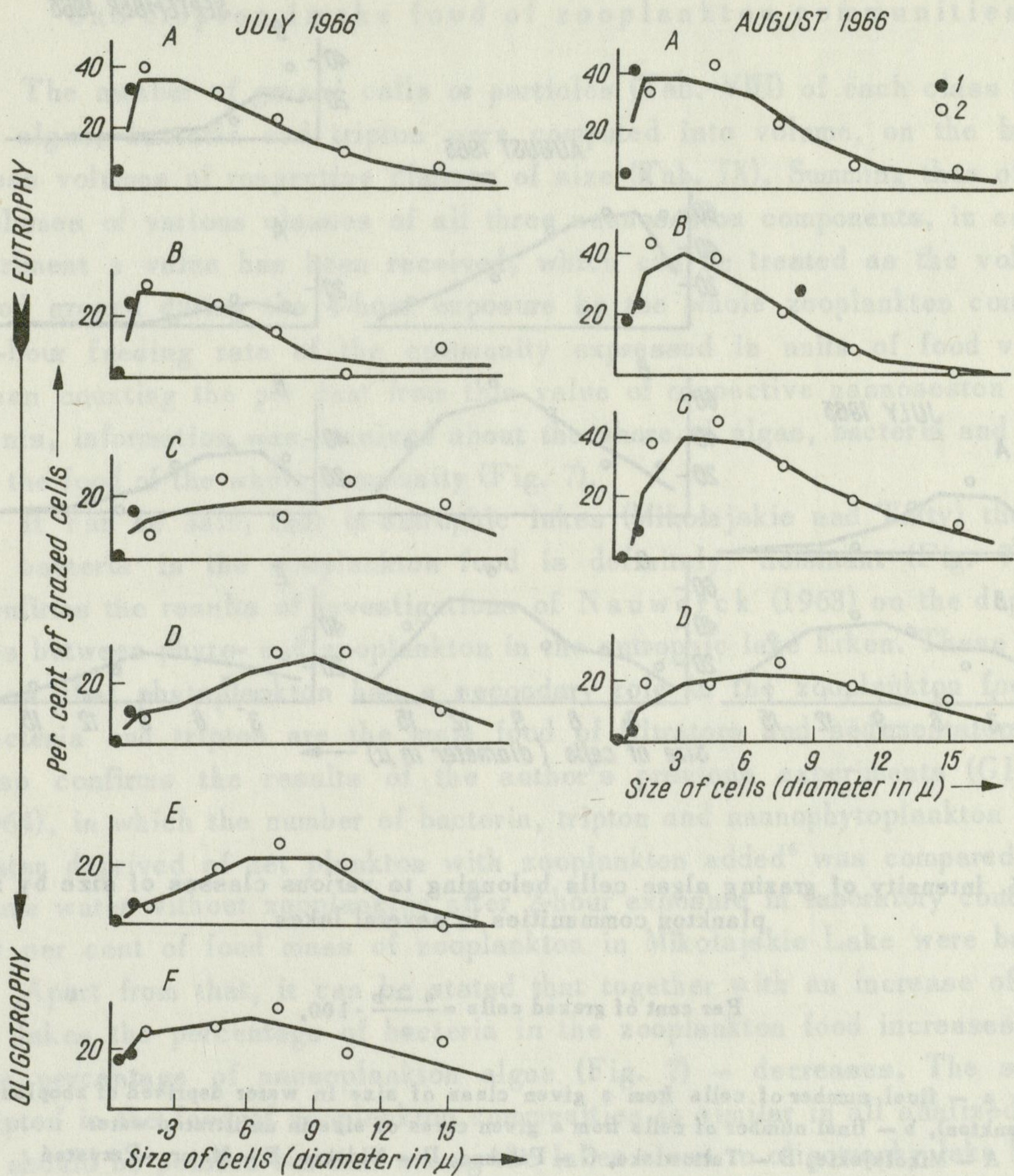


Fig. 5. Intensity of grazing the algae and bacteria cells belonging to various classes of size by zooplankton communities in the investigated lakes

$$\text{Per cent of grazed cells} = \frac{a - b}{a} \cdot 100,$$

where: a — final number of cells from a given class of size in the experimental variant (anaesthetized zooplankton), b — final number of cells from a given class of size in the control variant (active zooplankton)

1 — per cent of grazed bacteria cells from a given class of size, 2 — per cent of grazed algae cells from a given class of size

A — Międzybóże, B — Tałty, C — Tałtowisko, D — Piłakno, E — Wukśniki, F — Mamry-Przystań

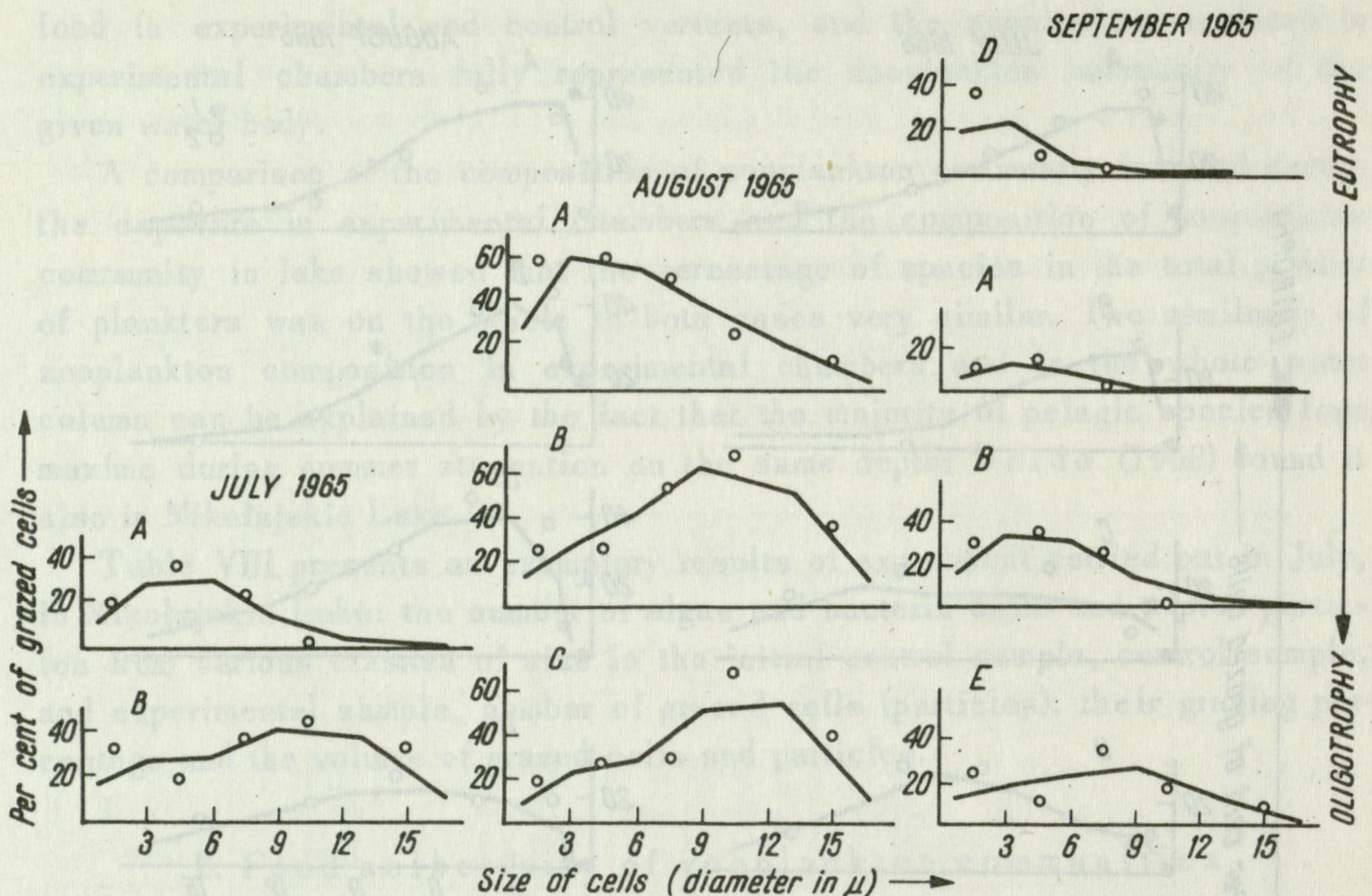


Fig. 6. Intensity of grazing algae cells belonging to various classes of size by zooplankton communities in several lakes

$$\text{Per cent of grazed cells} = \frac{a - b}{a} \cdot 100,$$

where: a — final number of cells from a given class of size in water deprived of zooplankton (net plankton), b — final number of cells from a given class of size in unfiltered water

A — Mikołajskie, B — Tałtowisko, C — Piłakno, D — Nidzkie, E — Mamry-Przystań

bolting cloth No. 25 placed on their lower openings. But the water in the experimental variant was also deprived of other elements of net seston, and that is why the results of these experiments do not include bacteria (Gliwicz 1968). The comparison of the number of algae in the same classes of size allowed to count, in an identical way as in the experiments with physostigminum, the per cent of grazed cells from various classes of size.

It may be assumed that as a result of different food selectivity of zooplankton communities, the food composition of respective communities in eutrophic lakes and those of lower trophy varies.

3. Share of nanoplankton algae, bacteria and tripton in the food of zooplankton communities

The number of grazed cells or particles (Tab. VIII) of each class of size of algae, bacteria and tripton were computed into volume, on the basis of mean volumes of respective classes of size (Tab. IX). Summing thus obtained volumes of various classes of all three nanoseton components, in each experiment a value has been received, which can be treated as the volume of food grazed during the 4-hour exposure by the whole zooplankton community (4-hour feeding rate of the community expressed in units of food volume). Then counting the per cent from this value of respective nanoseton components, information was received about the share of algae, bacteria and tripton in the food of the whole community (Fig. 7).

It can be said, that in eutrophic lakes (Mikołajskie and Tałty) the share of bacteria in the zooplankton food is definitely dominant (Fig. 7). This confirms the results of investigations of Nauwerck (1963) on the dependences between phyto- and zooplankton in the eutrophic lake Erken. These results show that phytoplankton has a secondary role in the zooplankton food, and bacteria and tripton are the main food of filtrators and sedimentators. This also confirms the results of the author's previous experiments (Gliwicz 1964), in which the number of bacteria, tripton and nanophytoplankton in lake water deprived of net plankton with zooplankton added⁶ was compared in the same water without zooplankton after 2-hour exposure in laboratory conditions. 90 per cent of food mass of zooplankton in Mikołajskie Lake were bacteria.

Apart from that, it can be stated that together with an increase of trophy in lakes the percentage of bacteria in the zooplankton food increases, while the percentage of nanoplankton algae (Fig. 7) – decreases. The share of tripton in the food of zooplankton communities is similar in all analyzed lakes. It should be pointed out that among the lakes close to oligotrophy lake Mamry–Przystań is an exception. This lake has a definitely greater percentage of bacteria and tripton in the food of zooplankton community (Fig. 7).

V. SUMMARY AND DISCUSSION OF THE RESULTS

Different share of nanoplankton algae and bacteria in the food of communities of filtrators and sedimentators in lakes with varying trophy can be conditioned, as it seems, chiefly by two factors: 1) various food selectivity of communities and 2) various abundance of minute algae and bacteria in the

⁶ When separating zooplankton from the other seston components the positive phototropism of animals was used; the light traps were applied.

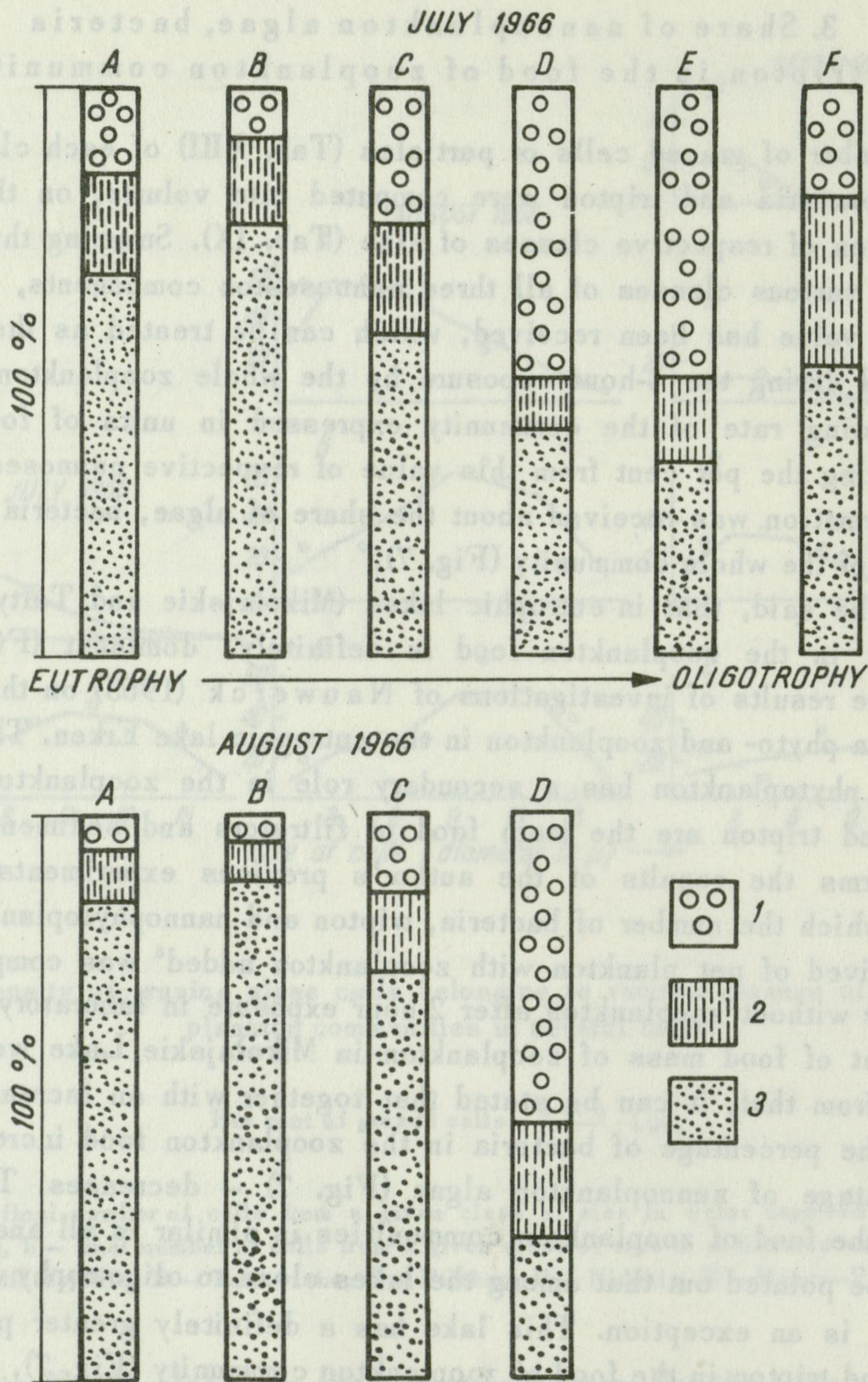


Fig. 7. Percentage share of the mass of alive nannoplankton algae (1), organic tripton (2) and bacteria (3) in the food of zooplankton communities of investigated lakes A - Mikołajskie, B - Tałty, C - Tałowisko, D - Piłakno, E - Wukśniki, F - Mamry-Przystań

pelagial of the given lake, available as food for the dominant plankter species.

The effect of the former factor on food composition of zooplankton communities can be observed when comparing the food selectivity of communities (Fig. 5) with the food composition of these communities (Fig. 7). Bacteria definitely dominate (Fig. 7) in eutrophic lakes (Mikołajskie Lake and lake

Tały, and in the experiments in 1965, also Nidzkie Lake), in which the smaller seston particles rather than the bigger ones are more intensively grazed (Fig. 6). But in lakes of a lower trophy (Piłakno and Wukśniki), where bigger food particles are more intensively grazed than the smaller ones (Fig. 5 and 6), the main food component are minute algae, while the percentage of bacteria in the food remains quite high (Fig. 7).

The main reason of the various food selectivity of zooplankton communities should be found in the species composition of these communities, as it does not seem possible that different behaviour of species in different lakes could decide about it. The results of the experiment with the suspension of sand grains and diatomite showed that the food selectivity of respective species essentially differs (Fig. 4). Therefore, it can be assumed, that the dominance of sedimentators and microfiltrators (*Rotatoria*, *Chydorus sphaericus* and *Bosmina* genus) in zooplankton community conditions the more intensive grazing of bigger rather than smaller food particles. But the dominance of macrofiltrators (*Eudiaptomus graciloides*, and also probably *E. gracilis* and *Eurytemora lacustris*) conditions more intensive grazing of bigger food particles than smaller ones.

When comparing the food selectivity of various zooplankton communities (Fig. 5) with the species composition of these communities (Tab. III) it can be said, that together with an increase of the grazing intensity of bigger food particles and parallel lowering of trophy of the lake, definite changes in zooplankton composition take place:

1) Decreasing percentage of *Rotatoria* (chiefly *Keratella cochlearis*), *Bosmina* genus and *Chydorus sphaericus* (in case of that one down to zero), i.e. species collecting the minute food particles;

2) Increasing percentage of 3 *Calanoida* species: *Eudiaptomus graciloides*, *E. gracilis* and *Eurytemora lacustris* (in case of that one from zero), out of which the first one displays a tendency to collect the biggest food particles. The food selectivity of the two remaining species seems to be similar in character, as all *Calanoida* species analyzed from the feeding point of view were found to be macrofiltrators (e.g. *E. gracilis* and *E. graciloides* – Malovickaja and Sorokin 1961a, *Eurytemora velox* – Lowndes 1935, *Calanus finmarchicus* – Marshall and Orr 1955);

3) Increasing percentage of *Dreissena polymorpha* larvae; lack of data in literature on their feeding. It can be assumed that they are microfiltrators. The following observations are in the favour of this opinion: a) grazing intensity of the minute particles in lake Mamry-Przystań, where is a definite dominance of these larvae (72.7 per cent of the total number of zooplankters), is very big and b) in August, in lake Tałtowisko, where the larvae are 37.3 per cent



Fig. 8. Intensity of grazing food particles of various size by zooplankton communities in investigated lakes

Intensity of grazing (expressed in the filtering rate of particles of various size out of the environment) calculated on the basis of laboratory data on the character of food selectivity (Fig. 4) and filtering rate (Erman 1956, Beljackaja-Potaenko 1964) of dominant species 1 — calculated for the zooplankton community out of the volume of 1 l of water isolated in experimental chambers (July 1966), 2 — calculated for the zooplankton community from the whole column of water of a given lake under 1 dcm² of the lake area (July 1966)

A — Mikołajskie, B — Tały, C — Tałtowisko, D — Piłakno, E — Wukśniki

of the total number of plankters, the community grazes smaller particles more intensively than in July, when the percentage of larvae in the total number of plankters is only 7.8 per cent (Fig. 5).

The dependence of the character of food selectivity of the community on the community species composition is confirmed more precisely by the comparison of curves illustrating the grazing intensity of food particles of various size by zooplankton communities obtained empirically (in the experiment with the parallel exposure of lake water with active and anaesthetized zooplankton — Fig. 5) with theoretical curves illustrating the same dependence (grazing intensity of food particles in dependence on their size) for the same communities and calculated on the basis of laboratory data on each species dominating in the given community (Fig. 8).

When calculating the theoretical curves characterizing the grazing intensity of food particles of various size by entire zooplankton communities the following points were taken into consideration:

- 1) character of food selectivity of each dominant species (Fig. 4);
- 2) the rates of filtering out of water food particles of a determined size by the dominant species, adopted on the basis of the results of laboratory experiments of Beljackaja-Potaenko (1964) and Erman (1956);
- 3) composition of zooplankton communities, for which empirical results were obtained, i.e. number of individuals of each dominant species (Tab. III). All *Cyclopoida* stages, naupliar *Calanoida* stages, embryos and young *Cladocera* individuals and all *Dreissena polymorpha* individuals were not taken into consideration as there is no data available on the subject. On account of the dominance of *D. polymorpha* in lake Mamry-Przystań (more than 70 per cent of the total number of plankters) the theoretical curve was not calculated for the community of this lake.

An example of such calculation is described in detail by Gliwicz (in press).

The curves illustrating the theoretical food selectivity of communities (Fig. 8) are in their general outlines like those obtained empirically on the basis of the results of experiments with active and anaesthetized zooplankton (Fig. 5). In both cases together with the trophy of lakes decrease the grazing intensity of smaller food particles decreases and of bigger ones increases. The comparison of median values for empiric curves and "theoretical curves" (Tab. X) points to the same thing. The differences in the course of empirical and "theoretical" curves are surely not only the result of some working presuppositions when calculating the latter, but also of not taking into consideration the adult and copepod *Cyclopoida* stages, as well as the naupliar stages of all *Copepoda* species and *Dreissena polymorpha* larvae.

Considering the same parameters the theoretical food selectivity of zooplankton communities from the whole water column of the given lake under 1 dcm² of area (Tab. III) was calculated using the same method (Gliwicz in press). And in this case (Fig. 8) high compatibility of the course of curves for different lakes was found, which once again confirms the representativeness of results obtained in the experiments with zooplankton communities characteristic for these lakes.

Recapitulating all that has been said, it can be stated that the character of food selectivity of zooplankton communities in the investigated lakes is determined by the communities composition: dominance of macrofiltrators or microfiltrators and sedimentators in the zooplankton communities.

Analyses of the dependence of the dominative relations in zooplankton communities on the trophic type of lake are also known from other fields.

Numerical comparison of curves illustrating the food selectivity of zooplankton communities, obtained as results of experiments with natural food (a) and (b) calculated on the basis of laboratory data for dominant species, with the help of median expressed in microns

On X-axis (Fig. 5 and 8) are presented the sizes of food particles in microns

Tab. X

Lake and date of experiment (1966)	a	b
Tały 10 VII	4.22	3.70
Mikołajskie 9 VII	6.03	5.48
Piłakno 5 VII	8.13	6.45
Tałowisko 11 VII	8.57	6.59
Wukśniki 8 VII	7.10	6.91

Patalas (1954) carried out such investigations in a group of 28 Pomeranian lakes, which trophic types are according to the Stangenberg's (1936) typology α -mesotrophic, β -mesotrophic and eutrophic. Among other things the author found that *Eurytemora lacustris* is a dominant species only in some α -mesotrophic lakes, while it does not occur at all in lakes having different trophic character. Species from the *Eudiaptomus* genus and *Daphnia cucullata* dominate in α -mesotrophy and β -mesotrophy; *Diaphanosoma brachyurum* – only in β -mesotrophy; *Chydorus sphaericus* – only in eutrophy and sporadically in β -mesotrophy and was not found at all in α -mesotrophy. In the range of lakes from α -mesotrophy to eutrophy a small increase was also observed of the share of *Cyclopoida* in the *Crustacea* community (chiefly species from the *Mesocyclops* genus).

Changes in dominative relations depending on the type of trophy, described by Patalas (1954), correspond in general to the changes found in the lakes analyzed in this paper. This suggests, that the discussed dependences have a character of general regularity. As it has been said before, the species composition of the community decides about its food selectivity, which in turn is one of the factors conditioning the composition of the food of zooplankton community. Therefore it can be anticipated that the dependence of zooplankton food composition on the trophic type of the water body in the lakes analyzed in this paper shall be also true in other lakes.

Certainly the food composition of zooplankton is conditioned not only by the food selectivity of communities, but also by another factor mentioned before, i.e. by the abundance of algae and bacteria in the pelagial of the given water body, available for dominant zooplankton species.

This abundance may be estimated on the basis of measurements of the production of nanoplankton algae and bacteria. As far as the investigated

lakes are concerned there are no direct data on the size of production of these organisms. Data on their number and biomass (Tab. IX and X) do not entitle to deduce the amount of phytoplankton and bacterial food available for zooplankton, because the number, which in some situations may be a production measure, in this case also depends on the grazing intensity (filtering rate) of reproductive cells of algae and bacteria, and as it is known is not identical in various water bodies.

On the basis of investigations on the primary pelagial production of analyzed lakes the indicator showing the share of minute nannoplankton algae in the production of whole phytoplankton communities in pelagial (Gliwicz 1967b) has been determined. Analysis of this indicator showed that the share of nannoplankton in the total primary pelagial production is the greatest in α -mesotrophic lakes (Piłakno and Mamry-Przystań), smaller in β -mesotrophic lakes (Tałtowisko) and the smallest in eutrophic lakes (Mikołajskie and Tały). Thus it has been stated that the share of minute, available for zooplankton algae decreases in the total primary pelagial production together with an increase of trophy of lakes. Nannoplanktonic algae are, as it is known, the exclusive producers in extremely oligotrophic bodies of water. This is proved by the results of investigations by Rodhe (1955, 1962), Juriš (1964), Whitford (1964), Nauwerck (1966) and Gliwicz (1967a), who in lakes of this type found total or almost total absence of net phytoplankton.

There is a lack of data on the production of bacteria in pelagial of the lakes analyzed in this paper. On the basis of data from literature (Petrovič 1961, Romanenko 1965, Sorokin 1967) it can be stated, however, that the bacteria production is considerably greater in eutrophic lakes than in meso- and oligotrophic lakes. Different bacteria production in lakes of various trophic type is probably connected with the value of primary production and with ways of its utilization. As it can be seen from numerous data from literature, primary pelagial production is greater in eutrophic than in oligotrophic lakes. Similar regularity has been observed in the lakes (Tab. I) analyzed in this work. On the other hand the share of available for animals nannoplankton in primary production is smaller in eutrophy. Therefore in eutrophy much more of substrate is produced for bacteria than in oligotrophy. This shows that zooplankton in eutrophic lakes has a greater amount of available bacterial food than in oligotrophic lakes.

As it has been discussed before, in the food of zooplankton communities of eutrophic lakes bacteria dominate, but in the food of zooplankton communities of lakes close to oligotrophy — nannoplankton algae. From the material presented here it results that the food composition of zooplankton in lakes of various trophic type can be conditioned by:

1) Character of food selectivity of communities, which as it has been shown depends on their species composition. Food particles smaller than 3μ , i.e. chiefly bacteria, are most intensively grazed in eutrophy. But in lakes close to oligotrophy more intensively grazed are particles bigger than 3μ , and so first of all minute algae;

2) The value and character of phytoplankton and bacterioplankton production. Little share of nanoplankton algae in the total primary production and high bacteria production are typical for eutrophic lakes, while in case of pelagial of lakes close to oligotrophy – great share of nanoplankton algae in the total primary production and low bacteria production.

It is difficult to decide, which of these factors is more important in conditioning the food composition of zooplankton communities. It seems possible that these both factors are mutually dependent. One might think that the different character of primary production, and what follows, different production value of nanoplankton algae on one hand, and bacteria production on the other in eutrophic and oligotrophic lakes may be one of the essential factors conditioning the occurrence or dominance of determined species, or whole systematic groups in zooplankton communities. At the same time the possibility of the effect of zooplankton on the character of primary production and the value of bacteria production should not be excluded. Perhaps the dominance of macrofiltrators, which more intensively consume minute algae than bacteria, conditions more intensive development and greater nanophytoplankton production. On the other hand the dominance of microfiltrators and sedimentators, which graze bacteria more intensively than algae, may stimulate bacteria development.

It seems that the different share of algae and bacteria in the food of zooplankton communities in eutrophic and oligotrophic lakes is not without significance for the "economics" of the energy flow through lake ecosystems.

Primary pelagial production is high in eutrophy, but its considerable part consists of big, unavailable to zooplankton, forms of net phytoplankton. Organic mass produced by these big forms may be used by zooplankton only after partial destruction, or in the form of bacterial cells or not completely decomposed fragments of plant cells (which has been already pointed by Edmondson 1957, Suščenija 1961 and Sorokin 1967), or coagulates of dissolved organic matter of plant or bacterial origin. Besides the food selectivity of zooplankton communities typical for these lakes is "set" on these minute bacteria cells (Fig. 5). Of course considerable amount of energy enclosed in phytoplankton is thus dispersed, as a result of intensive metabolism of microorganisms included in destruction processes, what has been already pointed out by Elster (1963) and Nauwerck (1963).

Primary production is smaller in oligotrophy, but consists chiefly or even exclusively of the production of directly available as food to zooplankton nanoplankton forms. Apart from that, in zooplankton communities of lakes close to oligotrophy macrofiltrators prevail (Tab. III), which graze more intensively algae cells measuring from several to 20 microns than bacteria cells measuring 1 micron or even less (Fig. 5).

Here is probably the reason of higher efficiency of utilizing the primary production by primary consumers in lakes with less advanced trophic than in eutrophic lakes, which has been already pointed out by Thienemann (1926). Thienemann's theory which says that the energy flow through successive trophic levels is less complicated in oligotrophy than in eutrophy, and therefore the efficiency of utilizing producers by consumers is also higher in oligotrophy, was confirmed by Hutchinson's (acc. to Lindeman 1942) comparative analysis of the phyto- and zooplankton biomass in several lakes of various trophic types. A comparison made by Petrovič (1953) also shows the varied degree of utilizing primary pelagial production depending on the trophic type of the lake. The author calculated the percentage share of zooplankton in the entire seston mass in 18 Byelorussian lakes. It has been found that this share in oligotrophy is on average 47 per cent, in mesotrophy — 44 per cent, and in eutrophy — only 11 per cent. In his later work Petrovič (1961) compared the yearly production of phyto- and zooplankton in 3 lakes: Naroč (mesotrophy), Mjastro (eutrophy) and Batorin (strong eutrophy). This comparison confirms also the differences in the efficiency of utilizing the primary pelagial production by plankton consumers in lakes with varying trophic type. The proportion of yearly zooplankton production (net) to yearly phytoplankton production (gross)⁷, calculated out of Petrovič's material, is 0.0446 for the mesotrophic lake, and accordingly 0.0133 and 0.0142 for eutrophic lakes. Differences in the efficiency of utilizing the primary pelagial production by zooplankton were also observed in one body of water. Straškraba (1966) found that in the dam reservoir Slapy, in the years 1961–1963, the value of primary production decreased as a result of disappearance of "water blooms" of blue-green algae some 35 per cent, while the annual mean zooplankton biomass — only 10 per cent. Thus a conclusion that the degree of utilization of primary production by zoo-

⁷Proportion of net zooplankton production to gross primary production: $P_z : (P_{ph} + R_{ph})$ is a good indicator of this efficiency only at an assumption that in all lakes the proportion of net primary production to gross primary production: $P_{ph} : (P_{ph} + R_{ph})$ has the same value. The best indicator would be here the proportion of gross pelagic zooplankton production to net primary pelagial production: $(P_z + R_z) : P_{ph}$, or eventually the proportion of net zooplankton production to net primary production: $P_z : P_{ph}$, but there are no data in literature, which could be used to calculate such indicator for lakes with varying trophic type.

plankton increased in that period and that this increase is most probably the result of better availability of algae to zooplankton (disappearance of "water blooms" of uneatable blue-green algae).

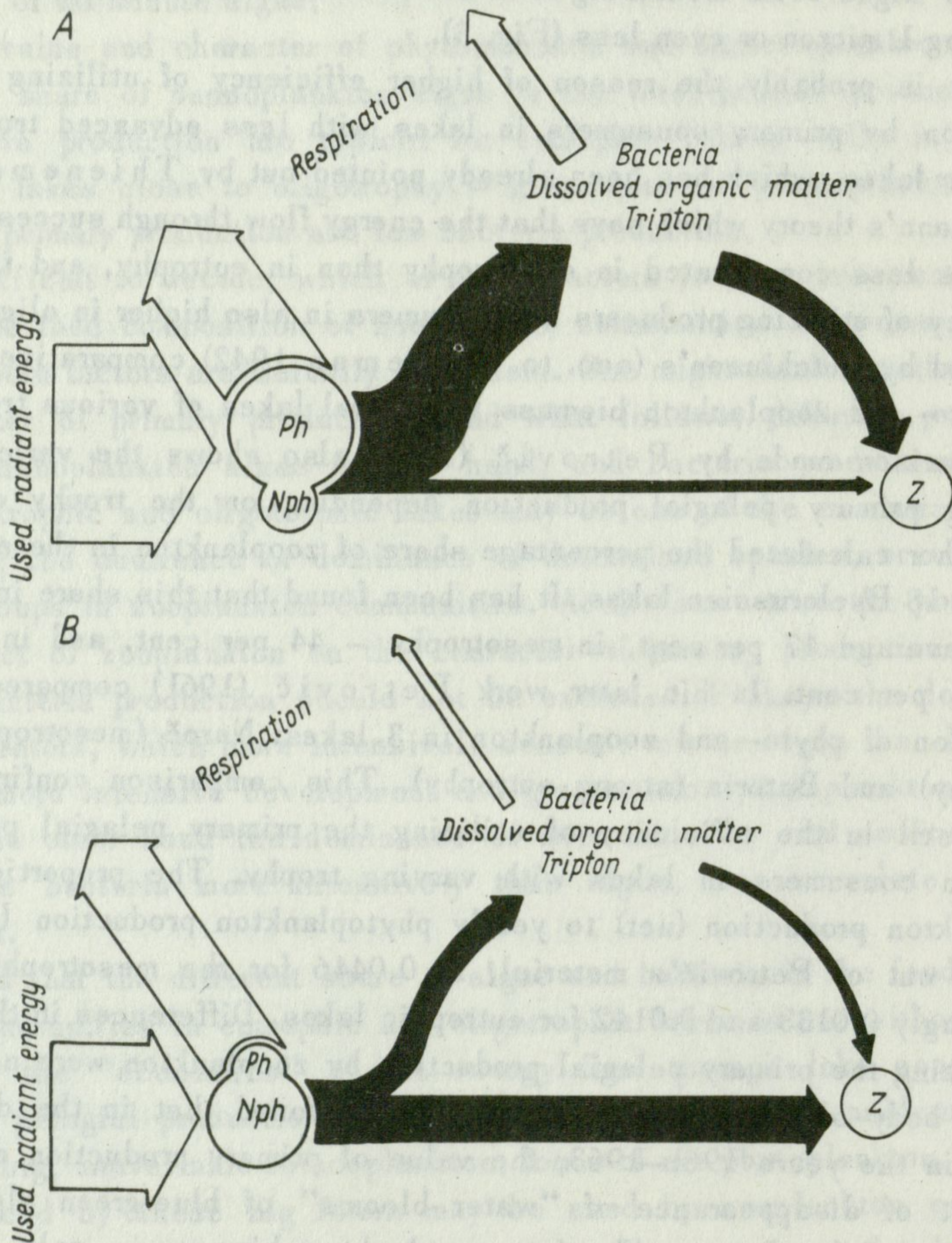


Fig. 9. The schematic diagram of main paths of energy flow between the producers and consumers level in the pelagial of eutrophic (A) and oligotrophic (B) lakes.

Ph - phytoplankton, Nph - nannophytoplankton, Z - zooplankton

In the view of material presented in this paper and literature data the definition of plankton filtrators and sedimentators as "primary consumers" or "phytophagous" does not seem to be very accurate. Between the level of producers and "primary consumers" additional trophic levels are engaged - various physiological bacteria groups. Closer analysis of this problem made

among others by Sorokin (1967) and Gliwicz (1969a) showed that these additional, intermediate levels may form a quite complicated system (microorganisms + dissolved organic matter + its coagulates + tripton particles). According to the conception of Saunders (in press) this system may have buffer significance for zooplankton: when the period of high primary pelagial production finishes, the energy bounded during that time in organic compounds is still for a long time available to zooplankton in the form of components of this system.

Nevertheless the functioning of such system is quite expensive (metabolism of microorganisms) for the ecosystem. Therefore the greater is the amount of energy transferred from producers to plankton consumers in that way – through bacteria – and the smaller the amount supplied directly to consumers, the lower must be the efficiency of utilizing primary production by zooplankton. Comparing from this point of view oligotrophic and eutrophic lakes (Fig. 9), it can be said, that the efficiency of utilizing primary production by zooplankton is greater in the former than in the latter.

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BADANIA NAD ODŻYWIANIEM SIĘ ZOOPLANKTONU PELAGICZNEGO W JEZIORACH O RÓŻNEJ TROFII

Streszczenie

Badania, których głównym celem było określenie roli fitoplanktonu, bakterii i tryptonu organicznego w odżywianiu się zooplanktonu pelagicznego jezior o różnej trofii, przeprowadzono w 6 jeziorach Pojezierza Mazurskiego (tab. I, fig. 1–2) w latach 1963–1966.

Analizowano: 1) skład pokarmu i wybiórczość pokarmową dominujących w pelagialu tych jezior gatunków skorupiaków i wrotków oraz 2) wybiórczość pokarmową i skład pokarmu całych zespołów zooplanktonu, charakterystycznych dla tych jezior.

1) Dla określenia składu pokarmu dominujących gatunków zooplanktonu i charakteru ich wybiórczości pokarmowej zastosowano mikroskopowe analizy zawartości przewodów pokarmowych żywych zwierząt, odławianych bezpośrednio ze środowiska, oraz eksperyment laboratoryjny. Eksperyment ten polegał na ekspozycji zwierząt w zawiesinie piasku o różnej wielkości ziaren i sprawdzaniu, jakie wielkości ziaren wyjadane są bardziej a jakie mniej intensywnie przez dany gatunek. Informacje te otrzymywano licząc ziarna z różnych klas wielkości w środowisku i w przewodach pokarmowych zwierząt. Z uzyskanych w ten sposób informacji wynika, że:

- a) Wybiórczość pokarmową typowych filtratorów (skorupiaki z rodzajów: *Eudiaptomus*, *Daphnia*, *Diaphanosoma*, *Bosmina* i *Chydorus*) i sedymentatorów (wrotki z rodzajów *Keratella* i *Conochilus*) ma pasywny, mechaniczny charakter, tzn. zależy w pierwszym rzędzie od dostępności pokarmu, a nie od preferencji pokarmowej zwierząt (np. tab. VI). Dostępność pokarmu jest z kolei uzależniona od wielkości cząstek potencjalnego pokarmu: komórek glonów i bakterii oraz cząstek martwej materii organicznej;
- b) U wszystkich wymienionych rodzajów skorupiaków i wrotków górna granica wielkości dostępnych jako pokarm cząstek sestonu wynosi około 16 μ średnicy (tab.

IV–V, fig. 3). Wynika z tego, że duże, kilkudziesięciomikronowe formy fitoplanktonu (tzw. fitoplankton sieciowy) nie są dla dominujących gatunków zooplanktonu dostępne, że zatem tylko formy drobne (nannofitoplankton) mogą być przez planktonowych konsumentów bezpośrednio wykorzystywane jako pokarm;

c) Wrotki (*Keratella* i *Conochilus*) i mniejsze wioślarki (*Bosmina* i *Chydorus*) najintensywniej wyjadają ze środowiska cząstki mniejsze od $2\ \mu$ (sedymentatory i mikrofiltratory), większe wioślarki (*Daphnia* i *Diaphanosoma*) – cząstki o wielkości $1\text{--}5\ \mu$, natomiast widłonogi (*Eudiaptomus*) – cząstki o wielkości $4\text{--}12\ \mu$ (makrofiltratory) (fig. 4).

2) Dla określenia charakteru wybiórczości pokarmowej i składu pokarmu całych zespołów zooplanktonu w badanych jeziorach zastosowano eksperyment terenowy. Zasadą tego eksperymentu było porównanie liczebności komórek drobnych glonów, bakterii i cząstek tryptonu z różnych klas wielkości w wodzie jeziornej z zooplanktonem aktywnym i wodzie jeziornej z zooplanktonem inaktywowanym, nie pobierającym pokarmu, po określonym czasie ekspozycji tej wody in situ. Z eksperymentów tych wynika, że:

a) Charakter wybiórczości pokarmowej zespołów zooplanktonu jest odmienny w jeziorach eutroficznym i jeziorach zbliżonych do oligotrofii. Zespoły charakterystyczne dla jezior eutroficznym wykazują tendencję do intensywniejszego wyjadania mniejszych od $3\ \mu$ cząstek nannosestonu. Zespoły charakterystyczne dla jezior bliższych oligotrofii wykazują tendencję do wyjadania większych od $3\ \mu$ cząstek nannosestonu (fig. 5–6);

b) Odmienny jest również skład pokarmu zespołów zooplanktonu w jeziorach eutroficznym i jeziorach zbliżonych do oligotrofii (fig. 7). W pierwszych w pokarmie zespołów dominują zdecydowanie bakterie, w drugich natomiast w pokarmie zespołów przeważają glony nannoplanktonowe, przy czym udział bakterii pozostaje dość duży. Udział tryptonu w pokarmie zespołów jest we wszystkich analizowanych zbiornikach zbliżony.

Udział glonów, bakterii i tryptonu organicznego w pokarmie zespołów zooplanktonu uwarunkowany jest przez dwa czynniki:

1) Charakter wybiórczości pokarmowej tych zespołów (fig. 5), który zależy z kolei od składu gatunkowego zespołów: dominacji makrofiltratorów (oligotrofia) lub mikrofiltratorów i sedymentatorów (eutrofia) w zespołach konsumentów planktonowych (tab. III);

2) Wielkość i charakter produkcji pierwotnej oraz produkcji bakterii w pelagialu: pelagial jezior eutroficznym charakteryzuje się małym udziałem glonów nannoplanktonowych w ogólnej produkcji pierwotnej i wysoką produkcją bakterii, natomiast pelagial jezior bliskich oligotrofii – dużym udziałem glonów nannoplanktonowych w ogólnej produkcji pierwotnej i niską produkcją bakterii.

W związku z powyższym wydaje się, że stopień bezpośredniego wykorzystania produkcji pierwotnej przez konsumentów jest większy w pelagialu jezior zbliżonych do oligotrofii, niż w pelagialu jezior eutroficznym, w których znaczna część wyprodukowanej przez producentów masy organicznej może być przez zooplankton wykorzystana dopiero po częściowej destrukcji, bądź w formie komórek bakteryjnych, bądź też niecałkowicie rozłożonych fragmentów komórek roślinnych lub też koagulatów rozpuszczonej materii organicznej pochodzenia roślinnego, bakteryjnego lub zwierzęcego. Wiąże się to ze znacznym rozproszeniem energii na skutek intensywnego metabolizmu mikroorganizmów stanowiących pośrednie ogniwa pomiędzy poziomem producentów i konsumentów (fig. 9).

Nie jest to bez znaczenia dla efektywności wykorzystania produkcji pierwotnej przez konsumentów planktonowych w pelagialu jeziornym. W świetle przedstawionych w pracy wyników można sądzić, że efektywność ta jest większa w jeziorach zbliżonych do oligotrofii niż w jeziorach eutroficznych.

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