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ECOLOGICAL CHARACTERISTICS OF LAKES IN NORTH-EASTERN POLAND VERSUS THEIR TROPHIC GRADIENT

VII. VARIATIONS IN THE QUANTITATIVE AND QUALITATIVE STRUCTURE OF THE PELAGIC ZOOPLANKTON (ROTATORIA AND CRUSTACEA) in 42 LAKES*

ABSTRACT: Changes in species structure and changes in numbers and biomass of Rotatoria and Crustacea in lakes varying as to trophic state, morphometry and degree of pollution have been analysed. On the basis of changes in the dominance of particular species in the biomass of communities ecological groups of organisms were distinguished among Rotatoria and Crustacea, characteristic of lakes of a low and high trophic state. The numbers increased, and to a smaller extent the biomass of Rotatoria as the trophic state increased, but such relation was not observed in the case of Crustacea.

KEY WORDS: Lakes, eutrophication, zooplankton, Rotatoria, Crustacea, bioindication.

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1. INTRODUCTION

First attempts to determine the relation between the trophic state of lakes and the zooplankton colonizing them have been based on a faunistic analysis, thus on searching for a relation between the occurrence (presence or absence) of a given species in the lake and the trophic state. For the first time in Poland investigations of this type have been conducted by Lityński (1925). He has distinguished three ecological zooplankton groups typical of oligotrophic, eutrophic lakes and for water bodies of pond type. Bowkiewicz (1938) has distinguished a community of indicatory organisms (the so-called complex of Entomostraca) consisting of 8 taxonomic units. The full composition of the complex corresponds to oligotrophic lakes and the number of complex species decreases in the eutrophication process. Among later Polish publications one should mention first of all those by: Patalas (1954), Gieysztor (1959), Patalas and Patalas (1966), Radwan (1973) - in which the indicatory character of particular species has been determined on the basis of their frequency of occurrence in a large number of lakes of a different trophic state. These publications give to a greater extent the quantitative data, e.g., numbers of zooplankton or dominance degree of particular species. But as these authors use various methods for estimating the trophic state of lakes und differ in analyses of various elements of zooplankton structure these results are often very difficult to compare.

The aim here is a comprehensive analysis of zooplankton structure (numbers, biomass, specific and group structure) and its changes together with increasing trophic state of lakes differing in morphometry and degree of pollution. Two basic groups forming this community, i.e., Rotatoria and Crustacea, have been taken into consideration.

The material has been obtained during complex studies in order to give ecological characteristics of lakes differing in their trophic state (K a j a k and Z d a n o w s k i 1983).

2. MATERIAL AND METHODS

Zooplankton samples were taken using the 5 l Bernatowicz type sampler. Samples were taken always near the maximal depth of the lake, every 1 metre, and then they were poured together for the layers: epi-, meta- and hypolimnion. In shallow water bodies samples were taken every 0.5 or 0.25 m. These samples were elaborated according to the generally used method (H i l l-b r i c h t - I l k o w s k a and P a t a l a s 1967). However, when estimating the numbers of large and relatively rare species (Leptodora kindtii, Bythotrephes longimanus, Heterocope appendiculata) the whole sample was again surveyed.

The individual weight of particular species was determined according to the relation: length-weight (P e č e n 1965, K l e-k o w s k i and Š u š k i n a 1966, K a r a b i n 1974, R u t t n e r - K o l i s k o 1977). Measurements, including development stages - nauplii, copepodites and adult (Copepoda) or juvenile and adult stages (Cladocera), were made separately for each zooplankton community of lakes examined.

Investigated were shallow water bodies, polymictic ones and also deep dimictic lakes. In order to obtain comparable results, regardless of lake morphometry and degree of water stability, in case of polymictic lakes the data for the entire water column were analysed, whereas in case of dimictic lakes only the epilimnion layer was analysed. According to the thesis about the autonomy of epilimnion in relation to cycles of basic nutrients (G l i-w i c z 1979) the role of metalimnion in deep lakes is similar to that of the bottom in shallow water bodies. Thus during summer stagnation the epilimnion layer with its physico-chemical and biological conditions may be compared with the whole water column of polymictic lakes. And these factors determine significantly the abundance and structure of zooplankton communities (H i l l-b r i c h t - I l k o w s k a 1977).

In the lakes under discussion the samples were taken twice: during spring circulation and summer stagnation in 1977 (dimictic lakes) and in 1978 (polymictic lakes).

The differentiating influence of the climate and the differentiated morphometry of lakes (through various types of water stability) caused that in spring the differentiation of zooplankton structure was first of all due to the effect of abiotic factors (mainly temperature) and not trophic factors (Karabin 1982). Therefore summer stagnation was considered as the best period for a comparative analysis of zooplankton - the data presented in the paper are only for this period.

Table I. The division of lakes discussed into trophic groups

Total phosphorus concentration ($\mu g \cdot l^{-1}$)	Dimictic lakes		Polymictic lakes	
	group	number of lakes	group	number of lakes
< 50	D_I	10	-	-
50-100	D_{II}	6	P_{II}	6
100-300	D_{III}	5	P_{III}	8
> 300	D_{IV}	2	P_{IV}	5

Total phosphorus concentration in upper water layers during summer stagnation was used as a basis for arranging the lakes in the trophic gradient and to divide them into trophic groups (Table I).

3. RESULTS AND DISCUSSION

3.1. Specific and trophic structure of Rotatoria communities

In analysed water layers of lakes examined 54 taxons of rotifers were found. Four classes of their occurrence were distinguished. Class I - "very constant species" (61-100% of lakes examined) had 11 taxons of which only one Keratella cochlearis typica occurred in all lakes examined (Table II). All rotifers in this class were typical euplanktonic organisms. In the next two classes there were only euplanktonic rotifers. The class of "constant" species (41-60% of lakes examined) consisted of 4 species, and the class of "additional" species consisted of 6 species. All other species (61% of found taxons) as "adventitious" species belonged to class IV of constancy (less than 20% of lakes). This class, otherwise than the others, is abundantly represented by organisms for which the pelagial[1] is not the proper life environment. These are littoral or littoral-benthic species, e.g., rotifers of the genera Lecane, Microcodides, Rotaria or Trichocerca (T. porcellus, T. tigris, T. rattus). According to Čujkov (1975) water pollution is connected with the passage of littoral species to the pelagial. This has been also confirmed in lakes examined, where littoral organisms have occurred mainly in the pelagial of polluted or highly eutrophic lakes. Whereas among euplanktonic species from class IV there are rotifers which in the lake pelagial dominate usually in spring - Polyartha dolichoptera, species of the genus Synchaeta.

In order to determine the relation between the trophic state of lakes and the species structure of Rotatoria communities a dominance criterion of each species in the biomass of the whole community has been used, more precisely the character of changes in this dominance as the trophic state of lakes increases. Proper analysis on the basis of the contribution of particular species to their total biomass should have all elements of this biomass in a similar class of size. But heavy individual weight of species of the genus Asplanchna at their varying occurrence may affect significantly the absolute biomass of the whole community and, what is very important, the estimation of the degree of dominance of particular species in the biomass of rotifer community. Therefore when analysing the structure of this community on the basis of biomass the genus Asplanchna has not been taken into consideration, because it requires a separate approach.

The analysis of over 70 lakes (including those discussed here) arranged in the trophic gradient and according to the above criterion of species dominance in the biomass of the community has allowed to distinguish 3 ecological groups of Rotatoria having individual reactions to the directional change of lake trophic state (Karabin 1982). The relative biomass, i.e., percentage of the community of group I in biomass decreases as the trophic state increases, relative biomass of group II increases, where-

[1]For practical reasons the term "pelagial" is used also for shallow lakes.

Table II. Rotatoria species and their frequency in lakes examined

Class of constancy	Species	Number of lakes	Per cent of lakes
I Very constant	Keratella cochlearis typica Gosse	42	100.0
	K. c. tecta Gosse	33	78.6
	Kellicothia longispina (Kell.)	32	76.2
	Polyarthra vulgaris Carl.	31	73.8
	Synchaeta kitina Rouss.	31	73.8
	Trichocerca similis (Wierz.)	31	73.8
	Pompholyx sulcata Huds.	30	71.4
	Collotheca mutabilis (Huds.)	28	66.6
	Conochilus unicornis Rouss.	27	64.3
	Ascomorpha saltans Bartsch	26	61.9
	Trichocerca rousseleti (Voight)	26	61.9
II Constant	Keratella quadrata Müller	25	59.5
	Trichocerca capucina (Wierz. et Zach.)	22	52.4
	Polyarthra major Burck.	21	50.0
	Filinia longiseta (Ehrb.)	19	45.2
III Additional	Trichocerca pusilla (Jenn.)	16	38.0
	Asplanchna priodonta Gosse	16	38.0
	Anuraeopsis fissa (Gosse)	16	38.0
	Gastropus stilifer Imhof	14	33.3
	Polyarthra remata Skorikov	13	30.9
	Brachionus angularis Gosse	12	28.6
	Microcodides sp.	8	19.0
	Cephalodella catellina (Müller)	7	16.7
	Chromogaster ovalis (Berg.)	7	16.7
	Ascomorpha ecaudis Perty	4	9.5
	Trichocerca cylindrica (Imhof)	4	9.5
	Lecane (M.) arcuta (Bryce)	4	9.5
	Trichocerca porcellus (Gosse)	3	7.1
	Synchaeta pectinata Ehrb.	3	7.1

IV Adventitious	Euchlanis dilatata Ehrb.	3	7.1
	Brachionus calyciflorus Pall.	3	7.1
	Bdelloidae	3	7.1
	Conochilus hippocrepis (Schr.)	3	7.1
	Brachionus quadridentatus Herm.	3	7.1
	Asplanchna girodi Guerne	2	4.8
	Trichocerca tigris (Müller)	2	4.8
	Trichocerca stylata (Gosse)	2	4.8
	Synchaeta oblonga Ehrb.	2	4.8
	Proales sp.	2	4.8
	Lepadella patella (Müller)	2	4.8
	Brachionus diversicornis (Dad.)	2	4.8
	Polyarthra euryptera Wierz.	2	4.8
	Colurella uncinata (Müller)	1	2.4
	Trichocerca rattus (Müller)	1	2.4
	Synchaeta stylata Wierz.	1	2.4
	Lophoharis salpina (Ehrb.)	1	2.4
	Brachionus rubens Ehrb.	1	2.4
	B. budapestanensis Dad.	1	2.4
	Keratella testudo (Ehrb.)	1	2.4
	Testudinella patina (Herm.)	1	2.4
	Filinia terminalis (Plate)	1	2.4
	Hexarthra mira (Huds.)	1	2.4
	Rotaria neptunia (Ehrb.)	1	2.4
	Polyarthra dolichoptera Idelson	1	2.4

as species from group III show no relation between their contribution to the biomass of rotifer community and the trophic state. Thus the I ecological group can be considered as an indicatory one for lakes of a low trophic state, and group II - for lakes of a high trophic state.

Group I consists of 5 species: Chromogaster ovalis, Conochilus hippocrepis, Ascomorpha ecaudis, Gastropus stilifer and Polyarthra major. Only one of these species - Ch. ovalis - is considered as a typical indicatory organism of lakes having low trophic state (P e j l e r 1957, R a d w a n 1973). C h a b e r m a n (1975) has also connected the occurrence of C. hippocrepis with mesotrophic lakes. Other species are not considered as indicatory ones. But in the above mentioned papers the indicatory character of a given species has been judged by its frequency of occurrence

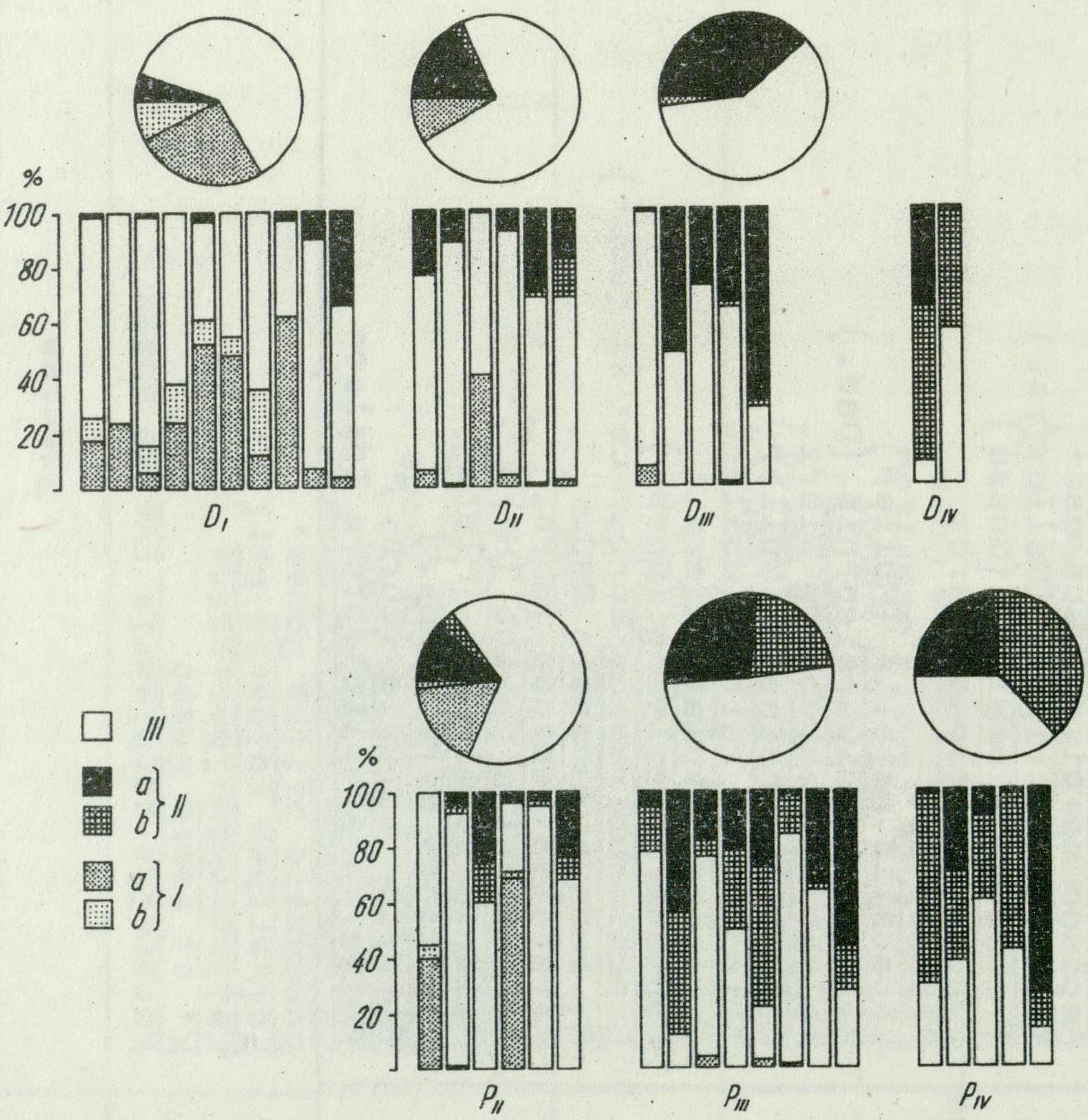

Fig. 1. Changes in dominance (per cent of biomass) of ecological groups of Rotatoria in particular lakes (columns) and mean values for distinguished trophic groups of lakes (circles)
I - I ecological group (a - Polyarthra sp., b - remaining species), II - II ecological group (a - Keratella cochlearis tecta, K. quadrata, Pompholyx sulcata, b - remaining species), III - III ecological group. D. and P explained in Table I

in lakes of a specified trophic state. And, e.g., Polyarthra major, a species dominant in the biomass of the I ecological group and deciding practically about its indicatory character (Fig. 1), has occurred in 50% of all lakes examined and in 78% of dimictic lakes.

The II ecological group of Rotatoria is quite abundant and consists of: Keratella cochlearis tecta, Keratella quadrata, Pompholyx sulcata, Filinia longiseta, Trichocerca pusilla, Anuraeopsis fissa, Brachionus angularis and other species of this genus, and also Microcodides sp. and Bdelloidae. Three first species, most abundant and frequently deciding about the biomass of this ecological group (Fig. 1), are also the most frequently occurring ones in lake pelagial (Table II). The majority of species forming this group are commonly considered as indicatory for highly eutrophic lakes (Järnefelt 1952, Pejler 1957, 1964, Radwan 1973). An exception are: Microcodides sp. and Bdelloidae - organisms typical of the littoral of shallow water bodies.

In all lakes with low trophic state (D_I) organisms from the I ecological group have been forming 4-62% of biomass of rotifer communities (33% on the average) (Fig. 1). In more eutrophic dimictic lakes (D_{II}) the significance of this group visibly decreases (only 10% of the biomass of the community). In polymictic lakes of a similar fertility (P_{II}) rotifers from the I ecological group have been found less frequently, although sometimes quite abundantly (up to 70% of biomass of the community). Whereas in polymictic and dimictic lakes, where phosphorus concentration exceeds 100 $\mu g \cdot l^{-1}$ the organisms from the I ecological group have been found sporadically and in small numbers (less than 4% of biomass), and in the most eutrophic lakes (D_{IV}, P_{IV}) they have not been found at all.

But in these lakes the II ecological group has been significant in the biomass of rotifer communities (Fig. 1). In most eutrophic lakes organisms from this group have constituted 41-92% of Rotatoria biomass. They do not always occur in not very fertile dimictic lakes (D_I), in lake groups D_{II} and P_{II} they are practically a constant element of rotifer communities, and in lakes of a phosphorus concentration exceeding 100 $\mu g \cdot l^{-1}$ (D_{III}, P_{III}) they are a significant part of community biomass (on the average 38 and 48%, respectively).

With the increasing lake trophic state the specific structure within the II ecological group is reconstructed. Most common species of this group: Keratella cochlearis tecta, K. quadrata, Pompholyx sulcata (Fig. 1) lose their dominance in favour of other species, especially Anuraeopsis fissa and Trichocerca pusilla. This phenomenon is characteristic mainly of many very eutrophic polymictic lakes (P_{III}, P_{IV}), although it has been observed in two extremely polluted dimictic lakes (D_{IV}).

Characteristic of polymictic lakes is also the less stable dominance structure of distinguished ecological groups as compared to dimictic water bodies of a similar degree of water fertility. A similar phenomenon has been observed by S p o d n i e w s k a (1983) for phytoplankton of these lakes.

The trophic status of Rotatoria species is much differentiated (G l i w i c z 1974). But here it has been necessary to distinguish on the basis of literature data (E r m a n 1962, G l i w i c z 1974, D u m o n t 1977, P o u r r i o t 1977) the two basic groups of organisms of a trophic status connected with two main components of rotifer food in the lake environment. These are: group I - organisms for which the main source of food is the nannophytoplankton. These are species of the genera Polyarthra and Synchaeta.

Group II - (a) species feeding on a suspension of bacteria and detritus (Anuraeopsis fissa, Keratella cochlearis, Conochilus unicornis, Brachionus angularis, Pompholyx sulcata, Filinia longiseta, (b) species which, apart from the suspension of bacteria and detritus, feed to a large extent on small algae typical of eutrophy (remaining species of the genus Brachionus).

In the phytoplankton of lakes having low trophic state usually small nannoplanktonic algae dominate (S p o d n i e w s k a 1983). Thus species of the genera Polyarthra and Synchaeta, organisms for which nannophytoplankton is the basic source of food, form in these lakes on the average 50% of biomass of rotifer zooplankton (Fig. 2). Also in polymictic lakes of a relatively low trophic state (P_{II}) phytophagous rotifers are almost 50% of Rotatoria biomass.

Together with the advancing eutrophication of lakes, when the dominance of small algae in phytoplankton decreases (S p o d n i e w s k a 1983), the dominance of phytophagous rotifer species also decreases. But the dominance of detritus eating species

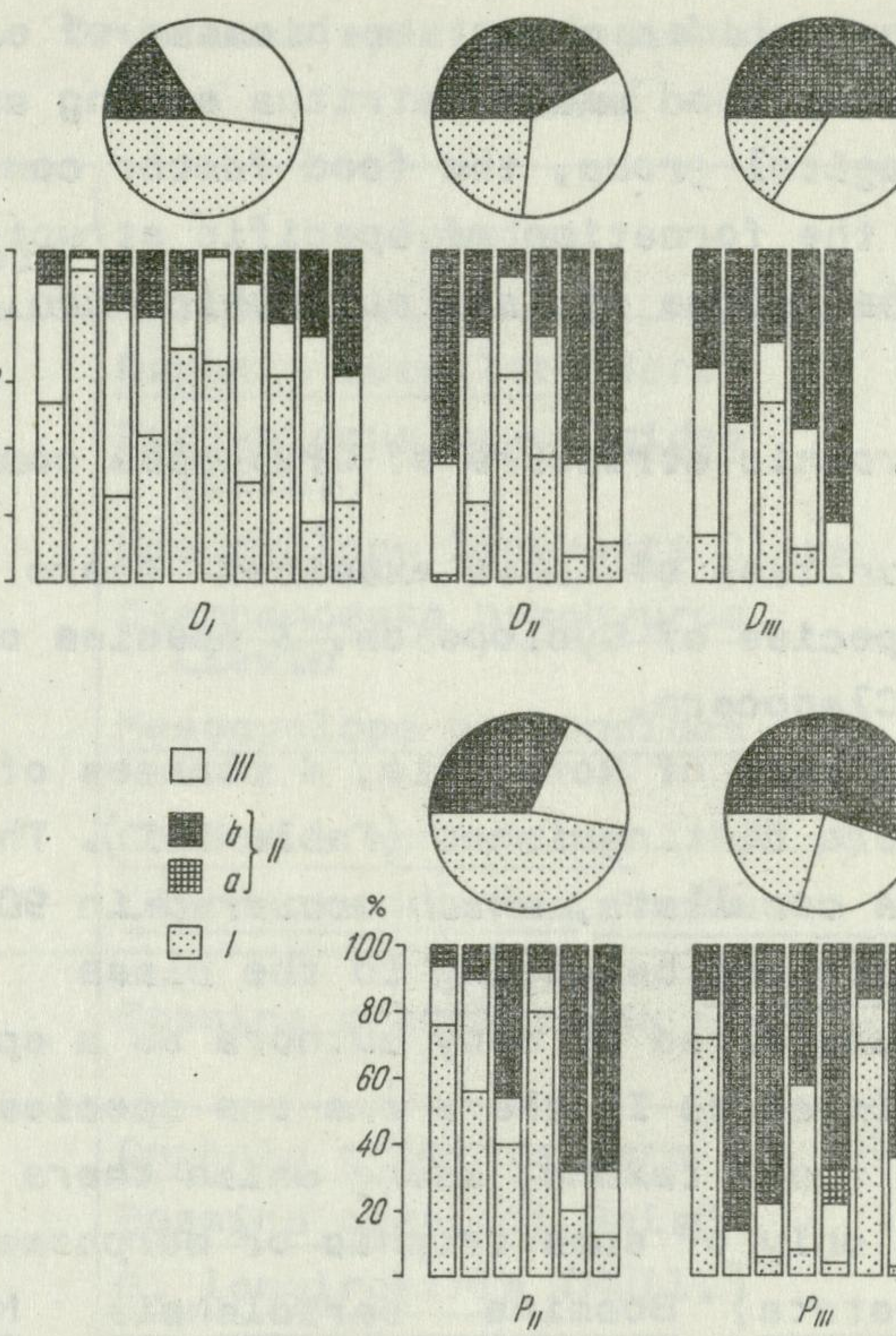

Fig. 2. Changes in dominance (per cent of biomass) of trophic groups of Rotatoria in particular lakes (columns) and mean values for distinguished trophic groups of lakes (circles)
I - I trophic group, II - II trophic group (a - Brachionus sp., b - remaining species), III - remaining species. D and P explained in Table I

increases probably due to the characteristic in highly eutrophic lakes greater significance of the suspension of bacteria and detritus in the food of zooplankton (H i l l b r i c h t - I l k o w s k a 1977). In lakes, where total P concentration exceeds 100 $\mu g \cdot l^{-1}$ the detritus eating rotifers are on the average 50--70% of biomass of the Rotatoria community, and in some cases even over 80% of biomass (Fig. 2). Apart from high dominance of typical detritus eating species in eutrophic polymictic lakes sometimes considerable numbers of species of the genus Brachionus appear, in the food of which, besides bacteria and detritus, quite significant are small algae typical of advanced eutrophy.

As a result of changes in abundance and structure of phytoplankton in the lake a significant reconstruction of trophic (food) structure of Rotatoria community takes place. As the phytophagous Polyarthra major decides about the biomass of early distinguished I ecological group, and small detritus eating species about the biomass of II ecological group, the food factor can be considered as significant in the formation of specific structure of Rotatoria community in the course of lake eutrophication.

3.2. Specific and trophic structure of Crustacea communities

In crustacean communities of lakes examined there were 21 Crustacea species: 5 species of Cyclopoida, 3 species of Calanoida and 13 species of Cladocera.

Similarly as in the case of Rotatoria, 4 classes of the constancy of occurrence were distinguished (Table III). The most common species was Daphnia cucullata, which occurred in 90% of lakes examined. Chydorus sphaericus belonging to the class of "very constant" species is considered by many authors as a species typical of the littoral. In class II there was one species, whereas class of constancy III had 7 taxons, among which there were organisms characteristic only of some trophic or morphometric types of lakes - Daphnia cristata, Bosmina beriolensis Mesocyclops hyalinus (P a t a l a s 1954, P a t a l a s and P a t a l a s 1966). In the IV class of constanty there were species occurring in less than 20% of lakes examined. This included littoral organisms (Acanthocyclops viridis, Ceriodaphnia quadrangula) and also Daphnia pulex - a species which does not rather occur in the pelagial of lakes of the temperate zone.

Similarly as in the case of rotifer zooplankton, the relation between the trophic state of lakes and the specific structure of pelagic Crustacea communities was assumed according to the dominance criterion of particular species in total Crustacea biomass. When analysing a large number of lakes of a differentiated trophic state three ecological groups of organisms were distinguished (K a r a b i n 1982).

The changes in relative biomass of these groups in lakes examined are given in Figure 3.

Group I, characteristic of mesotrophic lakes, is formed by: Heterocope appendiculata, Bythotrephes longimanus, Bosmina berolinensis and 3 Daphnia species (D. cristata, D. longispina hyalina galeata, D. cucullata). All these species have been found in the lakes examined. The two first species have been considered in

Table III. Crustacea species and their frequency in lakes examined

Class of constancy	Species	Number of lakes	Per cent of lakes
I Very constant	Daphnia cucullata Sars	38	90.5
	Eudiaptomus graciloides (Lill.)	35	83.3
	Mesocyclops leuckarti Claus	31	73.8
	Diaphanosoma brachyurum Lievin	31	73.8
	Mesocyclops oithonoides Sars	30	71.4
	Chydorus sphaericus (Müll.)	26	61.9
	Leptodora kindtii Focke	26	61.9
II Constant	Bosmina crassicornis	18	42.8
III Additional	Daphnia cristata Sars	16	38.0
	Bosmina coregoni Baird	15	35.7
	B. longirostris (Müll.)	11	26.2
	Daphnia longispina hyalina galeata (Leydig)	10	23.8
	Mesocyclops hyalinus (Rehberg)	9	21.4
	Eudiaptomus gracilis Sars	9	21.4
	Bosmina berolinensis Imhof	9	21.4
IV Adventitious	Ceriodaphnia quadrangula Sars	7	16.7
	Daphnia longispina hyalina pellucida (Leydig)	6	14.2
	Bythotrephes longimanus Leydig	5	11.9
	Cyclops kolensis Lillj.	4	9.5
	Heterocope appendiculata Sars	3	7.1
	Acanthocyclops viridis Jur.	1	2.4
	Daphnia pulex Leydig	1	2.4

Polish hydrobiological literature for many years as indicators of low trophic state (Lityński 1925, Bowkiewicz 1938, Patalas and Patalas 1966). This character is not attributed to B. berolinensis, but Pijanowska (1978) has stated that this species is most frequent in lakes of a low

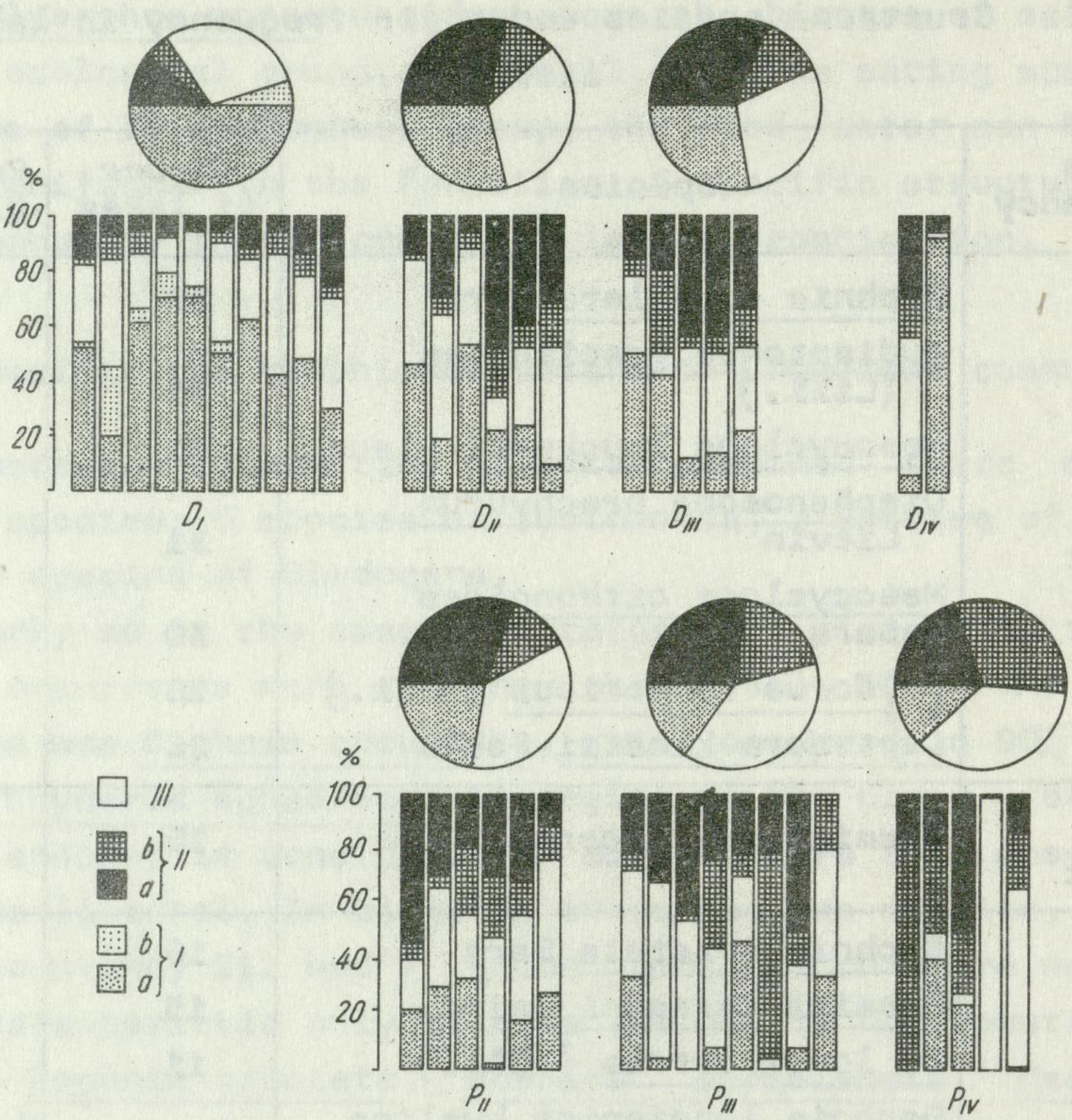

Fig. 3. Changes in dominance (per cent of biomass) of ecological groups of Crustacea in particular lakes (columns) and mean values for distinguished trophic groups of lakes (circles)
I - I ecological group (a - Daphnia sp., b - remaining species), II - II ecological group (a - Mesocyclops sp., b - remaining species), III - III ecological group. D. and P explained in Table I

trophic state. Still, these organisms do not decide about the biomass of the I ecological group and the degree of its dominance in crustacean communities of lakes examined, this is decided by species of the Daphnia genus (Fig. 3), and especially by D. cucullata. Pejler (1964) and Patalas and Patalas (1966) have said that D. cristata and D. longispina hyalina galeata are indicatory species for oligo- and mesotrophy. Although in the case of lakes examined these species occur in water bodies of an advanced trophic state, the decrease in the frequency of their occurrence as the phosphorus concentration in epilimnion increases points to the relation between these species and lakes of a low trophic state.

But the distinct character of relations with the trophic state is typical of the last species from the I ecological group - D. cucullata. Otherwise than other organisms from this group D. cucullata has occurred as frequently in lakes of low trophic state as in those of high trophic state. Thus the presence of this species in the lake does not have an indicatory character. But L i t y ń s k i (1925), B o w k i e w i c z (1938) and P e j l e r (1964) have placed D. cucullata among species indicating the eutrophy. It should be also mentioned that other species, when present in pelagial, have been connected by these authors with eutrophy (D. brachyurum, E. graciloides, L. kindtii), although in the lakes examined they have been most frequently occurring and are placed in the I class of constancy. These results confirm the opinion of P a t a l a s (1954) that species considered by L i t y ń s k i (1925) and B o w k i e w i c z (1938) as characteristic of the eutrophy are not indicatory organisms strictly speaking. The reason for placing D. cucullata in the I ecological group is the decrease in the dominance of this species as the trophic state in lakes increases (K a r a b i n 1982).

In the group of lakes having the lowest trophic state (D_I) D. cucullata covered 20-70% of biomass of the community of Crustacea (on the average 51%). With the advancing eutrophication the dominance of this species decreases, becoming on the average 29-28% of crustacean biomass in dimictic lakes (D_{II}, D_{III}) and 22, 16 and 13%, respectively, in polymictic lakes (P_{II}, P_{III}, P_{IV}). It is interesting that in 4 out of 13 polymictic lakes of a phosphorus concentration exceeding 100 $\mu g \cdot l^{-1}$ this species has not been found in the pelagial. An exception of this principle is the strongly polluted Sztumskie Lake from group D_{IV} in which D. cucullata is 92% of biomass of Crustacea.

The II ecological group consists of: Mesocyclops oithonoides, M. leuckarti, Diaphanosoma brachyurum, Chydorus sphaericus, Bosmina longirostris, B. coregoni thersites. The four first species, similarly as D. cucullata, are the "very constant" components of communities examined. Thus, neither their presence nor absence in lake pelagial but their contribution to biomass of communities decide about the indicatory character of these organisms and also of the entire group.

Increase of phosphorus concentration from 20-44 to 59-87 $\mu g \cdot l^{-1}$ in dimictic lakes is connected with a considerable, almost two-fold, increase of the significance of II ecological group in the formation of the biomass of crustacean community

(Fig. 3). Further, even very high, increase of phosphorus concentration does not cause such significant changes in the structure of the community; relative biomass (dominance) of II ecological group gradually increases, but these are not great changes. For this reason and because of great fluctuations in the dominance of this group in many extremely eutrophic and polluted lakes (P_{III}, P_{IV}, D_{IV}) changes in the dominance of II ecological group have an indicatory character only in the case of lakes having a relatively low trophic state.

As the trophic state increases the internal structure of II ecological group is being reconstructed (similarly as in the case of Rotatoria). Although in lakes of a lower trophic state species of the genus Mesocyclops decide primarily about the biomass of this group, in shallow, highly eutrophic lakes (P_{III}, P_{IV}), the increasing significance of Cladocera species is characteristic (Fig. 3). In two of these lakes B. longirostris population developed to such an extent that it was 75% of biomass of the whole crustacean community.

According to many authors (e.g., P a t a l a s and P a t a l a s 1966, B r o o k s 1969, C h a b e r m a n 1975) the increase in the dominance of Chydorus sphaericus is connected with the eutrophication process. Such relation has been also observed in lakes examined, but only in stratified (dimictic) water bodies. Still, in extremely eutrophic and polluted polymictic lakes, this species is again scarce - out of 5 lakes from group P_{IV} this species occurred only in one lake.

All the remaining crustacean species belong to the III ecological group - their occurrence and degree of dominance are not connected with the trophic state of lakes (Fig. 3). The dominant species in this group is Eudiaptomus graciloides, commonly occurring in lakes varying in trophic state, sometimes very numerously, up to 50% of biomass of the entire crustacean community.

Because of varying trophic degree and differentiation in dimictic and polymictic lakes, and because of no relation between the phosphorus concentration (as the trophic state indicator) and the changes in group structure in highly eutrophic lakes, the distinguished ecological groups of Crustacea in polymictic lakes do not have an indicatory character.

When analysing the zooplankton structure three groups of organisms: Cladocera, Calanoida and Cyclopoida, are usually distinguished. This commonly applied division, although based on taxonomic characters, is justified not only by biological and physiological differences, but also by the ecological ones of these groups. This is confirmed by the fact that species deciding about the biomass of taxonomic groups are simultaneously species deciding about the biomass, and thus about the indicatory character of distinguished ecological groups. In the majority of lakes discussed the basic biomass component of Cladocera are species of the Daphnia genus, which (especially D. cucullata) decide about the indicatory character of group I. On the other hand, organisms, which usually decide about the dynamics of dominance changes of II (Mesocyclops sp.) and III ecological group (Eudiaptomus sp.), are 90-100% of biomass of Cyclopoida and Calanoida. Thus, the conducted in a large number of lakes, analysis of contribution of Calanoida, Cyclopoida and Cladocera to the biomass of the community shows that only in the two latter groups there is a high, statistically significant correlation between their dominance in the community and the trophic state of lakes (K a r a b i n 1982).

As the considerable, but not connected with the trophic state, fluctuations in numbers of Calanoida, are responsible for the dominance degree of these two groups the relationship of Cyclopoida and Cladocera biomass ($B_{cyclop.} \cdot B_{cladoc.}^{-1}$) has been assumed as the indicator of changes of group structure of crustacean zooplankton. The character of changes of this indicator as the trophic state increases is due to regularities already observed, which concern changes in the dominance of distinguished ecological groups and species or genera belonging to them. And so, in dimictic lakes of a low trophic state (D_I), the biomass of Cladocera is on the average 4 times higher than the biomass of Cyclopoida, and this relation is relatively constant (Fig. 4).

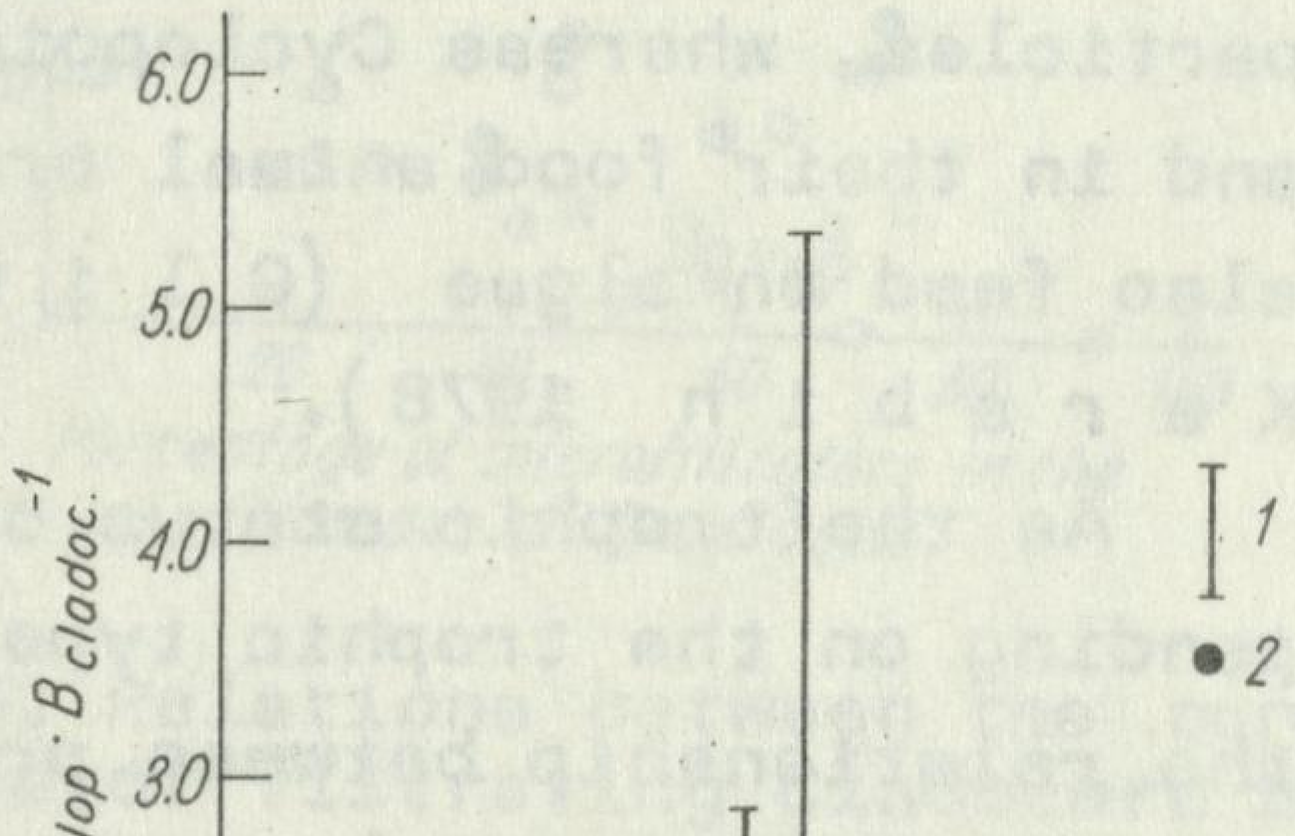

Fig. 4. The changes in the range (1) and of mean values (2) of biomass ratio of Cyclopoida and Cladocera in distinguished trophic groups of lakes D and P explained in Table I

With the increasing eutrophy of lakes the biomass of Cyclopoida increases proportionally, and in many moderately eutrophic lakes (P_{II}, D_{II}) it is equal or 1.5 times higher than the biomass of Cladocera. As it has been already observed, in highly eutrophic lakes (D_{III}, P_{III}), the dominance of Mesocyclops does not show a tendency to increase. Even the biomass of these organisms decreases (K a r a b i n 1982). Thus, apart from few lakes, where the biomass of Cyclopoida surpasses (2.8-5.8 times) that of Cladocera, this indicator in other lakes from group III does not increase or tends to decrease. In extremely eutrophic and polluted lakes (P_{IV}) this decrease is even greater. Owing to the growth of cladocerans characteristic of the eutrophy the total biomass of Cladocera is in these lakes again higher than that of Cyclopoida - twice on the average (Fig. 4).

The division on the basis of taxonomic criteria is almost such as the division into groups varying in their trophic status. Cladocera are microfiltrators feeding on nannoplankton and detritus, and Calanoida are macrofiltrators feeding on considerably big food particles, whereas Cyclopoida are animals which hunt actively and in their food animal organisms prevail, although they may also feed on algae (G l i w i c z 1974, M o n a k o v 1976, K a r a b i n 1978).

As the trophic status of Cyclopoida may change radically depending on the trophic type of the lake (G l i w i c z 1974), the relationship between predatory and non-predatory components of zooplankton under conditions of changing trophic state requires a detailed and comprehensive analysis, far beyond the subject of this paper.

In lakes examined the macrofiltrators are represented by 2 Eudiaptomus species. The analysis of a large group of lakes, consisting of lakes discussed here, has not shown a relation between the biomass and dominance of Eudiaptomus and the lake trophic state and phytoplankton biomass. No correlation has been observed with the nannophytoplankton biomass - basic food of these copepods (K a r a b i n 1982). These results do not allow to determine why the occurrence of Eudiaptomus has such a character, but may suggest that the food itself is not a limiting factor. Especially as in the majority of lakes examined the biomass of nannophytoplankton exceeds 1 mg $\cdot$ l^{-1} (S p o d n i e w s k a 1983), and this acc. to M a l o v i c k a and S o r o k i n (1961) satisfies the food requirements of Eudiaptomus. Perhaps the lack of relation between the trophic state of lakes and the biomass of macrofiltrators and their role in the community of Crustacea is due to the biology of their growth. The fluctuations of these two parameters may be the result of periodical decrease and increase in the numbers of Calanoida due to the cyclic character of their reproduction (cohorts).

The filtrating Cladocera in lakes examined have been divided according to works by G l i w i c z (1969, 1974, 1977) into two groups:

1. "Inefficient" microfiltrators. The largest food particles do not exceed 2-5 µm, narrow spectrum of the size of filtrated particles. To this group belong Chydorus sphaericus and Diaphanosoma brachyurum.

2. "Efficient" macrofiltrators. The biggest size of food particles is 10-12 µm, broad spectrum of the size of filtrated particles. This group contains the remaining pelagic species of Cladocera, mainly Daphnia.

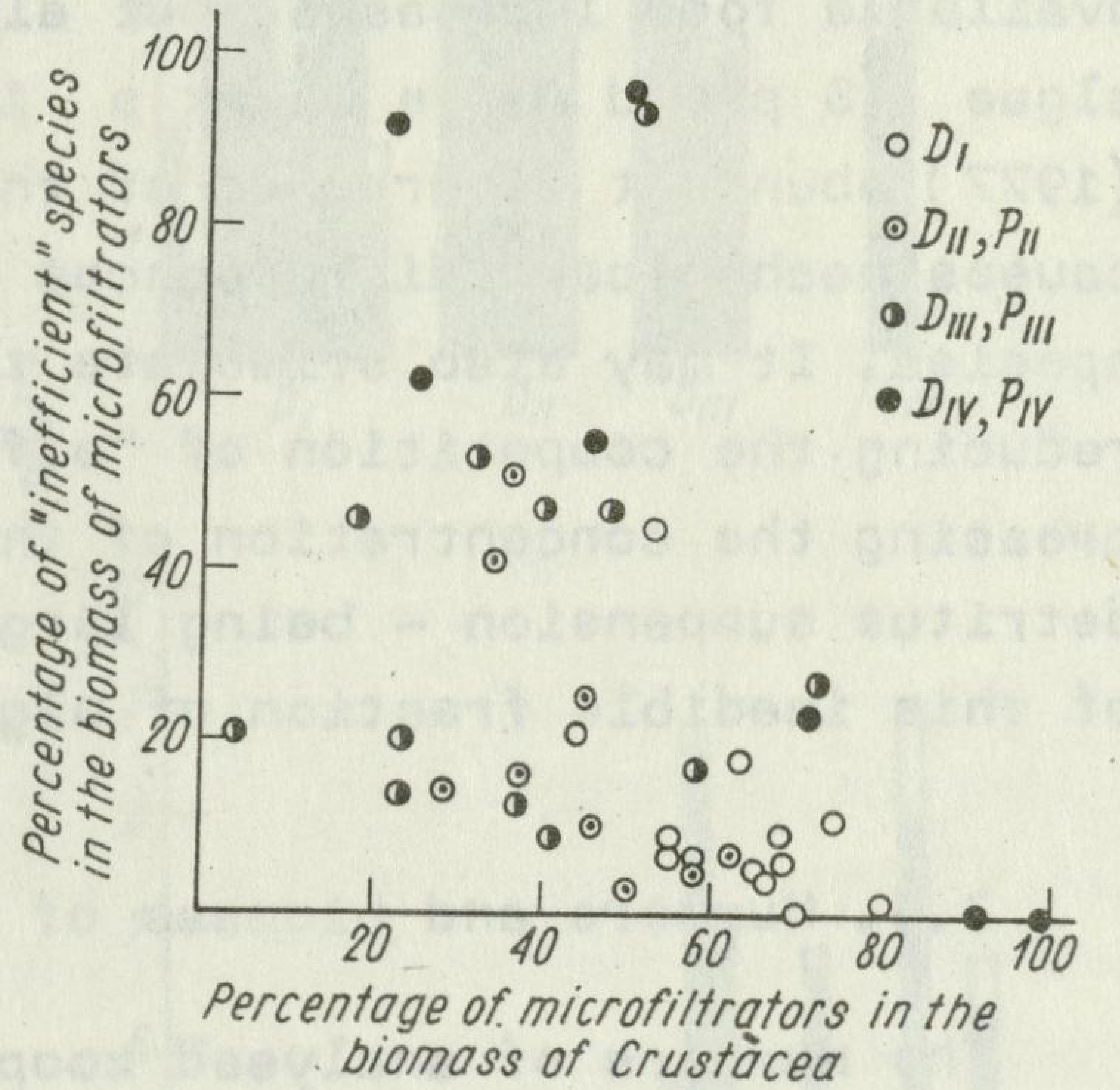

Fig. 5. Relations between the percentage of filtrating Cladocera in the biomass of Crustacea and the percentage of "inefficient" species in the biomass of these filtrators - in lakes of a different trophic state

D and P explained in Table I

The significance of distinguished groups of macrofiltrators and the relationships among them in water bodies of various trophic state are illustrated by Figure 5 showing the relations between the percentage of all microfiltraters in the biomass of Crustacea community and the percentage of "inefficient" species in the biomass of macrofiltrators. In all lakes of a low trophic state (D_I) the microfiltrators dominate covering over 50% of Crustacea biomass, and the percentage of "inefficient" species does not exceed 10% of biomass of macrofiltrators. With the increasing degree of eutrophication of lakes the dominance of macrofiltrators in the community decreases at a simultaneous increase in the significance of "inefficient" species.

The cause for such differentiated reaction of the distinguished group of microfiltrators to a trophic state increase may be structural changes within the phytoplankton. The "efficient" species, of a broader spectrum of the size of consumed particles, obtain from the same volume of filtrated water more food than the "inefficient" species. Thus in lakes of a low trophic state with low food concentration the "efficient" microfiltrators find relatively better food conditions and therefore become dominant. With the increasing trophic state not only the concentration of available food increases, but also the concentration of big "net" algae (S p o d n i e w s k a 1983). According to G l i w i c z (1977) abundant occurrence of these large phytoplankton forms causes mechanical disturbances in the filtration of "efficient" species. It may also stimulate the development of these species by reducing the competition of "efficient" microfiltrators and by increasing the concentration of their best food - a bacteria and detritus suspension - being largely the effect of decomposition of this inedible fraction of algae.

3.3. Numbers and biomass of zooplankton in lakes examined

The numbers of analysed zooplankton communities (Rotatoria and Crustacea) fluctuated in lakes examined between 221 and 16005 ind. $\cdot l^{-1}$ (Fig. 6). Rotifers decided aboud the abundance of the community, and especially about its high values exceeding 1000 ind. $\cdot l^{-1}$. In lakes of a low trophic state (D_I) the numbers of Rotatoria ranged between 128 and 409 ind. $\cdot l^{-1}$; 40-50% of all zooplankton numbers. Lake Bartąg was an exception. With the increasing trophic state the numbers of rotifers increased gradually so that in few shallow, highly eutrophic lakes (P_{III}, P_{IV}) the numbers exceeded 7000 ind. $\cdot l^{-1}$. In these lakes Rotatoria were over 90% of zooplankton numbers.

But no relation was observed between the lake trophic state and the numbers of Crustacea (Fig. 6). Independently of the phosphorus concentration it ranged between 35-634 ind. $\cdot l^{-1}$.

Because of great differences in the individual weight of Rotatoria and Crustacea the crustaceans decided practically about the biomass of pelagic zooplankton. Their biomass was 0.6--9.27 mg $\cdot l^{-1}$, and these changes, similarly as in the case of the numbers, were not connected either with the trophic state of lakes

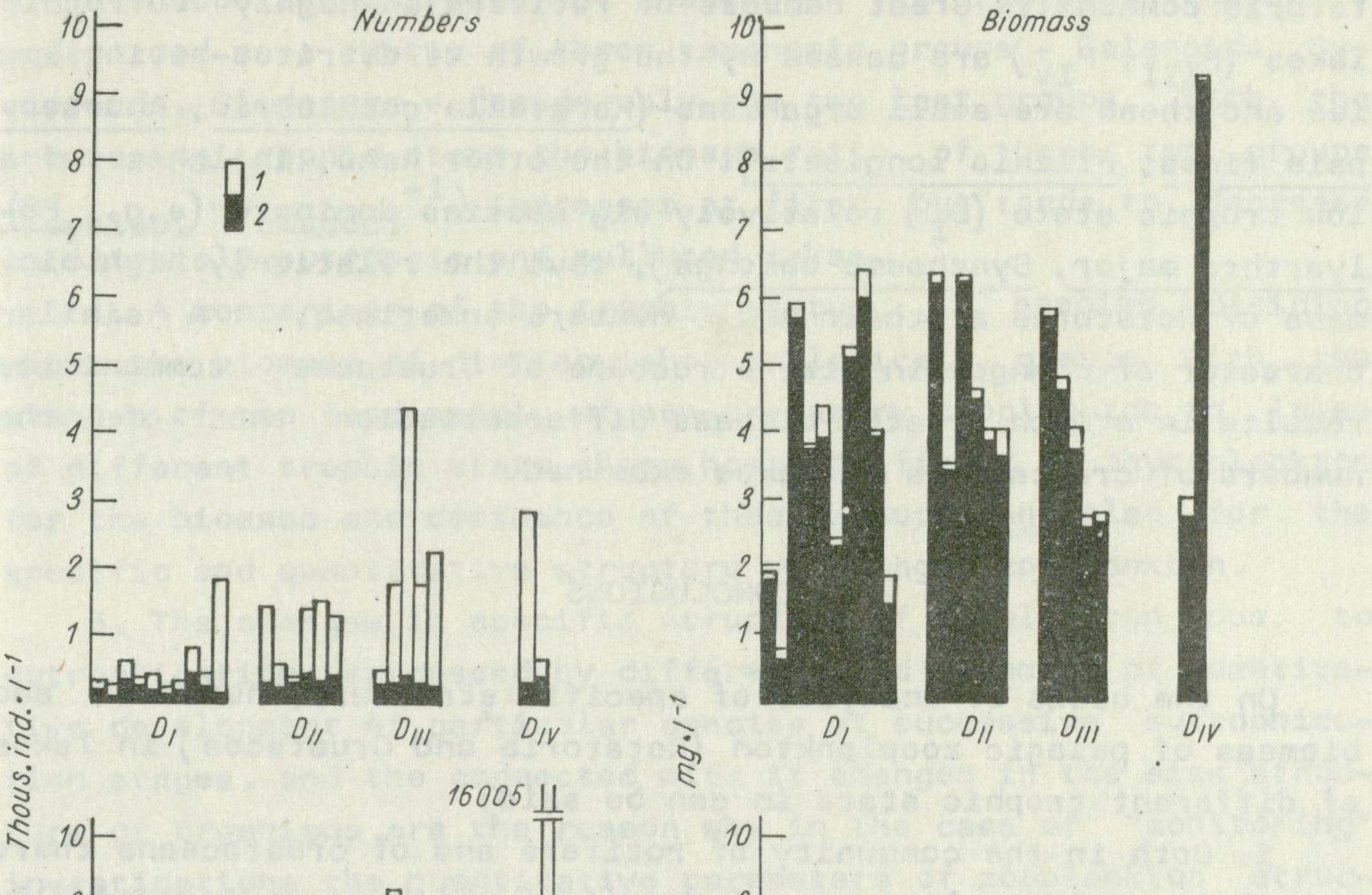

Fig. 6. Changes in numbers and biomass of Rotatoria (1) and Crustacea (2) in lakes examined
D and P explained in Table I

or with the degree of their pollution. But the biomass of Rotatoria increased with the trophic state. Especially in polymictic lakes.

As related to the rapidly increasing numbers of rotifers the increase of their biomass is relatively smaller. This is due to the above discussed changes in the specific structure of the Rotatoria community. Great numbers of rotifers in highly eutrophic lakes (P_{III}, P_{IV}) are caused by the growth of detritus-eating species and these are small organisms (Keratella cochlearis, Anuraeopsis fissa, Filinia longiseta). On the other hand, in lakes of a low trophic state (D_I) relatively big species dominate (e.g., Polyarthra major, Synchaeta oblonga), thus the relatively high biomass of Rotatoria at their small numbers sometimes. A similar character of changes in size structure of Crustacea communities results in a much greater biomass differentiation than of the numbers of crustaceans in lakes examined.

4. CONCLUSIONS

On the basis of analysis of specific structure, numbers and biomass of pelagic zooplankton (Rotatoria and Crustacea) in lakes of different trophic state in can be said:

1. Both in the community of rotifers and of crustaceans there are three ecological groups of organisms which react individually to changes in trophic state: group I - its dominance in the biomass of the community decreases as the trophic state increases, group II - the dominance increases, group III - no relation between the trophic state of lakes and the dominance in the biomass of the community.

2. Such character of reaction to changes in trophic state allows to acknowledge the I and II ecological group of rotifers and crustaceans as communities for trophic state indication. In lakes of north-eastern Poland the characteristic communities of lakes of a low trophic state (I group) are formed by: in rotifer zooplankton - Chromogaster ovalis, Conochilus hippocrepis, Ascomorpha ecaudis, Gastropus stylifer and Polyarthra major; in crustacean zooplankton - Heterocope appendiculata, Bythotrephes longimanus, Bosmina beriolinensis, Daphnia cucullata, D. cristata and D. longispina hyalina galeata. Whereas as characteristic of lakes of a high trophic state (II group) are: Keratella cochlearis tecta, K. quadrata, Pompholyx sulcata, Trichocerca pusilla, Anuraeopsis fissa, species of the genus Brachionus, and also Microcodides sp. and Bdelloidae (rotifer community) and Mesocyclops leuckarti, M. oithonoides, Diaphanosoma brachyurum, Chydorus sphaericus, Bosmina longirostris, B. coregoni thersites.

3. About the character of changes in the Crustacea community understood as a system of three taxonomic groups - Calanoida, Cyclopoida, Cladocera - decide only the two last groups. With the increasing trophic state the biomass ratio of these two groups ($B_{cyclop.} \cdot B_{cladoc.}^{-1}$) increases at first, but tends to decrease in extremely eutrophic and polluted lakes.

4. A comparison of the trophic status of species deciding about the biomass of distinguished ecological groups with the changes of the food supply of non-predatory zooplankton in lakes of different trophic state shows how significant is phytoplankton for the biomass and dominance of these groups, and also for the specific and quantitative structure of pelagic zooplankton.

5. The changes in specific structure of zooplankton due to eutrophication, expressed by differentiated dynamics of quantitative development of particular species at successive eutrophication stages, and the connected with it changes in the size structure of organisms are the reason why in the case of "monitoring" investigations the quantitative parameters of zooplankton structure (numbers, biomass) are not representative for a specific trophic type of lakes. Only changes in the numbers of Rotatoria are directly connected with the increasing trophic state in lakes.

5. SUMMARY

Changes in specific structure and in the abundance of pelagic zooplankton were analysed in 42 lakes, differentiated in their morphometry and trophic state (Table I). The presence of 54 taxons of Rotatoria and 21 taxons of Crustacea was recorded. Their frequency of occurrence was determined (Tables II, III).

Both in the rotifer and crustacean community of these lakes three ecological groups of organisms have been distinguished. The dominance of the I ecological group in the biomass of the community decreases together with the trophic state increase, the dominance of group II increases, whereas there is no relation between the trophic state and the dominance of the III group in the biomass of communities (Figs. 1, 3). This allows to acknowledge the I and II ecological group as communities indicating the low and high trophic state.

Comparison of changes in the trophic status of dominant species in rotifer and crustacean communities of lakes at particular eutrophication stages (Figs. 2, 5) proves the significance of phytoplankton in the formation of zooplankton structure.

The biomass ratio of Cyclopoida and Cladocera ($B_{cyclop.} \cdot B_{cladoc.}^{-1}$) increases at first with a trophic state increase, but tends to decrease again in extremely eutrophic lakes (Fig. 4).

Quantitative parameters of zooplankton structure (numbers, biomass) undergo considerable fluctuations, independently of lake trophic state. Only the changes in numbers of Rotatoria are connected with an increase in trophic state of water bodies examined (Fig. 6).

6. POLISH SUMMARY

Analizowano zmiany struktury gatunkowej i obfitości zooplanktonu pelagicznego w 42 jeziorach o zróżnicowanej morfometrii i trofii (tab. I). Stwierdzono obecność 54 taksonów Rotatoria i 21 taksonów Crustacea. Oceniono częstotliwość ich występowania (tab. II, III).

Zarówno w obrębie zespołu wrotkowego jak i skorupiakowego tych jezior wyróżniono 3 ekologiczne grupy organizmów. Dominacja I grupy ekologicznej w biomasie zespołu zmniejsza się wraz ze wzrostem trofii, dominacja grupy II wzrasta, natomiast brak jest zależności między trofią a dominacją II grupy w biomasie zespołów (rys. 1, 3). Pozwala to na uznanie I i II grup ekologicznych za zespoły wskaźnikowe niskiej i wysokiej trofii.

Porównanie zmian w statusie troficznym gatunków dominujących w zespołach wrotkowych i skorupiakowych jezior na poszczególnych etapach eutrofizacji (rys. 2, 5) świadczy o istotnej roli fitoplanktonu w kształtowaniu struktury zooplanktonu.

Stosunek biomass Cyclopoida i Cladocera ($B_{cyclop.} \cdot B_{cladoc.}^{-1}$) początkowo rośnie wraz ze wzrostem trofii, jednak w jeziorach skrajnie zeutrofizowanych wykazuje ponowną tendencję spadkową (rys. 4).

Stwierdzono, że ilościowe parametry struktury zooplanktonu (liczebność, biomasa) podlegają znacznym wahaniom, niezależnie od trofii jezior. Jedynie zmiany liczebności Rotatoria związane są ze wzrostem trofii badanych zbiorników (rys. 6).

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