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**PELAGIC ZOOPLANKTON (ROTATORIA + CRUSTACEA)
VARIATION IN THE PROCESS
OF LAKE EUTROPHICATION
II. MODIFYING EFFECT OF BIOTIC AGENTS***

ABSTRACT: In the lakes under study the pressure of planktivorous fish is not a factor causing changes in the quantifiable and structural characteristics of the zooplankton. Neither is the action of invertebrate predators. The results, obtained from the study indicate that the possible causes of changes in the zooplankton numbers, biomass and structure should be found on the one hand in changes in the size structure and biomass of the phytoplankton, and on the other – in the nature of the relationship between the phytoplankton and zooplankton.

KEY WORDS: Lakes, zooplankton, Rotatoria, Crustacea, eutrophication, zooplankton grazing, invertebrate predators, fish pressure.

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1. INTRODUCTION

The pelagic zooplankton community is characterized by the existence of many connections and interrelationships between it and many abiotic and biotic elements of the lake ecosystem, which may in different ways affect the structure, numbers and biomass of this community during the eutrophication process. Among the biotic factors the following must be considered most important: (1) trophic conditions, (2) impact of invertebrate predators, (3) planktivorous fish pressure.

The importance of the effect of food on the numbers and species structure of the zooplankton has been stressed many times (e.g., Nauwerck 1963, Edmondson 1965, Gliwicz 1969a, 1977, Hillbricht-Ilkowska 1977, Hillbricht-Ilkowska, Spodniewska and Węgleńska 1979). As the phytoplankton is the only producer of organic matter in the pelagic zone, it is also the only (leaving out the allochthonous matter) source of food for the zooplankton – direct for phytophagous species, indirect – for detritus-feeders. For this reason, changes that take place in the phytoplankton during eutrophication must be reflected in quantitative and qualitative changes of the non-predatory zooplankton, and consequently, of the predatory zooplankton. There is, however, a feedback here – an important role in determining the species diversity and numbers is attributed to the effect of invertebrate predators (Dodson 1974, Karabin 1974, 1978, Giljarov 1977a, Lane 1978, Matveev 1980). For this reason, the latter type of influence cannot be ignored in any correct assessment of the controlling effect of the biotic factors on the zooplankton communities.

In any analysis of the effect of eutrophication on the zooplankton those biotic factors must also be taken into account which, though not being directly related to the trophic state, can often exert an influence on the zooplankton, thus “masking” the direct effect of the trophic state. Planktivorous fish pressure no doubt should be included among the most important factors of this type. According to the widely accepted Brooks and Dodson's (1965) theory, the pressure of these fish is the main factor affecting the species composition and structure of the crustacean zooplankton. The latter authors and many others (Hrbáček 1962, Sprules 1975, Grygierek 1979, Węgleńska et al. 1979) are of the opinion that a selective feeding mode of fish consisting in preferring large species in the food leads on to a change of the species structure of the crustacean community. On the other hand, Gliwicz and Prejs (1977) have demonstrated that in the Masurian and Pomeranian lakes fish pressure is not a factor that could cause changes in numbers and structure of the crustacean zooplankton.

In the present study an assessment was made of the effect of the above-enumerated biotic factors as the cause of the changes taking place during the lake eutrophication process.

2. MATERIAL AND METHODS

The study covered 64 lakes differing in morphometry, trophic state and degree of pollution (K a r a b i n 1985). Zooplankton samples were collected at the deepest sites of the lakes and studied by routine methods. The results presented cover the summer stagnation period (August), and in the case of the stratified lakes they only concern the epilimnion. Secchi's disc visibility was used for lining up the lakes into a gradient of rising trophic state as expressed by the trophic state index (TSI_{SD}) — C a r l s o n (1977). A detailed description of the methods, and justification of the choice of: a trophic state index, phenological period and the pelagic zone — best for a comparative analysis of the zooplankton can be found in the paper by K a r a b i n (1985).

3. RESULTS AND DISCUSSION

3.1. AN ANALYSIS OF THE EFFECT OF PLANKTIVOROUS FISH ON THE CRUSTACEAN COMMUNITY STRUCTURE

In Polish lakes the following fish species should be considered typically planktivorous: the vendace (*Coregonus albula* L.), lavelat (*Coregonus lavaretus* L.), smelt (*Osmerus eparlanus* L.) and the bleak (*Alburnus alburnus* L.). As there were no other, accurate data, the actual numbers of these species were assessed on the basis of data of the Inland Fisheries Institute, given as average catches of these fish species ($\text{kg}\cdot\text{ha}^{-1}$) over several-year periods. Data for 42 lakes were obtained. The vendace is known to live and reproduce naturally in deep, well-oxygenated water bodies, i.e., usually low-trophic-state lakes. Its occurrence in the lakes under study confirmed this (Fig. 1 A). As the TSI_{SD} increases, the average catches of vendace diminish, and at the same time there are more and more lakes where it does not occur. The vendace is practically already absent from lakes with a TSI_{SD} above 60. A certain increase of catches in lakes with fairly high TSI_{SD} values such as Mikołajskie, Ryńskie, Tałtowisko is the result of a continual introduction of vendace into these lakes, and higher than average efficiency of catches in these lakes (G l i w i c z and P r e j s 1977). But there is no such clear relationship between the trophic state and the size of catches of all planktivorous fish (Fig. 1 B). An initial decrease in catches in lakes with a TSI_{SD} range of 50–60 was followed by their rapid growth to 20 and even up to $60\text{ kg}\cdot\text{ha}^{-1}$ (Lake Mikołajskie). The cause of this growth is disproportionately high bleak catches. As it is a low-value fish, the bleak is not usually an object of intensive catches. For some of the lakes very large average catches of it were recorded. This was due to the fact that some catches were deliberately aimed at catching the largest possible number of bleak. As the

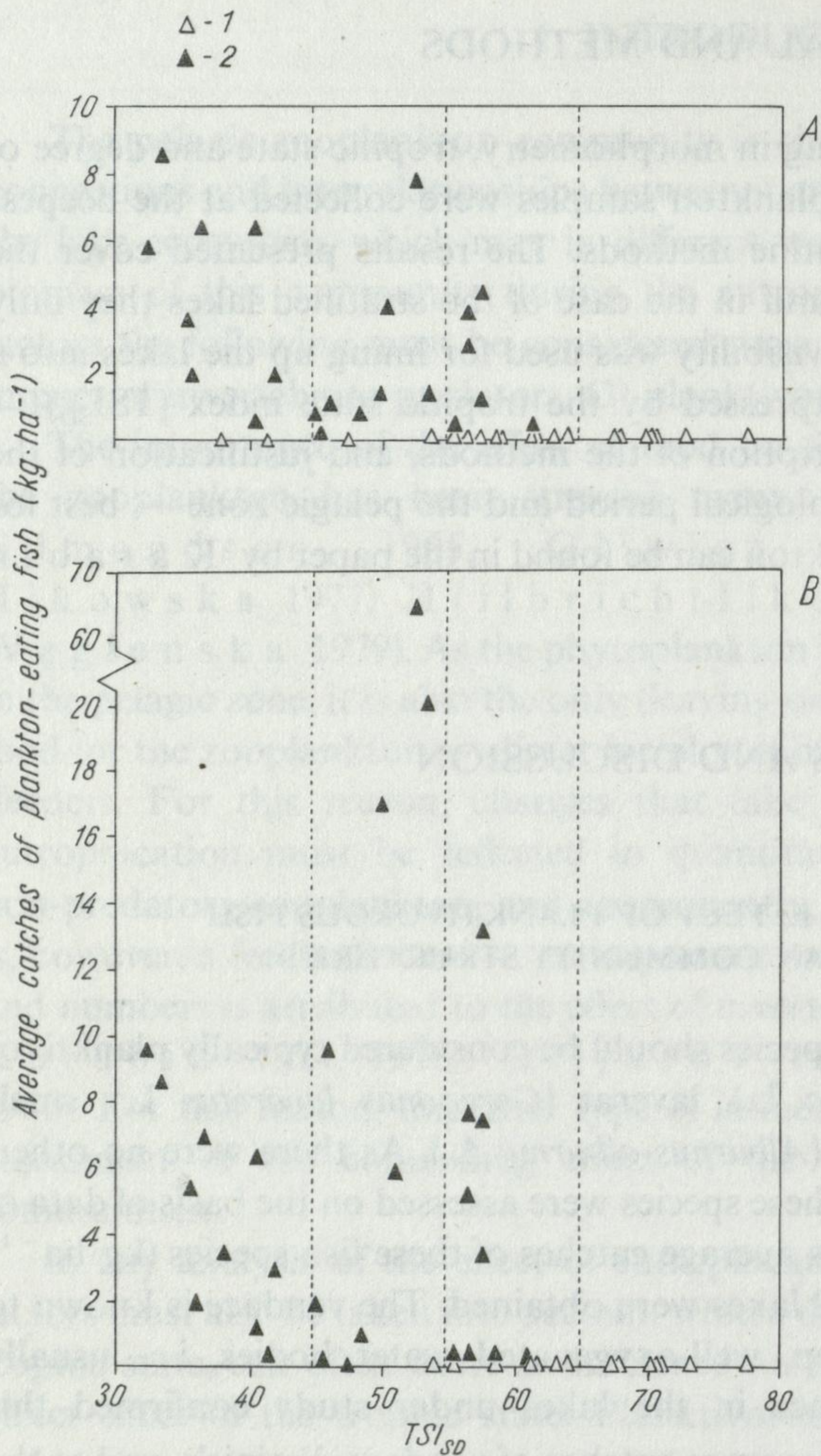


Fig. 1. Occurrence and yearly catches of the vendace (A) and all the plankton-eating fish analysed (B) in the lakes under study — mean values for several years

1 — lakes without plankton-eating fish stock, 2 — lakes stocked with plankton-eating fish

catching efficiency varied from lake to lake, these data can only be used for drawing some rough conclusions on the density of fish in the lakes. For the same reason, it is only possible to make a tentative comparative analysis of the planktivorous fish pressure on the zooplankton.

Following Brooks and Dodson's (1965) hypothesis, it should have been expected, however, that in the group of lakes for a long time inhabited by fish feeding on zooplankton the structure of the crustacean communities would be different from the structure of the communities in the group of lakes without planktivorous ichthyofauna.

Presented in Figure 2 is variation of the structure parameters selected, in relationship to the TSI_{SD} in three groups of lakes with a different abundance of planktivorous fish. As has been found earlier on, a rise in the lake trophic state leads, to a limited extent though, to a growth in numbers of the crustaceans (Karabin

1985). As can be concluded from Figure 2 A, this tendency can be seen in all the three lake groups, regardless of the size of the fish stock. In the eutrophic lakes and in those approaching eutrophy, for instance, large numbers of crustaceans were found, although there were among them lakes devoid of planktivorous fish and lakes where very large numbers of fish were caught. There was no clear impact of fish on the crustacean biomass either (Fig. 2 B) — the biomass does not show any relationship to the trophic state of the lakes or the numbers of planktivorous fish living in them. The results seem to indicate that the presence of planktivorous fish does not decisively affect the numbers or biomass of the crustacean communities of the lakes under study. This agrees with the results obtained by Gliwicz and Prejs (1977). These authors have found that in lakes Mikołajskie and Tałtowisko planktivorous fish pressure is not a biomass-eliminating factor, or one that causes changes in numbers or mortality

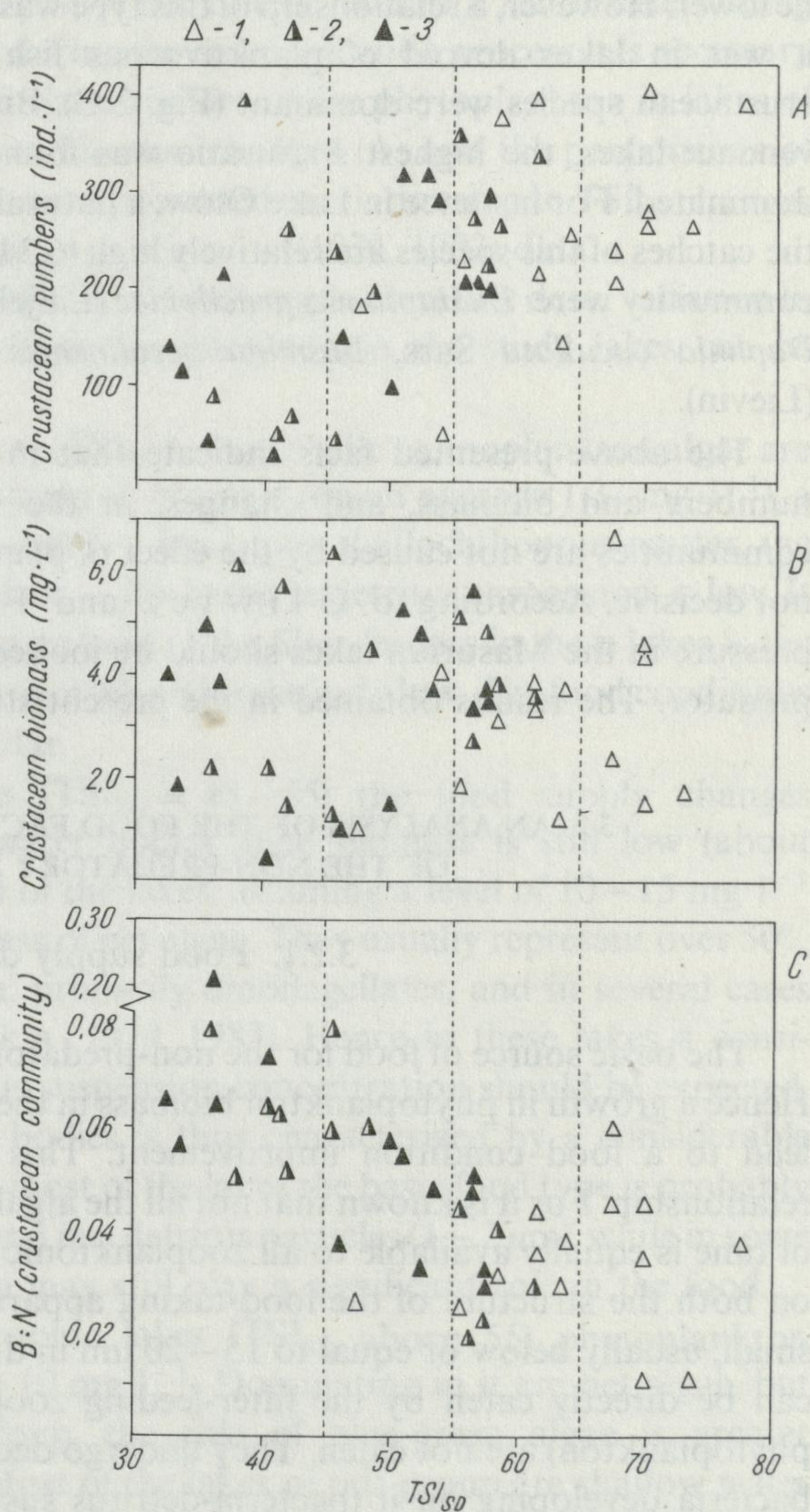


Fig. 2. Variation of the selected structure parameters of the crustacean community (A, B, C) in relation to TSI_{SD} changes in three groups of lakes differing in their plankton-eating fish stock

1 — lakes without plankton-eating fish,
 2 — average annual fish catch below $5 \text{ kg} \cdot \text{ha}^{-1}$,
 3 — average annual fish catch above $5 \text{ kg} \cdot \text{ha}^{-1}$

of the crustaceans during the growing season. Also an analysis of many-years' changes in the zooplankton of Lake Mikołajskie (H i l l b r i c h t-I l k o w s k a, S p o d n i e w s k a and W ę g l e ń s k a 1979) has shown that these changes cannot be attributed to the impact of fish. It must be noted here that for Lake Mikołajskie the highest planktivorous fish catches are recorded of all the study lakes.

A lack of a strong fish pressure in the lakes considered is most clearly indicated by changes in the average individual body weight of the crustaceans. According to the B r o o k s and D o d s o n ' s (1965) "size efficiency" hypothesis, a lack of fish pressure is the main factor making it possible for large-bodied crustaceans to successfully compete for food with small species. Thus in lakes devoid of planktivorous fish large species should be dominant, and thereby the $B:N$ ratio for the crustaceans should be the highest. Conversely, in lakes with a strong fish pressure this ratio should be lower. However, a relationship of this type was not found in the lakes under study — it was in lakes devoid of planktivorous fish (but eutrophic) that small-bodied crustacean species were dominant (Fig. 2 C). But in the mesotrophic lakes, typically vendace-lakes, the highest $B:N$ ratio was found, for it was here that large species dominated. For instance in Lake Ołów, a natural "nursery" of the vendace, and where the catches of this species are relatively high ($6.3 \text{ kg} \cdot \text{ha}^{-1}$), dominant in the crustacean community were: *Eudiaptomus graciloides* (Lilljeborg), *Heterocope appendiculata* Sars, *Daphnia cucullata* Sars, *Bosmina berolinensis* Imhof, *Diaphanosoma brachyurum* (Lievin).

The above-presented facts indicate that in the lakes under study variation in numbers and biomass, and changes, in the species structure of the crustacean communities are not caused by the effect of planktivorous fish; anyway, this factor is not decisive. According to G l i w i c z and P r e j s (1977), the planktivorous fish pressure in the Masurian lakes should be looked at as the action of an unspecialized predator. The results obtained in the present study seem to confirm this hypothesis.

3.2. AN ANALYSIS OF THE FOOD FACTOR ON THE STRUCTURE OF THE NON-PREDATORY ZOOPLANKTON

3.2.1. Food supply description

The basic source of food for the non-predatory zooplankton is the phytoplankton. Hence a growth in phytoplankton biomass in the course of lake eutrophication should lead to a food condition improvement. This is not, however, a straightforward relationship. For it is known that not all the algal biomass that there is at a given point of time is equally available to all zooplanktonic organisms. This availability depends on both the structure of the food-taking apparatus and the food particle size. Only small, usually below or equal to $15 - 20 \mu\text{m}$ in diameter, algae (nannophytoplankton) can be directly eaten by the filter-feeding zooplankton, whereas larger forms (net phytoplankton) are not eaten. They undergo decomposition, and only as detritus and bacteria developing on it (bacteria-detritus suspension) can they be utilized by the

non-predatory zooplankton (Hillbricht-Ilkowska 1977). However, the role of net algae is not restricted to the contributing to the abundance of the bacteria-detritus suspension. A high concentration of these algae causes disturbances in the filtering mechanisms of some cladoceran species (*Daphnia*, *Bosmina*), thereby causing a deterioration of their food conditions, and as a result the numbers of these crustaceans decrease (Gliwicz 1977). There are, therefore, three factors on which all the food conditions for the non-predatory zooplankton depend. Two of them: the minute nanoplankton algae and the bacteria-detritus suspension directly determine the amount and quality of food in the environment. The third factor — large, net algae — acts in two ways. On the one hand, a growth in their density leads on to a food condition improvement (through a detritus concentration increase), and on the other — to a food condition deterioration for some filter-feeders.

Because of this, for the determination of the role of food as a factor determining changes in the zooplankton structure during the eutrophication process it is necessary to analyse changes in the density and size structure of the phytoplankton in lakes of different trophic states. Phytoplankton biomass changes (A) and the proportions of large, net algae in the biomass (B) have been presented in relationship to TSI_{SD} changes in Figure 3 on the basis of Spodniewska's (1979, 1983) data.

Taking into account the relationships found, and ample literature data, variation in the supply of food for the non-predatory zooplankton in the study lakes can be described in the following way:

(1) In most of the mesotrophic lakes (TSI_{SD} below 45) the nanoplankton algae are dominant. Due to a low total phytoplankton biomass (on an average $1.33 \text{ mg}\cdot\text{l}^{-1}$), a small proportion of net algae and probably a low input of allochthonous matter, the concentration of the second food fraction — the bacteria-detritus suspension, is low. It may, therefore, be assumed that the basic food of the filter-feeders in these lakes is the nanophytoplankton the concentration of which is relatively low. The food conditions in all the lakes of this group are similar.

(2) In the meso-eutrophic lakes ($TSI_{SD} = 45 - 55$) the food supply changes radically. Though in some of the water bodies algal biomass is still low (about $2 \text{ mg}\cdot\text{l}^{-1}$), it clearly increases in most of the lakes, attaining a level of $10 - 15 \text{ mg}\cdot\text{l}^{-1}$ mainly through a growth of the biomass of net algae. They usually represent over 50% of the biomass of the phytoplankton, primarily dinoflagellates, and in several cases blue-green algae (Spodniewska 1979, 1983). Hence in these lakes a considerable growth of the bacteria-detritus suspension concentration should be expected. The group of meso-eutrophic water bodies is thus characterized by a considerable biomass and food supply diversity. In most of the lakes the basic food type is probably the suspension consisting of bacteria and fine detritus particles ($1 - 2 \mu\text{m}$), while in some of the lakes the nanophytoplankton may still play a significant role in the food.

(3) In the eutrophic and polytrophic lakes (TSI_{SD} above 55) phytoplankton biomass is as a rule very high, above $10 \text{ mg}\cdot\text{l}^{-1}$. Dominating in it are net algae, but by contrast to the former lake group, the role of blue-green algae is greater (Spodniewska 1979, 1983). Most of the lakes of this group are shallow water

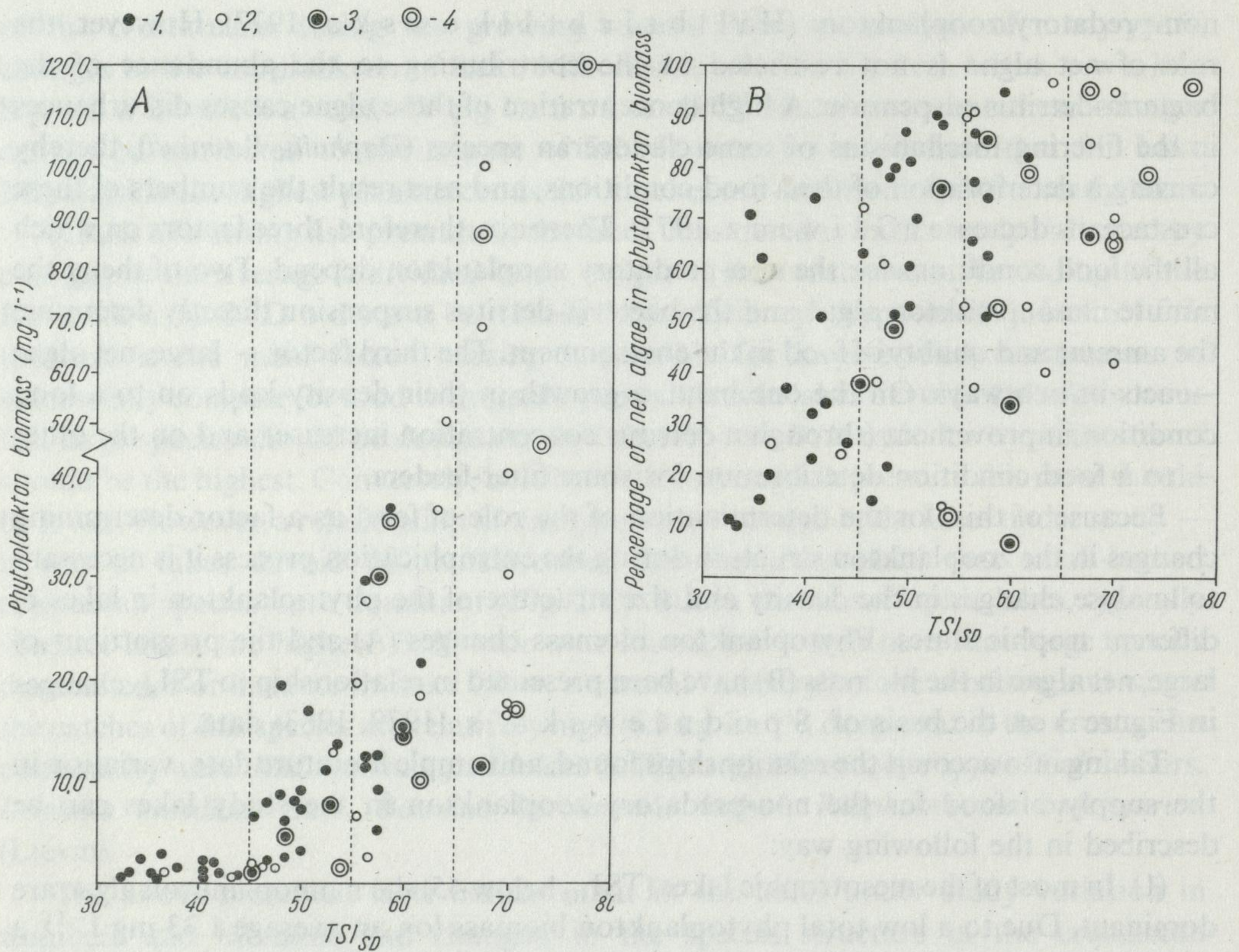


Fig. 3. Changes in phytoplankton biomass (A) and in the proportions of net algae in it (B) in lakes of different trophic states (after Spodniewska 1979, 1983)

1 — unpolluted stratified lakes, 2 — unpolluted nonstratified lakes, 3 — polluted stratified lakes, 4 — polluted nonstratified lakes

bodies with a well developed zone of littoral vegetation — the input of organic matter from this zone can be significant. The input of allochthonous matter in lakes of this type is also usually big. Because of these facts, in eu- and polytrophic lakes the basic food of the non-predatory zooplankton is the bacteria-detritus suspension of a variable, but always high concentration. In the lakes of this group changes in the food supply are thus mainly of quantitative nature.

The regularities discussed above concern the unpolluted lakes. However, in the polluted lakes, too, changes of the phytoplankton structure parameters discussed follow a similar course, although the oscillations are greater than in the “clean” lakes.

3.2.2. Trophic groups of the rotifer community

The main factor determining the trophic status of the different rotifer species is the structure and functioning of the food-collecting organs — the corona and mastax (Dumont 1977, Pourriot 1977). On this basis two groups of organisms

with different food-collecting mechanisms can be distinguished within the rotifer community (without *Asplanchna*). One of the groups (microfilter-feeders — sedimentators) includes rotifers possessing a mastax of the malleate, malleoramate, ramate and uncinata type. The size of the food particles collected by these organisms is no larger than 15–20 μm , and depends on the mouth size, thereby indirectly on the body size. The second group (macrofilter-feeders — raptors) consists of rotifers with a virgate type of mastax. The size of the food particles collected by them varies very widely (from several to over 50 μm), and does not always depend on the body size of a rotifer.

Most numerous among the sedimentators are species whose basic food is the bacteria-detritus suspension. According to P o u r r i o t (1977) they are: *Anuraeopsis fissa* (Gosse), *Pompholyx sulcata* Hudson, *Filinia longiseta* (Ehrenberg), *Conochilus unicornis* Rousselet, *Brachionus angularis* Gosse and *Keratella cochlearis* (Gosse). These species, except *C. unicornis*, are recognized as index organisms for high-trophic-state lakes (K a r a b i n 1985). G l i w i c z (1969b) and H i l l b r i c h t - I l k o w s k a (1972) report that the size of the food particles eaten by *Keratella cochlearis* is usually equal or below 1–2 μm . The bacteria-detritus suspension is readily eaten by species of the genus *Brachionus* which develop in large numbers in highly eutrophic lakes. However, an important role in the diet of the latter species is played also by minute algae — Chlorococcales, Volvocales and Euglenoides, typical of eutrophy. But species, like *Keratella quadrata* (Müller), *Kellicottia longispina* (Kellcott), feeding primarily on the nannophytoplankton occur in small numbers in the sedimentator group. A similar type of feeding is probably also peculiar to *Conochilus hippocrepis* (Schrank). The trophic status of this species is not clear. P o u r r i o t (1977) includes it among detritus-feeders, while N a u m a n n (1923) maintains that the genus *Conochilus* feeds on fine algae. Nauwerck (according to P e j l e r 1965) says that *C. unicornis* feeds on detritus and bacteria, whereas *C. hippocrepis* also ate minute algae. P e j l e r (1965) found that in some cases both species fed on algae, and in others — on detritus. Thus the diet of both species probably depends on the trophic conditions. But because the body size of *Conochilus hippocrepis* is larger, and consequently the species eats relatively larger particles and occurs in mesotrophic lakes (i.e., with low detritus concentrations), it may be presumed that in the lakes under study the role of nannoplankton algae in its diet is important.

The trophic status of species that do not feed on sedimented material is different. Due to the active grasping of food, very small, 1–2 μm , food particles are not available to these organisms. For this reason, the bacteria-detritus suspension does not actually play any role in their food.

The trophic status of the raptors varies widely, in respect of both the composition and size of the food particles collected. Thus species of the genus *Polyarthra* feed chiefly on the fraction of minute nannoplankton algae (E r m a n 1962, G a l k o v s k a j a 1963, P o u r r i o t 1977), while the food of *Synchaeta* consists of algae of various size — from several to over 50 μm . The trophic status of the pelagic *Trichocerca* species is not very clear. Although they can feed on animal food (e.g., eggs of other rotifer species), their basic food is net algae, both minute forms and filamentous

algae (Pouillot 1970, 1977). In the case of *Trichocerca* the collecting of food does not depend on the food item size, for these rotifers tear the cell membranes and suck out the cell contents.

On the basis of the above-discussed data, the following trophic groups have been distinguished in the rotifer communities of the lakes under study:

(A) Microfilter-feeders — sedimentators.

(1) The basic, often the only kind of food is the bacteria-detritus suspension, of particles not exceeding several μm in diameter — *Anuraeopsis fissa*, *Brachionus angularis*, *Keratella cochlearis*, *Conochilus unicornis*, *Hexarthra mira* (Hudson), *Pompholyx sulcata*, *Filinia longiseta*.

(2) The bacteria-detritus suspension and minute algae typical of eutrophy — the remaining species of the genus *Brachionus*.

(3) Nannophytoplankton below 20 μm , but bacteria and detritus may sometimes constitute a significant proportion of the food — *Keratella quadrata*, *Conochilus hippocrepis*, *Kellicottia longispina*.

(B) Macrofilter-feeders — raptors.

(4) Small and large net algae, including filamentous algae, sometimes animal food as well — species of the genus *Trichocerca*.

(5) Nannophytoplankton and net algae, with a maximum food particle size of over 50 μm — species of the genus *Synchaeta*.

(6) Only nannoplankton algae of maximum size of 20–30 μm , food particle size depending on the size of the consumer — species of the genus *Polyarthra*.

(7) Of a separate trophic status are highly specialized Gastropodidae species of the genera: *Ascomorpha*, *Gastropus*, *Chromogaster*, feeding on different dinoflagellate species, mainly *Peridinium*.

The nature of the changes in biomass and dominance of the rotifer trophic groups distinguished indicates a clear dependence of these changes on the amount and quality of food in the environment (Fig. 4). In the mesotrophic lakes (TSI_{SD} below 45), where the nannophytoplankton dominates, and the amount of detritus may be low because of a low algal biomass, it is nannoplanktivorous species of the genus *Polyarthra* (trophic group 6) that dominate. Of the genus *Synchaeta* (trophic group 5) common in the lakes under study was *Synchaeta kitina* Rousselet, a small species, probably also feeding on the nannophytoplankton. For this reason, these two groups were considered jointly. In the mesotrophic lakes their contribution to the biomass is relatively stable, as it diminishes on an average from 75 to 62%, in spite of a considerable rise in the TSI_{SD} values (from 32.2 to 45.0).

In the meso-eutrophic lakes ($\text{TSI}_{\text{SD}} = 45 - 55$) there occurs a significant growth in biomass of the net algae which already definitely dominate in the phytoplankton and determine its biomass. In these lakes the biomass of nannophytoplanktivorous species is still at a level specific to mesotrophy; but their contribution to the biomass of rotifers was nearly a half lower, for it fell from 58% to 32%. At the same time there is an increase in biomass and dominance of those organisms whose trophic status is directly or indirectly connected with a high concentration of net algae. There is, therefore, a clear

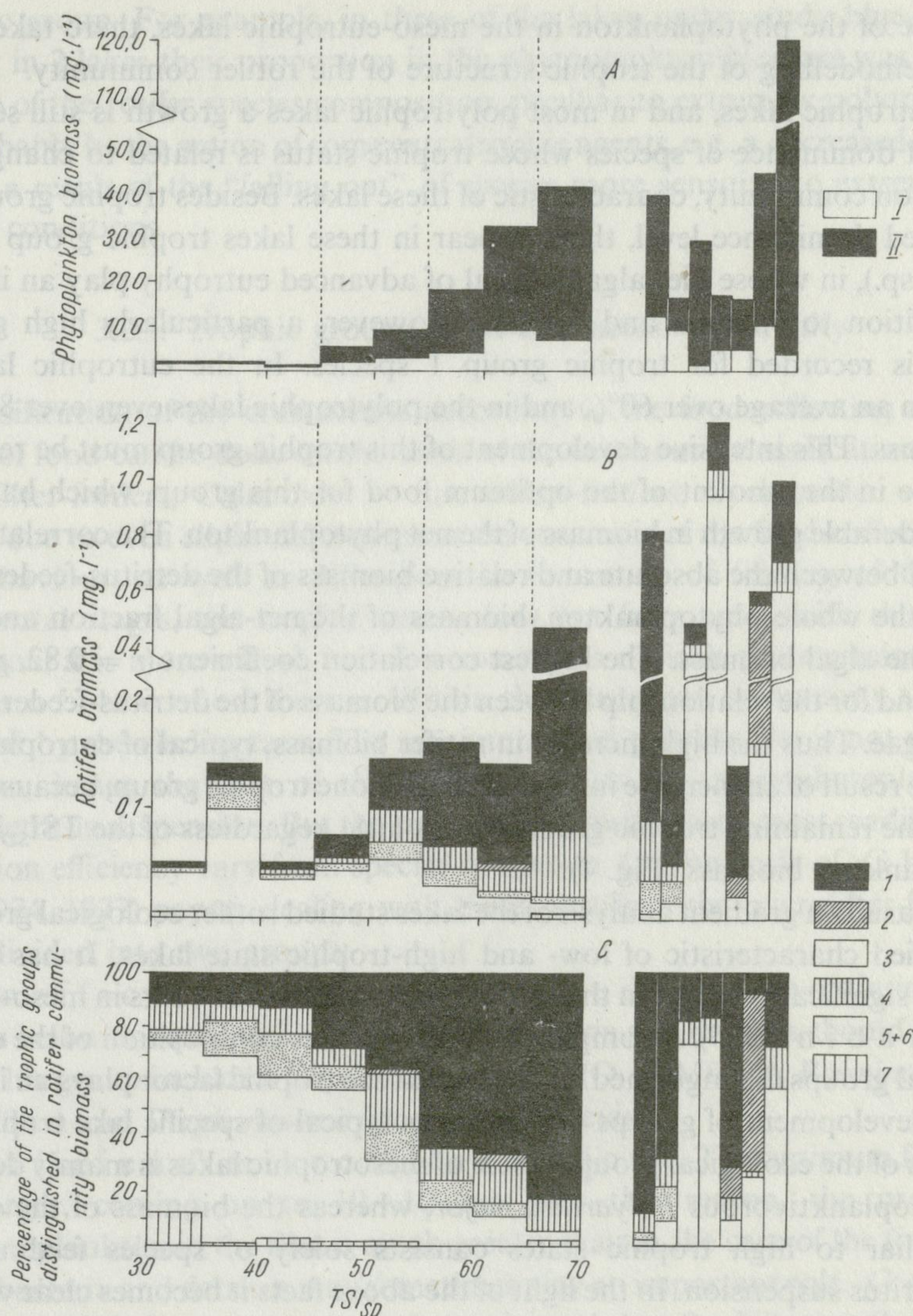


Fig. 4. Dynamics of phytoplankton biomass (A) and of the biomass of the rotifer trophic groups distinguished (B) and of their percentage in the biomass of this community (C) in lakes of different trophic states. A group of 7 extremely polytrophic lakes has been distinguished; I — nannophytoplankton, II — net algae, 1 — 7 rotifer trophic groups (see the text)

growth in biomass and dominance of species of the genus *Trichocerca* (trophic group 4). This is understandable, because their basic food is net algae, which also provide a substrate on which most pelagic *Trichocerca* lay their eggs. There is a parallel growth in the rotifer community of detritus-feeding species (trophic group 1). Because of this, in the mesotrophic lakes the proportions of both groups in the rotifer biomass remained at a stable and low level — about 20%, while in lakes approaching eutrophy they accounted for nearly 60% of the rotifer biomass. As a result of changes in biomass and

size structure of the phytoplankton in the meso-eutrophic lakes, there takes place a significant remodelling of the trophic structure of the rotifer community.

In the eutrophic lakes, and in most polytrophic lakes a growth is still seen of the biomass and dominance of species whose trophic status is related to changes in the phytoplankton community, characteristic of these lakes. Besides trophic group 4, with an unchanged dominance level, there appear in these lakes trophic group 2 rotifers (*Brachionus* sp.), in whose diet algae typical of advanced eutrophy play an important role, in addition to bacteria and detritus. However, a particularly high growth in abundance is recorded for trophic group 1 species. In the eutrophic lakes they constitute on an average over 60%, and in the polytrophic lakes even over 80% of the rotifer biomass. This intensive development of this trophic group must be related to a high increase in the amount of the optimum food for this group, which has resulted from a considerable growth in biomass of the net phytoplankton. The correlations have been studied between the absolute and relative biomass of the detritus-feeders and the biomass of the whole phytoplankton, biomass of the net-algal fraction and its proportion in the algal biomass. The highest correlation coefficient ($r = 0.82$, $p < 0.001$) has been found for the relationship between the biomass of the detritus-feeders and that of the net algae. Thus the high increase in rotifer biomass, typical of eutrophication, is first of all the result of an increase in biomass of this one trophic group, because the joint biomass of the remaining trophic groups varies little, regardless of the TSI_{SD} values or the phytoplankton biomass (Fig. 4).

On the basis of a gradient analysis of the lakes studied rotifer ecological groups have been identified characteristic of low- and high-trophic state lakes. It has also been found that a significant change in the rotifer species structure occurs in meso-eutrophic lakes (Karabin 1985). A comparison of the species composition of the ecological and trophical groups distinguished indicates that the trophic factor plays an important role in the development of groups of organisms typical of specific lake trophic states. The biomass of the ecological group typical of mesotrophic lakes is mainly determined by the nannoplanktivorous *Polyarthra major*, whereas the biomass of the ecological group peculiar to high trophic states consists solely of species feeding on the bacteria-detritus suspension. In the light of the above facts it becomes clear why it is in the meso-eutrophic lakes that the species structure of the pelagic rotifer communities is changed so significantly and rapidly.

The relationships discussed apply in principle to the whole lake pool studied except some extremely polytrophic shallow lakes (Fig. 4). In three out of 7 lakes with TSI_{SD} values above 70 species feeding on the nannophytoplankton (eutrophic groups 5 and 6) dominate — as in the mesotrophic lakes. However, the species structure of these groups is different. In the mesotrophic lakes they are usually made up of 3 — 4 species, while in the polytrophic lakes a high dominance of these groups is determined by one, usually small species — *Synchaeta kitina*, *Polyarthra remata*, *P. vulgaris*. In the analysis of the food relationships the species composition of the phytoplankton has not been taken into account, and under extremely polytrophic conditions this composition varies considerably between lakes, and is usually characterized by a strong dominance of one

taxonomic group. For example, in three of the lakes under study blue-green algae dominate; in 2 lakes their proportion in the phytoplankton biomass was above 90%. The cause of the rotifer species composition, peculiar to extremely polytrophic lakes, could probably be the action of some extratrophic agents, e.g., a decreased competitive action as a result of the "falling out" of species more sensitive to extreme physico-chemical conditions.

3.2.3. Trophic groups of the crustacean community

A classification of the crustaceans according to the food collecting mechanisms and kind of food can be done on the basis of the taxonomic classification; Cladocera – microfilter-feeders, Calanoida – macrofilter-feeders, Cyclopoida – predators. However, due to even slight differences in the structure of the food-collecting organs, varied behaviour, as well as differences in the mode of feeding of the different developmental stages, the trophic status does not fully agree with the taxonomic classification; it is more varied, and it is sometimes difficult to determine it exactly.

M i c r o f i l t e r - f e e d e r s. Within the crustacean community this group is represented by the cladocerans. The maximum food particle size is not greater than 15–20 μm , hence the diet of this group consists of: nannophytoplankton and bacteria-detritus suspension. But the size of the particles eaten most readily, as well as the filtration efficiency vary from species to species. On the basis of G l i w i c z ' s (1969b, 1974, 1977) papers dealing with these problems the microfilter-feeders have been subdivided into two groups:

(1) "I n e f f i c i e n t" m i c r o f i l t e r - f e e d e r s. The optimum food particle size is below or equal to 2–5 μm , hence bacteria and detritus should dominate in the diet. This group includes: *Chydorus sphaericus* (O. F. Müller), *Basmina longirostris* (O. F. Müller) and *Diaphanosoma brachyurum* (Lievin).

(2) "E f f i c i e n t" m i c r o f i l t e r - f e e d e r s. The optimum food particle size is larger, coming up to 10–12 μm . For this reason, the proportion of nannophytoplankton in the diet is much greater than in the case of the former group, although bacteria and detritus may sometimes play an important role. G e l l e r and M ü l l e r (1981), for instance, have demonstrated that *Daphnia cucullata* Sars feeds on much smaller, on an average, particles than does *Daphnia longispina hyalina* v. *galeata* (Leydig), and besides, *D. cucullata* filters bacteria and detritus more efficiently than *D. l. h. galeata*. Of the cladocerans found in the lakes studied the following have been included in the "efficient" microfilter-feeder group: species of the genera *Daphnia* and *Bosmina* (except *B. longirostris*), and *Ceriodaphnia quadrangula* (O. F. Müller) (K o m a r o v a 1966).

Variation in the biomass of the "efficient" and "inefficient" microfilter-feeders, in relationship to phytoplankton biomass changes, has been presented in Figure 5. In low-trophic-state lakes, where dominant in the small phytoplankton biomass (below 3–4 $\text{mg}\cdot\text{l}^{-1}$) is nannoplankton, "inefficient" microfilter-feeders as a rule occur in small numbers or are absent. This does not apply to the polluted Lake Niegocin,

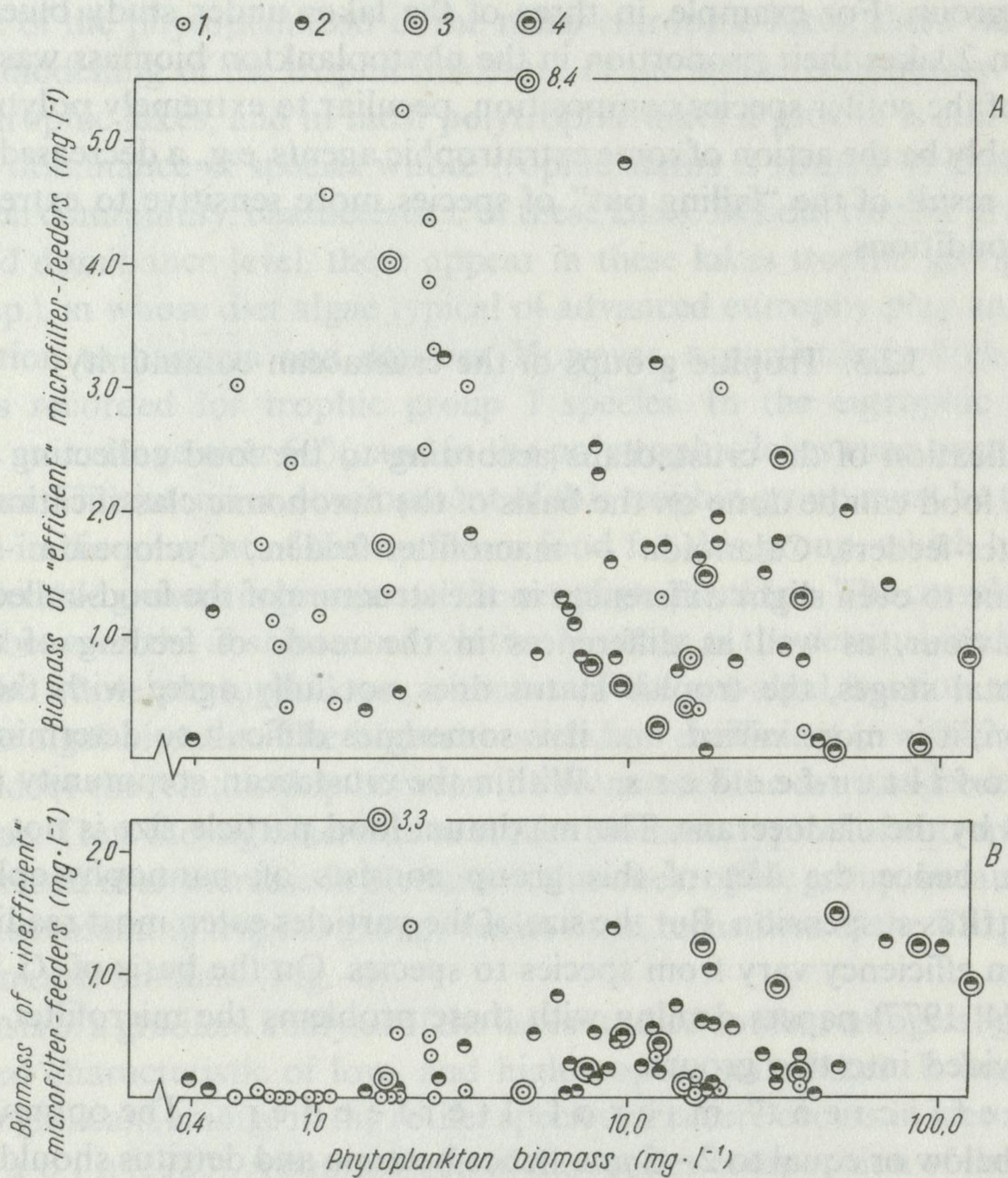


Fig. 5. Variation in the biomass of "efficient" (A) and "inefficient" (B) microfilter-feeders in relationship to changes in the phytoplankton biomass of the lakes under study

Unpolluted lakes in which net algae represent $> 50\%$ (1) and $< 50\%$ (2), and polluted lakes in which net algae represent $> 50\%$ (3) and $< 50\%$ (4)

where, because of an abundant development of *Chydorus sphaericus*, the biomass of these microfilter-feeders is disproportionately high. In the lakes mentioned above "efficient" microfilter-feeders are dominant. Their biomass grows at first as the phytoplankton biomass increases. However, with further growth of the algal biomass (above $4.0 \text{ mg}\cdot\text{l}^{-1}$), and a simultaneous rise in the dominance of the net-algal fraction, the biomass of the "efficient" microfilter-feeders drops. But there occurs an increase in the biomass of the "inefficient" microfilter-feeders, in some lakes up to $1.0 - 1.5 \text{ mg}\cdot\text{l}^{-1}$. The values are not high, but the organisms contributing to them are relatively small.

Conclusions on the role of the microfilter-feeder groups discussed, in unpolluted lakes at different eutrophication stages can be drawn on the basis of the relationships between: (a) the contribution of the microfilter-feeders to the crustacean biomass, and (b) the proportion of the "inefficient" microfilter-feeders in the microfilter-feeder biomass (Fig. 6). In the mesotrophic-lake crustacean communities the microfilter-

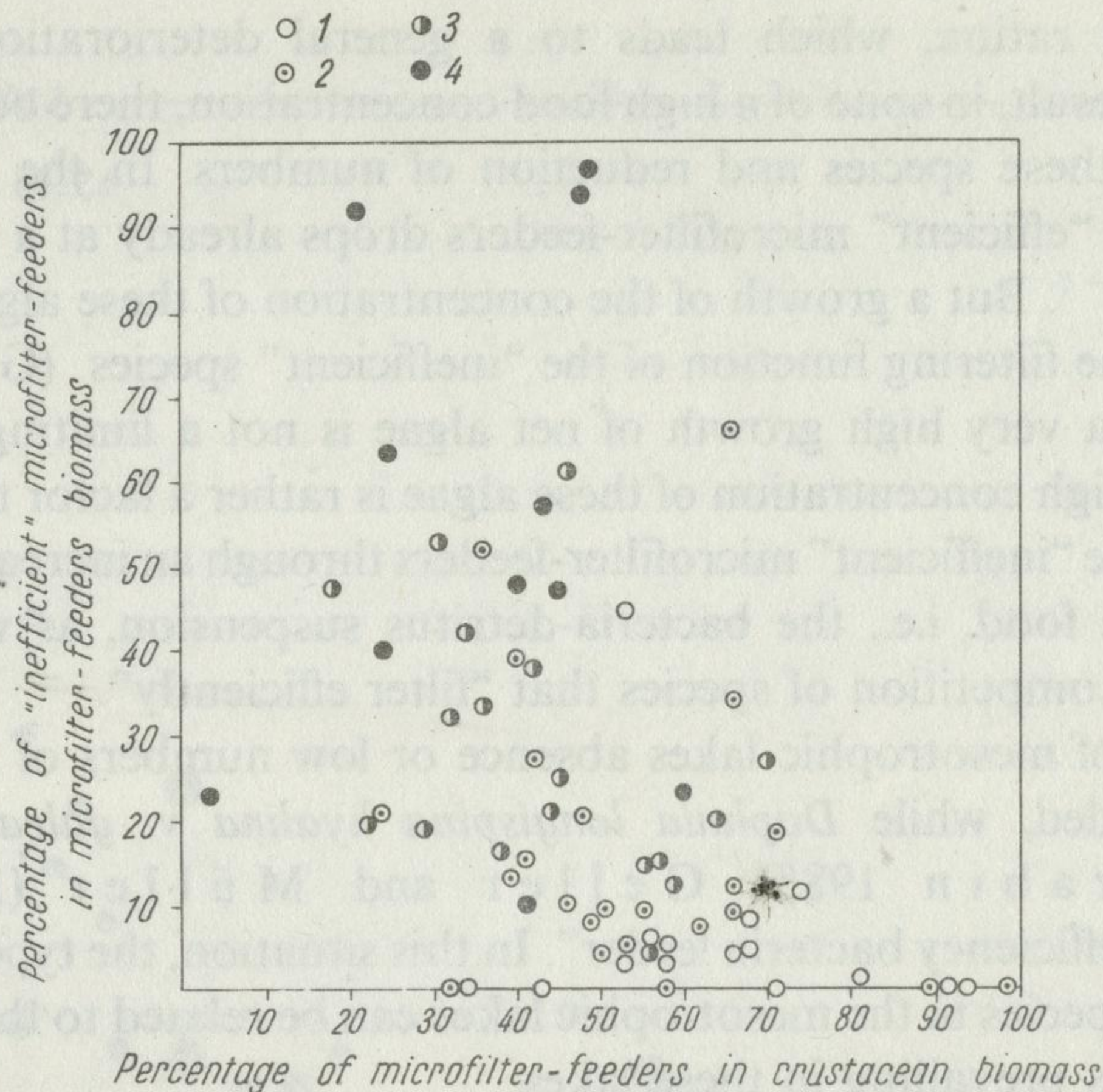


Fig. 6. Relationship between the proportion of microfilter-feeders in crustacean community biomass and the proportion of "inefficient" microfilter-feeders in the biomass of microfilter-feeders — in unpolluted lakes of different trophic states

1 — mesotrophic lakes, 2 — meso-eutrophic lakes, 3 — eutrophic lakes, 4 — polytrophic lakes

-feeders definitely dominate, usually representing over 50% of the biomass of these communities, and they mainly consist of "efficient" microfilter-feeders. With a progressing lake eutrophication the role of the microfilter-feeders in determining the level of the crustacean biomass diminishes, while the importance of the "inefficient" filter-feeders grows. As a result, in most of the polytrophic lakes the microfilter-feeders account for less than 50% of the crustacean biomass, and dominant among them are "inefficient" species.

The causes of the different response of these two microfilter-feeder groups to a trophic state rise should be found first of all in phytoplankton size-structure changes. In low-trophic-state lakes, where food concentration is low, the dominant component being the nannophytoplankton, there virtually occur only "efficient" microfilter-feeders. Because they are able to filter off a larger amount of biomass from the same water volume (Gliwicz 1977), these species find in low-trophic-state lakes relatively better food conditions than do the "inefficient" microfilter-feeders. This should explain, on the one hand, the sporadic occurrence of the "inefficient" filter-feeders in low-trophic-state lakes, and on the other — the biomass growth of the "efficient" filter-feeders with improving trophic conditions (increasing nannophytoplankton concentration). However, a further rise of the lake trophic state is followed by a growth in abundance of the net algae. Gliwicz (1977) is of the opinion that an abundant occurrence of large phytoplankton forms causes mechanical disturbances in the filtration by "efficient" microfilter-feeders. This reduces the filtration rate, and

thereby the food ration, which leads to a general deterioration of the trophic conditions. As a result, in spite of a high food concentration, there occurs a decrease in the fecundity of these species and reduction of numbers. In the lakes studied the abundance of the "efficient" microfilter-feeders drops already at a net-algal biomass content of $5 \text{ mg} \cdot \text{l}^{-1}$. But a growth of the concentration of these algae does not cause disturbances in the filtering function of the "inefficient" species (G l i w i c z 1977), this is why even a very high growth of net algae is not a limiting factor for them. Conversely — a high concentration of these algae is rather a factor that stimulates the development of the "inefficient" microfilter-feeders through an increased concentration of their optimum food, i.e., the bacteria-detritus suspension, as well as through a reduction in the competition of species that "filter efficiently".

In a number of mesotrophic lakes absence or low numbers of *Daphnia cucullata* have been recorded, while *Daphnia longispina hyalina* v. *galeata* was relatively numerous (K a r a b i n 1985). G e l l e r and M ü l l e r (1981) consider *D. cucullata* a "high efficiency bacteria feeder". In this situation, the type of co-occurrence of both *Daphnia* species in the mesotrophic lakes can be related to the above-discussed trophic conditions prevailing in these lakes.

M a c r o f i l t e r - f e e d e r s. In the lakes under study this group includes various copepod species and developmental stages, but its biomass is in principle determined by two species: *Eudiaptomus graciloides* (Lilljeborg) and *Eudiaptomus gracilis* (Sars). Included in this group are also *Limnocalanus macrurus* Sars and cyclopoid and calanoid nauplii (M o n a k o v 1976). It has also been accepted that the youngest cyclopoid copepodid stages (I — III) should be included among macrofilter-feeders. The food particle size available to the macrofilter-feeders ranges from $4 - 5 \mu\text{m}$ to $40 - 50 \mu\text{m}$ (G l i w i c z 1969b, 1977, M o n a k o v 1976), the dominant food item being nannoplankton algae. Bacterioplankton and detritus are only to a small extent available to these organisms (as aggregates).

In the lakes studied no relationship has been found between the biomass of this group and its proportion in the crustacean biomass, and the biomass of the whole phytoplankton, or its size fractions.

It is difficult to unequivocally establish the causes of this. In most of the lakes the nannophytoplankton biomass, the basic food item of the macrofilter-feeders, exceeds $1.0 \text{ mg} \cdot \text{l}^{-1}$. These are quantities which, according to M a l o v i c k a j a and S o r o k i n (1961), meet the food requirements of *Eudiaptomus*. Some rotifers (*Polyarthra*, *Synchaeta*), dominant in mesotrophic lakes, can be significant "rivals", competing with the macrofilter-feeders for food. The competitive role should also become evident of the "efficient" microfilter-feeders, primarily in the mesotrophic lakes, where the concentration of food is low, the food mainly consisting of minute algae. Presented in Figure 7 are changes of the biomass ratio of these two crustacean trophic groups in relationship to increasing nannophytoplankton biomass, i.e., a food item for which they may compete. In most of the lakes in which the biomass of minute algae does not exceed $2 - 3 \text{ mg} \cdot \text{l}^{-1}$ the "efficient" microfilter-feeders dominate, whereas in other lakes their biomass is equal to or lower than that of the macrofilter-feeders. This

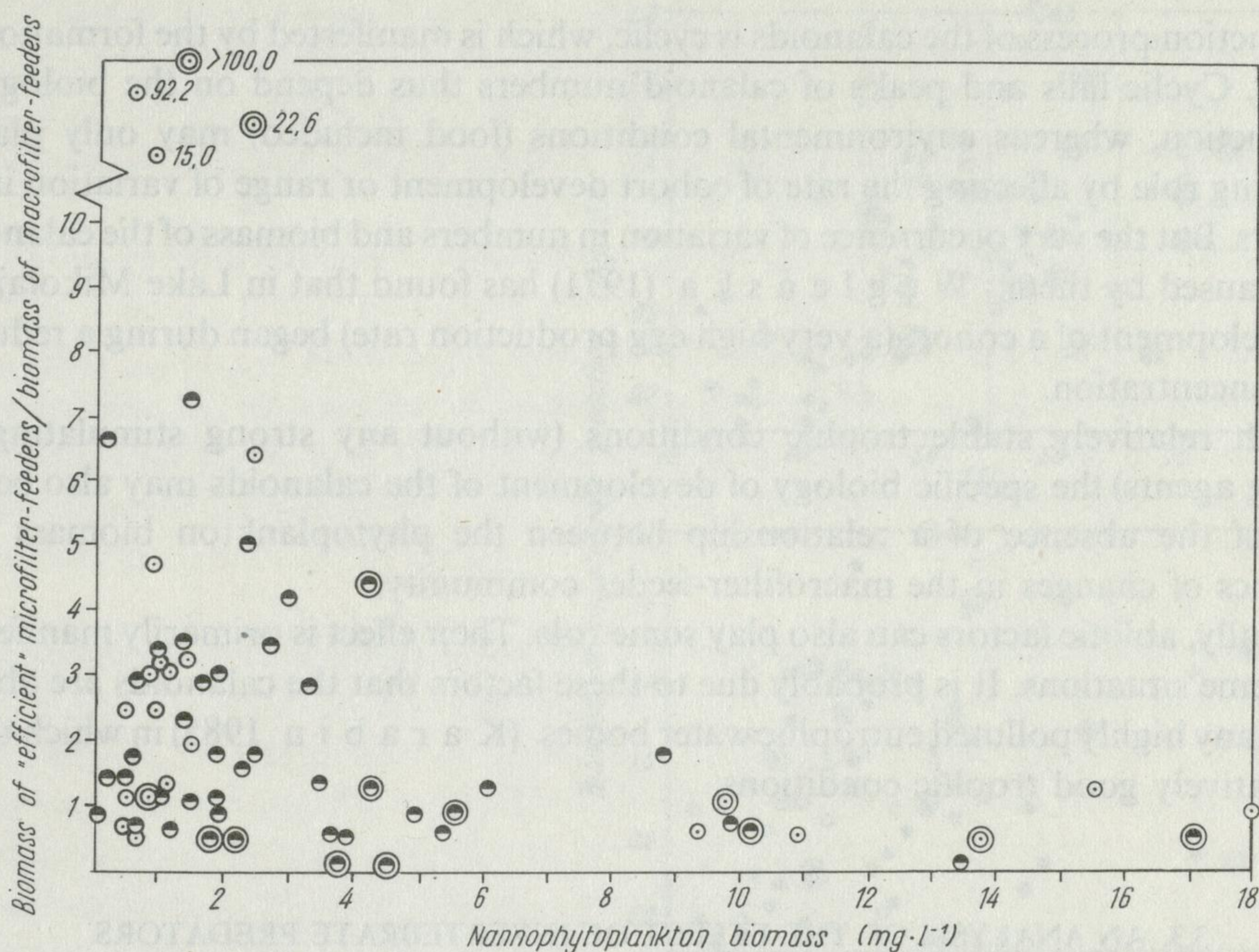


Fig. 7. Changes in the biomass ratio — “efficient” microfilter-feeders to microfilter-feeders in relationship to changes in nannoplankton biomass
Lake denotations as in Figure 5

is, of course, the result of the decreasing numbers of “efficient” cladocerans. But even this simple index confirms the presumption that it is particularly in phytoplankton-rich lakes approaching eutrophy, and ones that are already eutrophic, that the competition of microfilter-feeders need not play a significant role. Changes of the biomass ratio of these two trophic groups indicate rather a relative improvement in the trophic conditions for the macrofilter-feeders in these lakes, the more so as in the case of these crustaceans there is no adverse effect of the net algae.

In the light of the data on nannophytoplankton biomass changes and competition of other trophic groups a growth in macrofilter-feeder density should be expected as the lake trophic state rises. But no such relationship has been found. There may be several causes of this. According to M o n a k o v (1976) the calanoids show food preference, but this preference is not of a purely mechanical nature, the limiting factor is not the food particle size alone. It may thus be assumed that optimum trophic conditions for the macrofilter-feeders depend not only on the abundance of food, but on its quality as well. This also applies, to a lesser extent though, to the microfilter-feeders. However, in the case of the latter the disturbing effect of large forms of algae seems strong enough to level the effect of other factors.

The lack of a relationship between the lake trophic state and the biomass of the macrofilter-feeders may also result from the impact of extratrophic factors. The

reproduction process of the calanoids is cyclic, which is manifested by the formation of cohorts. Cyclic falls and peaks of calanoid numbers thus depend on the biology of reproduction, whereas environmental conditions (food included) may only play a modifying role by affecting the rate of cohort development or range of variation in its numbers. But the very occurrence of variation in numbers and biomass of the calanoids is not caused by them. Węgleńska (1971) has found that in Lake Mikołajskie the development of a cohort (a very high egg production rate) began during a reduced food concentration.

With relatively stable trophic conditions (without any strong stimulating or limiting agents) the specific biology of development of the calanoids may also be the cause of the absence of a relationship between the phytoplankton biomass and dynamics of changes in the macrofilter-feeder community.

Finally, abiotic factors can also play some role. Their effect is primarily manifested in extreme situations. It is probably due to these factors that the calanoids are absent from many highly polluted eutrophic water bodies (Karabin 1985) in which there are relatively good trophic conditions.

3.3. AN ANALYSIS OF THE EFFECT OF INVERTEBRATE PREDATORS ON THE ZOOPLANKTON STRUCTURE

The trophic status of species commonly included among "predators-raptors" is particularly difficult to determine unequivocally, for it is only the predatory cladocerans: *Leptodora kindtii* (Focke) and *Bythotrephes longimanus* Leydig that can be recognized as obligatory predators. In the lakes under study these two species occur, however, in small numbers. But the cyclopoids (IV–VI copepodids and adults) determining the predator biomass, are in the pelagic zone of these lakes represented by species of the genus *Mesocyclops*. They can feed on very diverse food – from bacterial aggregates through varied-sized animal organisms to large net algae (Fryer 1957, Monakov and Sorokin 1971, Monakov 1973, 1976, Karabin 1978). *Mesocyclops* species are thus facultative predators, which, as suggested by Gliwicz (1974), can be real predators only in low-trophic-state lakes. *Heterocope appendiculata* is also characterized by a similar mode of feeding (Monakov 1972, 1976).

In addition to the above-enumerated crustacean species included in the predator group discussed have been two rotifer species: *Asplanchna priodonta* Gosse and *A. girodi* Guerne. They are also facultative predators in whose diet algae may play an important role (Ejmont-Karabin 1974, Guiset 1977).

Changes in the biomass of the predator community distinguished, in relationship to TSI_{SD} changes, have been presented in Figure 8 A. In the mesotrophic lakes the biomass of invertebrate predators does not exceed $0.5 \text{ mg} \cdot \text{l}^{-1}$. This does not apply to two water bodies in which *Asplanchna* is dominant in this community. With a rising trophic state the biomass of these predators increases fairly quickly, primarily through a growth in

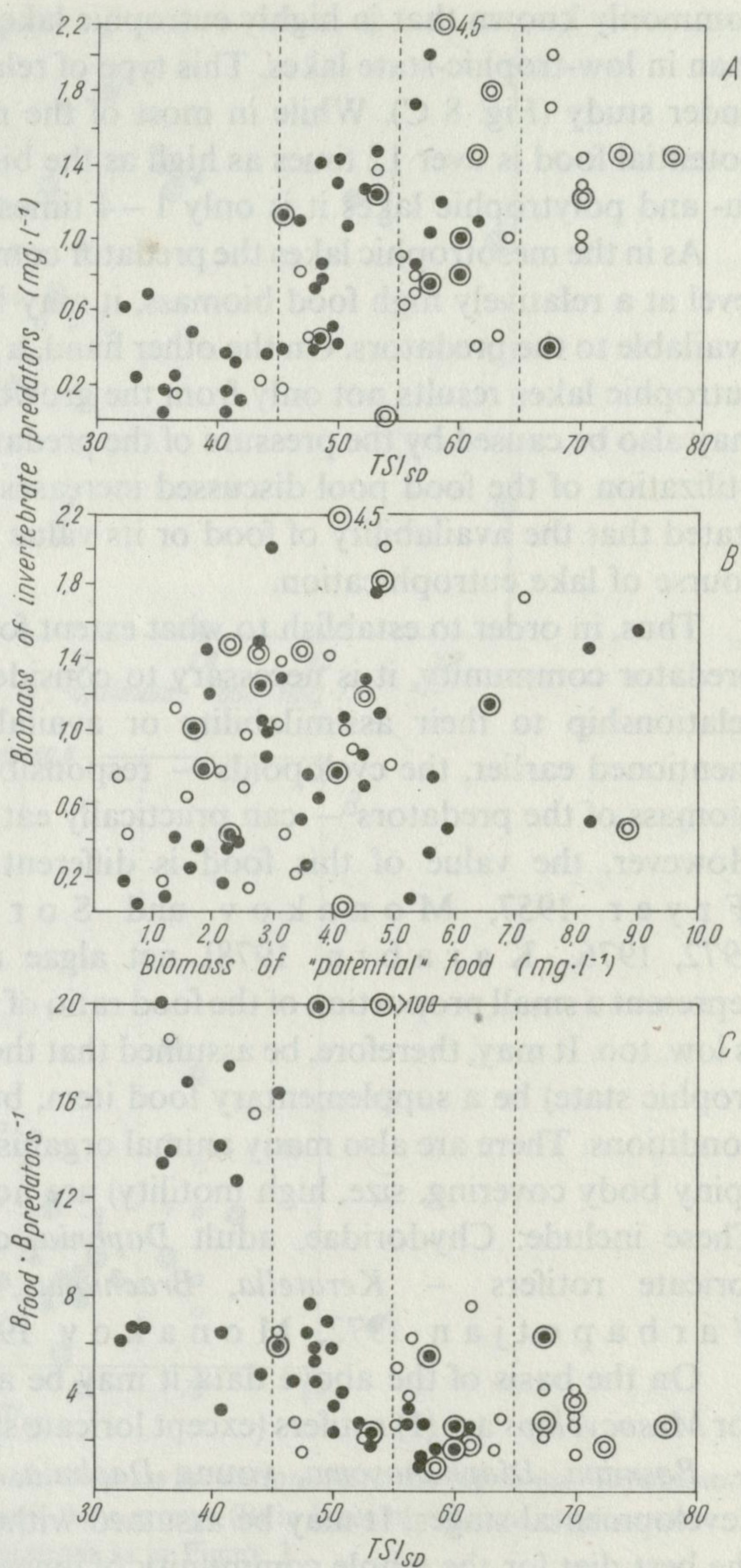


Fig. 8. Variation in invertebrate predator community biomass in relationship to the TSI_{SD} (A) and biomass of non-predator zooplankton (B), and the $B_{\text{food}}:B_{\text{predator}}$ ratio (C) in lakes of different trophic states

Lake denotations as in Figure 3

the biomass of *Mesocyclops* sp. But in the eutrophic and polytrophic lakes the biomass of the predators no longer shows a tendency to grow, being at the same time subject to variation: from about 0.4 to $2.0 \text{ mg}\cdot\text{l}^{-1}$.

To illustrate the effect of the trophic conditions on the abundance of predators, in Figure 8 B the value has been presented of the biomass of predators in relationship to biomass of their potential food — the non-predatory zooplankton (rotifers and crustaceans). In the lakes studied no relationship has been found between the biomass of the predators and that of their potential prey. Trophic conditions of the environment can also be inferred from the prey biomass to predator biomass ratio. It has been

commonly known that in highly eutrophic lakes the value of this ratio is much lower than in low-trophic-state lakes. This type of relationship has been found for the lakes under study (Fig. 8 C). While in most of the mesotrophic lakes the biomass of the potential food is over 12 times as high as the biomass of the predators, in most of the eu- and polytrophic lakes it is only 1–4 times as high.

As in the mesotrophic lakes the predator community attains a relatively low growth level at a relatively high food biomass, it may be presumed that the food is not fully available to the predators. On the other hand, a low value of the $B_{\text{food}} : B_{\text{pred.}}$ ratio in the eutrophic lakes results not only from the growth of the biomass of the predators, but may also be caused by the pressure of the predators on the prey. Since the efficiency of utilization of the food pool discussed increases with a rising trophic state, it may be stated that the availability of food or its value is subject to changes (it grows) in the course of lake eutrophication.

Thus, in order to establish to what extent food determines the development of the predator community, it is necessary to consider the value of different food items in relationship to their assimilability or availability to the predator. As has been mentioned earlier, the cyclopoids – responsible for the dynamics of changes in the biomass of the predators – can practically eat any food present in the environment. However, the value of this food is different. As indicated by numerous papers (Fryer 1957, Monakov and Sorokin 1971, 1972, Monakov 1972, 1976, Karabin 1978), net algae and the bacteria-detritus suspension represent a small proportion of the food ratio of the cyclopoids, and their assimilability is low, too. It may, therefore, be assumed that they can in certain situations (e.g., a high trophic state) be a supplementary food item, but not one ensuring optimum trophic conditions. There are also many animal organisms which for various reasons (hard or spiny body covering, size, high motility) are not practically eaten by the cyclopoids. These include: Chydoridae, adult *Daphnia*, copepodids and adults of calanoids, loricate rotifers – *Keratella*, *Brachionus*, *Kellicottia* (McQueen 1969, Varbapetjan 1972, Monakov 1976, Karabin 1978).

On the basis of the above data it may be assumed that the optimum food items for *Mesocyclops* are (1) rotifers (except loricate species), (2) easily available cladocerans – *Bosmina*, *Diaphanosoma*, young *Daphnia*, *Ceriodaphnia*, (3) youngest copepod developmental stages. It may be assumed without a risk of a grave error, that this is the best diet for the whole community of invertebrate predators (Morduchaj-Boltovskaja 1960, Galkovskaja 1963, Karabin 1974), although *Asplanchna* can also to a large extent use vegetable food (Ejmont-Karabin 1974, Giljarov 1977b). Also, as has been stated earlier, *Asplanchna* and predatory cladocerans only represent a small percentage of the biomass of invertebrate predators.

Predator biomass has been compared with the biomass of the optimum food (Fig. 9 A). This time a clear relationship has been found between both parameters (cf. Fig. 8 B). This relationship is statistically significant for all the unpolluted lakes ($r = 0.62$, $p < 0.001$). Though this does not apply to the polluted lakes, the results

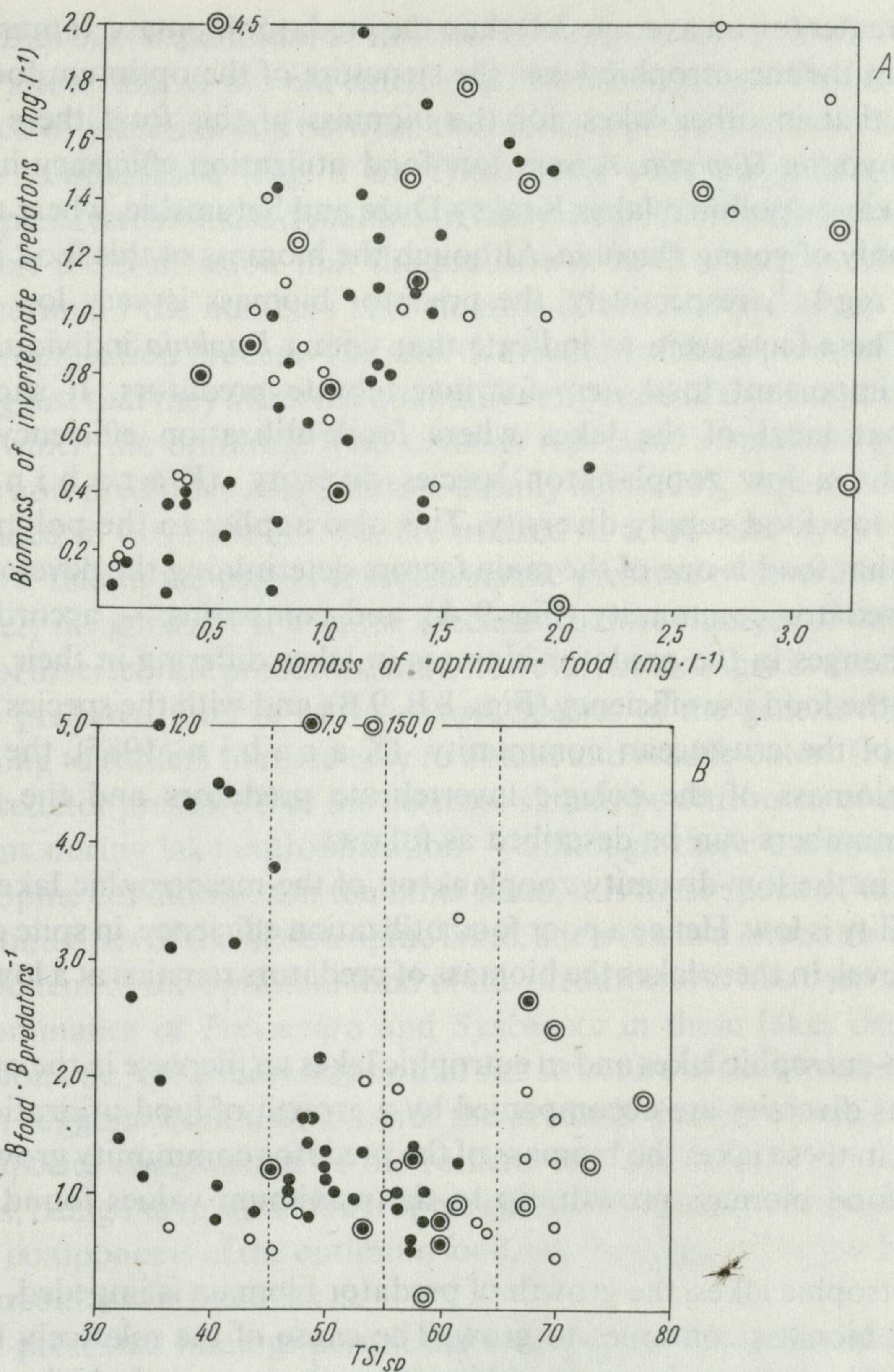


Fig. 9. Changes in invertebrate predator community biomass in relationship to the "optimum" food biomass (A), and changes in the biomass ratio of both these groups (B) in lakes of different trophic states
Lake denotations as in Figure 3

obtained seem to confirm that the assumption of a limited composition of the optimum food supply is right. At the same time, the results point to the role of the optimum food as a factor determining the development of the predator community discussed.

Assuming the food to predator biomass ratio to be a kind of food utilization efficiency index, the highest values of this index have been found for the predator communities in the meso-eutrophic and eutrophic lakes (Fig. 9 B). In 77% of the lakes the biomass ratio varies between 0.5 and 1.5, amounting on an average to 1.32 in the meso-eutrophic lakes, and 1.09 in the eutrophic lakes. The lowest food utilization efficiency has been found in the mesotrophic lakes. In most of them the food biomass is

several times greater (on an average 3.1) than the predator biomass. It must be stressed, however, that in the mesotrophic lakes the structure of the optimum food is slightly different from that in other lakes, for the biomass of this food there is primarily determined by young *Daphnia*. A very low food utilization efficiency has also been found in two heavily polluted lakes Kraksy Duże and Sztumskie, where the optimum food consists only of young *Daphnia*. Although the biomass of this food is fairly high, 2.01 and 3.53 mg·l⁻¹, respectively, the predator biomass is very low — 0.01 and 0.44 mg·l⁻¹. These facts seem to indicate that young *Daphnia* individuals are not a valuable and important food item for invertebrate predators. It should also be emphasized that most of the lakes where food utilization efficiency is low are characterized by a low zooplankton species diversity (Karabin 1985), and thereby also a low food supply diversity. This also applies to the polytrophic lakes.

Assuming that food is one of the main factors determining the development of the invertebrate predator community (Fig. 9 A), and comparing — accordingly — the dynamics of changes in the predator biomass in lakes differing in their trophic state (Fig. 8 A) with the food use efficiency (Figs. 8 B, 9 B), and with the species composition and diversity of the crustacean community (Karabin 1985), the relationship between the biomass of the pelagic invertebrate predators and the zooplankton structure and numbers can be described as follows:

Dominant in the low-diversity zooplankton of the mesotrophic lakes are species whose availability is low. Hence a poor food utilization efficiency, in spite of a relatively high biomass level. In these lakes the biomass of predators remains at a low level, below 0.5 mg·l⁻¹.

In the meso-eutrophic lakes and in eutrophic lakes an increase in the optimum food biomass and its diversity are accompanied by a growth of food utilization efficiency. Consequently, in these lakes the biomass of the predator community grows proportionately to the food biomass growth, up to the maximum values found in the lakes studied.

In the polytrophic lakes, the growth of predator biomass is impeded, although the optimum food biomass continues to grow. The cause of the relatively low predator biomass may be, in addition to extratrophic agents, the impact of which must be strong in extremely eutrophic lakes and in polluted lakes, a low food diversity, especially of the crustacean component. The fact must be taken into account here that in the polytrophic lakes a large, larger than in other trophic types of lakes, proportion of the optimum food biomass consists of young cyclopid developmental stages. In this situation it is necessary to accept that there is a strong self-limitation of the predator community (through cannibalism), or the optimum food biomass in these lakes has been overestimated.

For a correct assessment of the role of biotic factors in the determination of the zooplankton communities it is necessary to establish the effect of invertebrate predators on these communities. In the lakes under study the main component of the predator community is the cycloids (*Mesocyclops* sp.) which will determine the nature and intensity of the predator pressure on the zooplankton. As has been mentioned earlier, many of the zooplankters on which the biomass value of the

zooplankton (*Daphnia*, Calanoida) or its numbers (*Chydorus*, *Keratella*) often depend are utilized at a low rate, or are not eaten at all by *Mesocyclops*. This is probably the cause of the lack of a relationship between the biomass of the predators and that of the non-predatory zooplankton (Fig. 8 B). These facts, with the predatory and non-predatory zooplankton biomass dynamics in lakes of different trophic states taken into account, suggest the conclusion that the pressure of invertebrate predators is not a factor that determines the numbers and biomass of the non-predatory zooplankton during the eutrophication process. The selective feeding of these predators may, on the other hand, suggest that they affect the qualitative structure of the zooplankton. But the organisms of which the optimum food consists represent a small proportion of the biomass of the non-predatory zooplankton, usually below 25%. Apart from this, young *Daphnia*, included in this type of food, are utilized at a low rate by the predators. It seems, therefore, that in the case of crustaceans the pressure of invertebrate predators plays a relatively insignificant role in the species structure changes of this community.

The effect of invertebrate predators, may, however, be stronger in the case of rotifers which are the preferred food of *Mesocyclops*. Species of the genera *Polyarthra* and *Synchaeta* belong to rotifers that are easy to obtain and readily eaten. It is probably to the growing predator pressure that the decrease should be attributed of the biomass of these organisms during lake eutrophication — although there is a relative improvement of the trophic conditions. On the other hand, it is these species that dominate in the rotifer communities of the mesotrophic lakes, and even in a situation when they are the only component of the optimum food of the predators. As has been demonstrated earlier, the dominance of *Polyarthra* and *Synchaeta* in these lakes depends on the trophic conditions, i.e., the concentration and size structure of the phytoplankton. Thus the conclusion suggests itself that it is not the predator pressure that determines the biomass and species composition of the rotifers, but, the other way round — a low rotifer biomass, being the result of the trophic conditions in the mesotrophic lakes, and a lack of other components of the optimum food, are the cause of the low biomass of the invertebrate predators in these lakes.

The above-presented findings permit the conclusion that in the lakes studied the effect of invertebrate predators, even if significant in certain situations, does not determine the general regularities and nature of changes taking place in the zooplankton communities during the eutrophication process. The results obtained from the study seem to indicate that there is an opposite situation — that it is food (the biomass and composition of non-predatory zooplankton) that determines the development of the invertebrate predator community.

4. CONCLUSIONS

An analysis of selected biotic agents that may determine changes in numbers, biomass and structure of the zooplankton during eutrophication permits the following conclusions:

(1) In the lakes studied planktivorous fish pressure does not determine the nature of species structure changes in the crustacean communities. The results from the study seem to support the hypothesis put forward by Gliwicz and Preis (1977) that in the Masurian lakes the planktivorous fish pressure should be looked at as the action of an unspecialized predator.

(2) The cause of changes in numbers, biomass and species structure of the zooplankton should be looked for among factors directly associated with the lake trophic state, mainly in the above-discussed relationships between the phyto- and zooplankton, i.e., in changes in the food supply of the zooplankton. This is indicated, in addition to the data discussed above, by the following findings:

(a) In the lakes studied ecological groups have been identified of species specific to low- (group I) and high- (group II) trophic states. Changes in numbers and biomass of these groups determine changes in the species structure of the zooplankton in the course of eutrophication (Karabin 1985). The level of biomass of the group typical of low-trophic-state lakes depends on: in the rotifer community — *Polyarthra major*, a macrofilter-feeder feeding on nannophytoplankton, in the crustacean community — microfilter-feeders sensitive to high concentrations of net algae (*Daphnia*). The entire biomass of ecological rotifer group II consists of sedimentators feeding on the bacteria-detritus suspension, and the biomass of crustacean group II depends on facultative predators, and on those cladoceran filter-feeders which are not sensitive to the disturbing effect of high concentrations of net algae. A comparison of the trophic status of species determining the biomass of ecological groups I and II with changes in the food supply of the zooplankton in lakes of different trophic states thus points to the important role of the food factor modifying the dominance dynamics of these groups, thereby the species structure of the whole pelagic zooplankton.

(b) Changes in the species structure of the rotifers and crustaceans are step-like — structure remodelling takes place over a narrow range of TSI_{SD} variation, corresponding to meso-eutrophic lakes (Karabin 1985), i.e., lakes, where, due to considerable changes in numbers and size structure of the phytoplankton, there occurs a significant change in the food supply of the non-predatory zooplankton.

(c) The high and very high rotifer numbers and biomass found in the eutrophic and polytrophic lakes are the result of an intensive development in these lakes of species feeding on the bacteria-detritus suspension.

(d) A lack of unequivocal, directional changes in cladoceran numbers and biomass with rising lake trophic states (Karabin 1985) can be attributed to differences in the response of the microfilter-feeders (“efficient” and “inefficient”) of the groups distinguished to a growth in numbers of the net algae.

(e) The growth, following a trophic state rise, in the biomass to numbers ratio of the rotifers and crustaceans, i.e., in the average individual body weight of the communities (Karabin 1985) results from the increasing dominance of minute sedimentators and microfilter-feeders, and small facultative predators of the genus *Mesocyclops*.

(3) Food (non-predatory zooplankton biomass and composition) is also a factor determining the development of the predatory zooplankton in lakes differing in the

trophic state. But the effect of invertebrate predators on the pelagic zooplankton, even if significant in certain situations, does not determine the general regularities of changes in the zooplankton communities during the eutrophication process.

(4) Factors directly or indirectly related to the phytoplankton biomass and structure in lakes of different trophic states thus determine the numbers and species structure of the whole zooplankton, both non-predatory and predatory.

5. SUMMARY

The role has been evaluated of selected biotic factors (pressure of planktivorous fish, and of invertebrate predators, trophic conditions in the habitat) in the determination of the numbers and biomass, as well as structure of the zooplankton in lakes of different trophic states.

A comparison of the density of planktivorous fish with selected structure parameters of the crustacean community (numbers, biomass, average individual body weight) has shown that the pressure of planktivorous fish is not a factor determining changes in these parameters in the course of lake eutrophication (Fig. 2). For this reason, the causes of these changes were looked for in factors directly or indirectly associated with the trophic state, primarily in the phytoplankton-zooplankton interrelations. For the phytoplankton is (directly or indirectly) the basic source of food for the pelagic zooplankton. On the basis of data relating to the biomass and size structure of the phytoplankton the nature and changes of the food supply have been determined for lakes of different trophic states (Fig. 3). This in turn made it possible to establish the relationship between the trophic conditions of the habitat, and structure of the zooplankton. For on the basis of literature data concerning the way of food collecting and the diet seven rotifer and three non-predatory crustacean trophic groups have been distinguished. An analysis of biomass and dominance changes in these groups in relationship to changing trophic conditions in the environment (Figs. 4–7) permits the following conclusions:

(1) Large algae, the so-called net algae, play a significant role in the determination of the trophic conditions of the zooplankton.

(2) Food is the main factor determining changes in numbers, biomass and species structure of the zooplankton in the course of lake eutrophication.

By "controlling" the numbers, biomass and species composition of the non-predatory zooplankton the phytoplankton also determines, in an indirect way, the numbers and biomass of the invertebrate predators in the lakes under study (Figs. 8, 9). But the pressure of these predators on the zooplankton, even if significant sometimes, is not a factor responsible for the changes that the zooplankton is subject to as the lake eutrophication progresses.

6. POLISH SUMMARY

Oceniono znaczenie wybranych czynników biotycznych (presja ryb planktonożernych i drapieżników bezkręgowych, warunki pokarmowe w środowisku) w kształtowaniu liczebności, biomasy i struktury zooplanktonu w jeziorach różnej trofii.

Porównując zagęszczenie ryb planktonożernych z wybranymi parametrami struktury zespołu *Crustacea* (liczebność, biomasa, średni ciężar osobnika zespołu) stwierdzono, że presja ryb planktonożernych nie jest czynnikiem decydującym o zmianach tych parametrów w trakcie procesu eutrofizacji (rys. 2). Dlatego też przyczyn tych zmian poszukiwano w czynnikach związanych bezpośrednio z trofią, a głównie w

stosunkach fitoplankton-zooplankton. Jest bowiem fitoplankton (bezpośrednio lub pośrednio) podstawowym źródłem pokarmu dla zooplanktonu pelagicznego. Na podstawie danych dotyczących biomasy i struktury wielkościowej fitoplanktonu oceniono charakter i zmiany bazy pokarmowej w jeziorach różnej trofii (rys. 3). Pozwoliło to z kolei na określenie zależności między warunkami pokarmowymi w środowisku a strukturą troficzną zooplanktonu. Na podstawie danych literaturowych, dotyczących sposobu pobierania pokarmu i jego składu, wyróżniono bowiem w obrębie zespołu *Rotatoria* 7, a wśród niedrapieżnych *Crustacea* – 3 grupy troficzne. Analiza zmian biomasy i dominacji tych grup na tle zmieniających się warunków pokarmowych w środowisku (rys. 4–7) pozwala na sformułowanie wniosków, że:

1. Istotną rolę w kształtowaniu warunków pokarmowych zooplanktonu odgrywają duże glony, tzw. glony sieciowe.

2. Pokarm jest głównym czynnikiem determinującym zmiany liczebności, biomasy i struktury gatunkowej zooplanktonu w trakcie eutrofizacji jezior.

Fitoplankton – poprzez „kontrolę” liczebności, biomasy i składu gatunkowego zooplanktonu niedrapieżnego – decyduje też, choć w sposób pośredni, o liczebności i biomacie drapieżników bezkręgowych w badanych jeziorach (rys. 8, 9). Natomiast presja tych drapieżników na zooplankton, choć niekiedy znacząca, nie jest czynnikiem decydującym o zmianach, jakie zachodzą w zooplanktonie w miarę eutrofizowania się jezior.

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