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**PELAGIC ZOOPLANKTON (ROTATORIA + CRUSTACEA)
VARIATION IN THE PROCESS
OF LAKE EUTROPHICATION
I. STRUCTURAL AND QUANTITATIVE FEATURES***

ABSTRACT: Rotifer and crustacean ecological groups, distinctive of low-trophic-state lakes and eutrophic lakes have been identified. Zooplankton specific composition changes accompanying lake eutrophication occur in steps, over a narrow TSI_{SD} (45 – 55) range. An increasing dominance of small-bodied species must be looked at as the cause of differences in the response of numbers and biomass to a rising trophic state – a rising trophic state is accompanied by a diminishing of the biomass to numbers ($B:N$) ratio of the rotifers and crustaceans. On the basis of a statistical analysis a selection has been made of structural characteristics of high bioindicative values, most useful in ecological monitoring.

KEY WORDS: Lakes, eutrophication, polluted lakes, zooplankton, Rotatoria, Crustacea, zooplankton structure, bioindication.

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1. INTRODUCTION

The great majority of rotifer and crustacean species show a high tolerance of changes in environmental conditions. For this reason, trials for determining the relationship between the trophic state of lakes and the zooplankton inhabiting them, on the basis of a faunistic analysis (i.e., only by looking for relationships between the presence or absence of a species and a trophic state) make it only possible to identify groups indicative of extreme trophic types of lakes (Lityński 1925, Gieysztor 1959). It is practically impossible to establish specific characteristics of the zooplankton species structure, or the dynamics of this structure in a large group of intermediate lakes. This problem was studied by Bowkiewicz (1938). Within the crustaceans he identified an eight-unit complex of indicator species, the so-called complex of Entomostraca. Bowkiewicz (1938) assumed that a progressing lake eutrophication is accompanied by an impoverishment of the zooplankton species composition, which is manifested by a steady decrease of the number of species in a complex. Patalas (1954) has found, however, that Bowkiewicz's (1938) theory is only true in the case of low-trophic-state lakes.

The faunistic approach is also represented by studies in which the index value of particular species was determined on the basis of the frequency of their occurrence in lakes of different trophic states (Pejler 1965, Patalas and Patalas 1966, Radwan 1973). This method, as well as the use of the multiple analysis, or creating species matrices (Sprules 1977) increase the accuracy of choosing the most useful indicator species. However, the results obtained, and the possibility of using them for bioindication have the same limitations as have the results from the studies mentioned earlier.

When considering the possibility of using biological indices, it is necessary to take

into account geographical differences in the occurrence of organisms. This factor may play a particularly limiting role in the typically faunistic approach, where the presence or absence of a species is considered to indicate the trophic state of a lake. The effect of this agent can also be seen in areas located within the boundaries of Poland. For instance, the occurrence of *Limnocalanus macrurus* Sars (a species indicative of low trophic states) in Poland is limited to several water bodies in the Great Lake Country (Wierzbicka 1953). During their study of lakes in northern Poland Patalas and Patalas (1966) have found that *Daphnia cristata* Sars and *Bosmina berolinensis* Imhof occur only in Masurian lakes, while *Bosmina coregoni gibbera* (Schoedler) is sporadically found in lakes of this area.

The above-presented facts indicate that from the point of view of bioindication it is not sufficient to establish the relationship between the trophic state of lakes and the zooplankton living in them solely on the basis of a faunistic analysis. For this reason, there has been an increasing number of trials for relating the trophic state to a number of zooplankton structural characteristics on the basis of numerical data (structure analysis). This approach does not disprove the usefulness of a species in lake typology, yet in this case the nature and indicative value of a species depend on numeric ratios, e.g., absolute abundance or dominance degree in a community, and not its presence or absence. Looking for a relationship between the zooplankton and the lake trophic state, Patalas (1954) concentrated his attention primarily on communities of dominant species and their quantitative ratios expressed by their percentage in total numbers. He identified 4 crustacean indicator groups with different dominant-species proportions, characteristic of a-meso, b-meso-, eutrophic and highly eutrophic lakes. The above author also found that a rising trophic state is accompanied by a steady growth in numbers of the crustaceans; in highly eutrophic (disharmonic) lakes, however, the number of crustaceans decreases again. Long-term (many-year) studies of lakes undergoing a steady eutrophication have also revealed a steady growth in number and biomass of the zooplankton, especially of its rotifer component (e.g., Chaberman 1975, Petrovič 1975, Hillbricht-Ilkowska, Spodniewska and Węgleńska 1979). Patalas (1972) found a high correlation between the numbers of crustaceans and the concentration of total phosphorus and chlorophyll-a.

Many authors suggest that numeric ratios between taxa or trophic groups of the zooplankton should be used for bioindication (Gannon 1972, Giljarov and Gorelova 1974, Bespalov and Saprykina 1975, McNaught 1975, Ivanova 1976).

With a rising trophic state, changes in the species structure of the zooplankton are accompanied by a decrease in the number of species (Bowiekiewicz 1938, Patalas and Patalas 1966, Margalef 1968). At present, the community species diversity is assessed by many indices, of which the Shannon-Weaver index, derived from the theory of information and called the general index of diversity (\bar{H}), is most widely recognized. Giljarov (1972) tried to use this index for a trophical classification of lakes.

The above-discussed studies searching for relationships between the trophic state of lakes and the structure of the zooplankton inhabiting them indicate that the particular authors usually restrict their investigations to an analysis of some selected structure elements of this community. The studies mainly concern the crustacean component of the zooplankton, and are usually based on an analysis of a small group of lakes with a relatively low trophic-state diversity. Apart from this, due to the fact that the authors use different indices for lake trophic state determination, and different methods for zooplankton abundance assessment, the results are often difficult to compare and do not give a consistent, complex picture of changes in the zooplankton structure in the course of lake eutrophication.

For this reason, in the present study a comprehensive analysis has been attempted, on the basis of quantitative data, of the structure of zooplankton (numbers and biomass of the whole community and of particular taxonomic and ecologic groups, degree of their dominance in the community, species structure, species diversity indices, indicator-species), and of the nature of changes in this structure in lakes representing a trophic state gradient. Both the basic groups making up this community – rotifers and crustaceans, have been taken into account, and the analyses have been based on a large group of lakes with a wide trophic-state range, from a-mesotrophy to hypertrophy.

This will make it possible to look for, and precisely quantify the relationships between the above-enumerated structural characteristics of the pelagic zooplankton and the lake trophic state also expressed in terms of quantity, according to the index selected. The results obtained can be used for the selection of community structure features most useful as bioindicators.

2. AREA, MORPHOMETRICAL AND TYPOLOGICAL DESCRIPTION OF LAKES

Most of the lakes under study are located in the Masurian Lakeland, but some of them are within other geomorphological units – Iława Lake District and Lubawa Upland (Fig. 1). Such a large study area was needed for the analysis to cover a large number of lakes of different trophic states (from a-mesotrophy to polytropy) and at the same time differing with respect to stability (dimictic and polymictic lakes) and effect of pollution. The material has been collected from a total of 64 lakes (71 stations).

The study was carried out in the years 1976 – 1978. In 1976, the study covered water bodies of the Great Masurian Lakes (lakes 1 – 20). These lakes were chosen on account of their considerable recreation value and economic importance in the Masurian region. Most of them are large and very large water bodies – there are 11 lakes with a surface area of over 400 ha, and only 2 below 100 ha (Table I). They are at the same time deep lakes – only in three of them was not a thermal stratification found to form during the summer period.

When selecting lakes for studies in the years 1977 – 1978, the above-mentioned considerable diversity of the water bodies was taken into account. With regard to

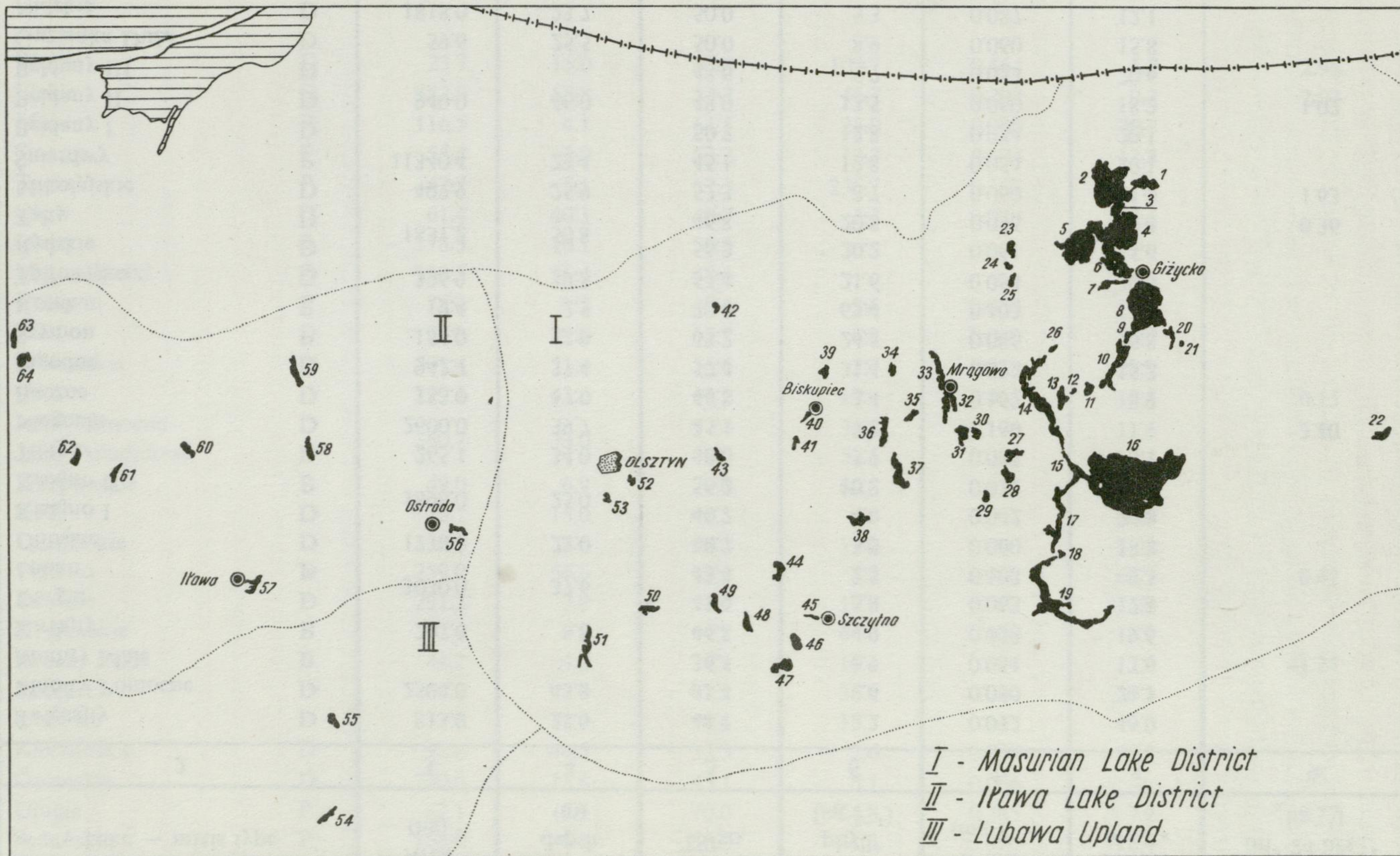


Fig. 1. Location of study lakes
 I – Masurian Lake District, II – Iława Lake District, III – Lubawa Upland (lake names and numbers assigned to them are listed in Table I)

Table I. Morphometric, physico-chemical and biological characteristics of the lakes under study

D – dimictic lakes, P – polymictic lakes

No. of lake acc. to map	Lake – mixis type	Area (ha)	Max. depth (m)	TSI _{SD}	Chloro-phyll* ($\mu\text{g}\cdot\text{l}^{-1}$)	P tot.* ($\text{mg}\cdot\text{l}^{-1}$)	N tot.: P tot.*	Sewage ($\text{m}^3\cdot 24 \text{ hrs}^{-1}\cdot \text{ha}^{-1}$)
1	2	3	4	5	6	7	8	9
1	Święcajty D	813.0	28.0	44.1	2.2	0.072	45.0	
2 a	Mamry Północne D	2504.0	43.8	35.4	2.6	0.050	21.5	
2 b	Mamry Małe P			36.5	1.9	0.051	17.6	
3	Kirsajty P	207.0	5.8	46.8	4.9	0.053	19.6	
4 a	Dargin D			41.9	5.8	0.063	17.9	
4 b	Łabab P	3030.0	37.6	43.4	2.5	0.103	9.5	
5	Dobskie D	1776.0	22.0	40.7	3.5	0.060	18.2	
6 a	Kisajno I D			40.7	4.0	0.042	24.8	
6 b	Kisajno II P	1896.0	25.0	56.2	10.2	0.071	16.2	
7	Tajty D	265.1	34.0	48.6	5.7	0.055	25.2	
8	Niegocin D	2600.0	39.7	45.1	7.8	0.160	1.1	3.10
9	Boczne D	183.0	17.0	46.8	2.4	0.157	8.9	
10	Jagodne D	942.7	37.4	57.4	31.4	0.092	15.2	
11	Szymon P	154.0	2.9	63.2	24.5	0.086	16.8	
12	Kotek P	19.4	2.5	70.0	63.4	0.103	13.9	
13	Tałtowisko D	326.9	39.5	57.4	21.6	0.054	30.6	
14 a	Ryńskie D			56.2	20.2	0.061	15.6	
14 b	Tały D	1831.2	50.8	46.8	20.8	0.036	29.4	0.36
15	Mikołajskie D	497.9	25.9	52.3	8.7	0.060	21.2	1.63
16	Śniardwy P	11340.4	23.4	45.1	12.8	0.054	20.1	
17 a	Bełdany I D			50.7	12.8	0.054	20.1	
17 b	Bełdany II D	940.0	46.0	48.0	13.5	0.060	18.2	1.02
17 c	Bełdany III D			48.6	5.7	0.053	20.6	
18	Guzianka Duża D	59.6	25.5	50.0	8.9	0.060	15.8	
19	Nidzkie D	1818.0	23.7	50.0	5.3	0.087	12.1	
20	Wojnowo D	176.3	14.2	58.6	42.2	0.092	13.7	

21	Wobel	D	23.7	15.0	67.4	109.7	0.464	5.7	2.95
22	Elckie	D	382.0	55.8	53.2	46.7	0.202	9.2	2.03
23	Mój	P	116.5	4.1	61.5	25.0	0.080	20.7	
24	Siercze	P	55.4	2.0	53.2	13.7	0.084	13.8	
25	Tuchel	P	42.7	5.1	67.3	236.7	0.357	7.2	
26	Ołów	D	61.4	40.1	40.7	3.4	0.029	58.6	
27	Inulec	P	178.3	10.1	58.6	—	—	—	
28	Majcz Wielki	D	163.5	16.4	48.6	—	—	—	
29	Kołowin	P	78.2	7.2	47.4	3.6	0.053	11.7	
30	Kuc	D	98.8	28.0	35.7	8.8	0.040	33.7	
31	Probarskie	D	201.4	31.0	36.5	3.7	0.038	28.9	
32	Czos	D	279.1	42.6	53.2	17.9	0.068	18.4	0.15
33 a	Juno Północne	D	380.7	33.0	57.4	32.8	0.175	11.4	5.97
33 b	Juno Południowe	D			60.0	53.6	0.282	7.1	
34	Warpuńskie	P	49.0	6.9	70.0	69.8	0.134	8.3	
35	Sarż	D	76.7	15.0	41.5	4.8	0.031	50.0	
36	Lampackie	D	198.6	38.5	56.2	17.0	0.073	13.4	
37	Pilakno	D	259.0	56.6	33.2	1.5	0.020	62.5	0.42
38	Rańskie	P	291.3	7.8	55.1	17.0	0.092	15.9	
39	Stryjewskie	P	67.4	6.2	64.1	64.0	0.160	7.9	
40	Kraksy Duże	P	44.2	4.0	54.1	10.1	0.594	7.5	41.24
41	Rzeckie	D	56.1	29.0	61.5	36.6	0.087	20.1	
42	Kokowo	D	37.2	11.7	58.6	18.7	0.147	10.3	
43	Kierzlińskie	D	92.8	44.5	32.3	2.6	0.038	32.9	
44	Gromskie	D	240.0	15.8	45.1	5.1	0.066	—	
45	Długie	P	62.1	5.4	70.0	74.8	0.285	7.2	2.77
46	Sędańskie	P	168.0	6.1	56.2	31.3	0.090	18.4	
47	Sasek Mały	P	319.1	3.7	58.6	25.0	0.142	22.4	14.02
48	Brajnickie	P	186.3	5.2	67.3	110.7	0.157	11.8	
49	Małszewo	D	202.0	16.9	56.2	33.7	0.137	9.8	
50	Gim	D	175.9	25.9	34.2	8.2	0.043	29.1	

1	2		3	4	5	6	7	8	9
51	Maróz	D	332.5	41.0	49.3	9.2	0.040	23.7	
52	Skanda	D	51.5	12.5	38.0	11.7	0.044	22.7	
53	Bartağ	D	72.3	15.2	50.0	—	—	—	
54	Lidzbarskie	D	121.8	25.2	60.0	61.5	0.222	—	8.20
55	Hartowiec	P	69.2	5.2	61.5	22.7	0.176	8.3	0.20
56	Szeląg Mały	D	83.8	15.2	57.4	21.6	0.062	18.5	0.47
57	Iławskie	P	154.5	2.8	77.4	167.5	0.420	8.5	12.45
58	Jańskowskie	D	152.5	16.5	48.0	8.3	0.059	33.1	
59	Sambród	P	128.4	4.3	70.0	77.8	0.161	14.0	0.20
60	Bądze	P	149.9	6.7	70.0	46.7	0.141	17.4	
61	Burgale	P	79.0	7.4	55.1	15.8	0.074	21.7	
62	Liwieniec	P	81.2	2.4	73.2	76.5	0.321	5.5	7.35
63	Sztumskie**	D	50.1	24.0	48.6	22.3	0.506	4.5	?
64	Barlewickie**	P	63.7	8.5	67.3	83.6	0.940	2.8	?

*According to Z d a n o w s k i (1983) and unpublished data. **Large amounts of sewage discharged in emergency situations, but no data on the actual quantities.

morphometry and thermal stratification type they can be divided into two separate groups. One of them (22 lakes) comprises deep lakes, up to 12.0–56.6 m, with a clear thermal-oxygen stratification during the summer stagnation. The second group (20 lakes) includes nonstratified, shallow water bodies, up to 2.4–10.1 m. In the choice of lakes for study in 1977–1978 care was taken to avoid too great surface-area differences between them. The area of the lakes ranges from 23.7 to 382.0 ha, lakes of 50–250 ha in area representing 75% of them (Table I).

Data from the papers by: Olszewski and Paschalski (1959) and Olszewski et al. (1978) have been used as a criterion for choosing lakes with a specific trophic state. The exact determination of the trophic state, needed for lining the lakes up into a trophic gradient, was based on parameters obtained during the study of the lakes. They were the following: Secchi's disc visibility (the author's own data), and the concentration of phosphorus and chlorophyll-a (Zdanowski 1983 and unpublished data) in the upper water layers (Table I).

Comparatively numerous among the study lakes are lakes receiving pollution from point sources – mainly municipal sewage. The total number of such lakes, including those into which even small amounts of pollutants are discharged, is 23. The amount of sewage input to the lakes during 24 hours, and the BOD₅ value (Giercuskiewicz-Bajtlik and Jabłoński 1977) have been presented in Table I. Municipal sewage and industrial effluents are characterized by a high phosphorus content (Kajak 1979). For this reason, many lakes polluted with sewage are characterized by a high concentration of this nutrient in the surface water layer. This applies to both total phosphorus and the inorganic fraction which often represents over 50% of the total amount of this element. At the same time, for these lakes a low N:P ratio is found, usually below 10.0 (Table I). Lakes of this type are: Niegocin, Wobel, Elckie, Juno, Kraksy Duże, Długie, Sasek Mały, Lidzbarskie, Hartowiec, Iławskie and Liwieniec – i.e., lakes receiving relatively high (above $1 \text{ m}^3 \cdot 24 \text{ hrs.}^{-1} \cdot \text{ha}^{-1}$) and very high (above $5 \text{ m}^3 \cdot 24 \text{ hrs.}^{-1} \cdot \text{ha}^{-1}$) amounts of sewage. This group includes the following lakes: Sztumskie and Barlewickie. Although there are no data on this, the amounts of sewage discharged into these lakes are probably very high, and it is known that the sewage is not treated. This is indicated by a very high concentration of total phosphorus in the surface water layers of the lakes Sztumskie and Barlewickie (0.51 and $0.94 \text{ mg} \cdot \text{l}^{-1}$), where phosphates represent 97 and 84%, respectively, of total phosphorus. The N:P ratio is very low: 3.6 and 4.5.

In the remaining lakes into which sewage is discharged the concentration of total and inorganic phosphorus and the N:P ratio do not differ from the average values found in unpolluted lakes. They are lakes receiving low amounts of effluents (below $0.5 \text{ m}^3 \cdot 24 \text{ hrs.}^{-1} \cdot \text{ha}^{-1}$), or through-flow water bodies with a short water exchange time.

For this reason, from this point on the term “polluted lakes” refers only to the above-enumerated 11 lakes receiving effluents characterized by a high P concentration and a low N:P ratio in the upper water layers.

3. MATERIAL AND METHODS

3.1. MATERIAL

Zooplankton samples were collected at the deepest place in a lake. In the case of lakes that differ greatly in respect of their morphometric characteristics, in several clearly outlined open water stretches samples were collected at several stations. A 5-litre sampler of the type designed by Bernatowicz was used. Samples were collected at 1 m intervals from the surface to the bottom, and were then pooled together for the layers: epi-, meta-, and hypolimnion. In the case of shallow, polymictic water bodies sampling was done at 0.5 m or 0.25 m intervals. After being fixed with 4% formalin the material was studied by routine methods (Hillbricht-Ilkowska and Patlas 1967). Individual body-weight was determined for each species on the basis of the relationship between body length and body weight (Pečen 1965, Klekowski and Šuškina 1966, Karabin 1974, Ruttner-Kolisko 1977).

3.2. CHOICE OF: TROPHIC STATE INDEX, PHENOLOGICAL PERIOD AND PELAGIC ZONE – BEST FOR A COMPARATIVE ANALYSIS OF THE ZOOPLANKTON

The aim of the study is to determine the relationship between quantifiable and structural characteristics of the zooplankton and the trophic state of lakes. Hence the necessity to choose an index that would make it possible to carry out a comparative analysis of the trophic state of lakes and line them up to form a trophic state gradient. The index should be: (1) synthetic, comprising as many different signs of eutrophication as possible, (2) stable for a relatively long period, (3) independent of lake morphometry and mictic status, (4) the range of variation of the index value should be relatively wide to cover all eutrophication stages.

It has been established that the above conditions are best satisfied by the water transparency, as determined by Secchi's disc visibility. In case of extensive studies, such as the investigations of the lakes considered, the commonly applied trophic state indices – phosphorus concentration, primary production, chlorophyll concentration or zooplankton abundance only reflect the situation at the time of measurement. Since the value of most of these indices are subject to great and fast variation during the summer season, a comparative analysis of lakes based only on measurements made once is difficult, and in many cases it may be misleading. Moreover, phosphorus concentration is in many cases only an indicator of the "potential" productivity of a lake, while the real productivity may vary. Indices based on chlorophyll concentration or primary production may be affected by extratrophic factors, e.g., light.

These reservations to a lesser extent apply to the visibility of Secchi's disc. Water transparency is primarily determined by phytoplankton abundance (Bul'ón 1977,

C a r l s o n 1977) at the measuring time. The value of this index depends, however, also on the subsequent "processing" of the primary production – abundance of all living organisms and dead organic matter concentration in the pelagic zone. Water transparency is thus the sum total of all the final effects of trophic-state determining factors – understood as the lake productivity. On account of the cumulative nature of this index, its oscillations during the growing season are not so rapid as are those of the phytoplankton abundance, and if a selected period of the growing season is considered (e.g., the summer stagnation peak), it may be expected that the oscillations will be yet lower.

In summer, it is the transparency of the water that most fully satisfies the conditions required of an index that is expected to make possible a comparative analysis of the trophic state – especially in the case of extensive investigations. For this reason in this paper this index became the basis of the degree of lake eutrophication. Secchi's disc visibility has been used for the calculation of the trophic state index (C a r l s o n 1977) for the lakes under study according to the formula:

$$\text{trophic state index (TSI}_{SD}) = 10 (6 - \log_2 SD)$$

where: SD – visibility of Secchi's disc in metres. The values of the index were used to line the lakes up into a gradient, in ascending order of the trophic state.

As indicated by C a r l s o n ' s (1977) paper, mesotrophic lakes are characterized by TSI values of about 40, eutrophic – about 60, whereas water bodies of an intermediate nature, meso-eutrophic correspond to a TSI value of about 50. Although a trophic state rise is a continuous process, intermediate TSI values were for practical reasons assumed to constitute the „borderlines" between the three lake types. According to this assumption, lakes with a TSI under 45 are mesotrophic, those with a TSI value of 45 – 55 are meso-eutrophic, whereas lakes with TSI values above 55 are eutrophic. It has also been assumed that lakes with a TSI value above 65 are polytrophic. Since this classification is consistently used hereafter, the lake trophic groups distinguished have been described in Table II, where the ranges and mean values of selected physico-chemical and biological parameters of the lakes have been presented. They are similar to the values given by many authors (D o b s o n, G i l b e r t s o n and S l y 1974, S p o d n i e w s k a 1979, 1983, V o l l e n w e i d e r 1979) to describe different trophic types of lakes.

In most of the study lakes the zooplankton was sampled twice – during the spring circulation and during the summer stagnation.

On account of the fast rise of temperature and water circulation, the spring is the period of dynamic changes in the communities of organisms inhabiting the pelagic zone. The changes occur over a comparatively short time, and the time of their start, and their rate primarily depend on abiotic factors such as the lake morphometry and climate variation.

The summer stagnation period is more stable – changes in the abiotic and biotic environmental conditions are small. Water stagnation leads to the accumulation of the effects of factors determining the trophic state of lakes and thereby to a considerable

Table II. Description of the trophic types of the study lakes, identified on the basis of the TSI_{SD} value during summer stagnation (in brackets — mean values)

Lakes	Stratification	TSI_{SD}	Trophic type	Number of lakes	Phosphorus ($mg \cdot l^{-1}$)		N:P	Chlorophyll ($\mu g \cdot l^{-1}$)
					total	mineral		
Unpolluted	stratified	45	mesotrophy	13	0.020–0.063 (0.040)	0.011–0.018 (0.015)	64.5–17.8 (32.8)	1.1–10.4 (3.8)
		45–55	meso-eutrophy	15	0.036–0.087 (0.058)	0.014–0.019 (0.012)	29.4–12.1 (20.3)	5.3–20.8 (10.1)
		55–65	eutrophy	9	0.054–0.092 (0.075)	0.007–0.025 (0.015)	30.6–14.0 (18.2)	11.1–42.2 (24.6)
	non-stratified	45–55	meso-eutrophy	4	0.038–0.084 (0.057)	0.002–0.053 (0.027)	24.5–11.7 (17.4)	3.6–11.8 (6.9)
		55–65	eutrophy	8	0.071–0.160 (0.093)	0.012–0.041 (0.026)	21.8–7.9 (16.7)	10.2–46.2 (22.3)
		65	polytropy	6	0.103–0.357 (0.175)	0.024–0.076 (0.049)	17.0–7.2 (12.1)	35.4–183.3 (74.4)
Polluted ($TSI_{SD} = 45.1–77.4$)				14	0.157–0.940 (0.347)	0.087–0.444 (0.257)	22.4–1.1 (7.6)	0.8–92.4 (33.2)

trophic diversity of the lakes, greater than in the spring period. By comparing plankton communities of the Great Masurian Lakes in different seasons, P i j a n o w s k a (1978) found that during the summer stagnation these communities became most diversified and attained the highest abundance level. In this period also the greatest differences were seen between lakes with the highest and lowest zooplankton numbers and biomass. For this reason, the summer stagnation period was considered best for a comparative analysis of the zooplankton.

The study covered both deep, stratified and shallow, nonstratified lakes. According to the assumption that the epilimnion is autonomous with regard to the cycling of the basic nutrients (G l i w i c z 1979, S c a v i a 1979), in deep lakes the metalimnion plays a role similar to that played by the bottom in shallow water bodies. Because of this, during the summer stagnation the epilimnion layer can be compared, in respect of both the physico-chemical and biological conditions, and the processes going on in it, to the entire water column of nonstratified lakes. On the other hand, since in the majority of the study lakes the epilimnion layer virtually overlaps the trophogenic zone, the production processes that occur in the epilimnion determine the productivity level of a whole water body. Secchi's disc visibility, used as the basis for lining up lakes into a trophic state gradient, as well as other productivity indices (e.g., amount of chlorophyll, phytoplankton biomass) are epilimnetic symptoms of eutrophication. For a correct analysis of the relationship between the trophic state of lakes and the structure of the zooplankton in morphometrically different lakes it seems, therefore, justified to restrict the analysis of the zooplankton in stratified lakes to the epilimnion layer alone.

4. RESULTS

4.1. ANALYSIS OF PARAMETERS CHARACTERIZING THE SPECIFIC AND GROUP STRUCTURE OF THE ZOOPLANKTON

4.1.1. Community structure of the rotifers

4.1.1.1. General

In many of the lakes under study one or two species of the genus *Asplanchna* were found. Because of their large body size, the individual body weight of *Asplanchna* is many times greater than that of other rotifer species, e.g., in Lake Tuchel the average individual body weight of *Asplanchna priodonta* Gosse was equal to the weight of 1318 individuals of *Keratella cochlearis* (Gosse). Thus the presence of even one individual in a sample can significantly affect the assessment of the dominance of other species in the community biomass. As it is the degree of dominance of individual species in the joint rotifer biomass that is used in the present study as the basis for the comparative analysis of the structure of rotifer communities, the genus *Asplanchna* has been excluded from the analysis and discussed separately (subsection 4.1.1.5).

4.1.1.2. Species structure — indicative species and species groups

In order to determine the nature of the relationship between the trophic state of lakes and the species that inhabit them, the following criteria have been used: presence or absence of a species, frequency of its occurrence, and above all, the degree of dominance of a species in the rotifer biomass — in lakes of different trophic states. On the basis of these criteria three ecological groups of rotifers have been distinguished, characterized by a different type of response to directional changes in the lake trophic state. With a rising trophic state of lakes the dominance of ecological group I in the biomass of the rotifers decreases, that of group II grows, whereas for organisms representing group III no relationship is found between the lake trophic state and their proportion in the biomass of the rotifer community (Fig. 2).

Species included in ecological group I occurred most often and most abundantly in the mesotrophic lakes, i.e., lakes the TSI_{SD} of which does not exceed the value of 45. They are: *Conochilus hippocrepis* (Schrank), *Chromogaster ovalis* (Bergendal), *Gastropus stylifer* Imhof, *Ascomorpha ecaudis* Perty, *Polyarthra major* Burckhardt (Fig. 2). It is therefore a group poor in species.

However, the rotifers are organisms rather typical of highly productive lakes, where they occur most abundantly and in the largest number of species. This accounts for the difficulty in distinguishing species characteristic of low-productivity waters, as well as for the discrepancies, found in the literature, in the evaluation of the usefulness of the particular rotifer species as indicators of low trophic states. Three of the species included in ecological group I — *Chromogaster ovalis*, *Conochilus hippocrepis* and *Gastropus stylifer* — are often mentioned as low trophic-state indicators (Pejler 1957, Hakkarı 1978, Mäemets 1983). But other species considered characteristic of low-productivity water bodies, such as *Kellicottia longispina* (Kellcott), *Conochilus unicornis* Rousselet, *Polyarthra remata* Skorikov (Berzins 1949) did not show in the Masurian lakes any clear connection with a specific trophic state, or such as *Synchaeta grandis* Zacharias, *Bipalpus hudsoni* (Imhof), *Keratella serrulata* (Ehrenberg), or *Asplanchna herricki* Guerne (Pejler 1965, Hakkarı 1978, Mäemets 1983) occurred sporadically, or were not encountered in the study lakes at all. Finally, *Polyarthra dolichoptera* Idelson, which Järnefelt (1952) regarded to be the only rotifer species indicative of low trophic states, was only found in an extremely polluted Lake Kraksy Duże, where it represented 22% of the biomass of non-predatory rotifers. *P. dolichoptera* is a species occurring in fairly large numbers in the winter-spring period (Miracle 1977). It is then encountered also in highly eutrophic and polluted lakes (A. Karabin — unpublished data), where oxygen deficits can be expected. This may indicate that this species is capable of adapting itself to waters with a low oxygen content, and would thereby explain the presence of *P. dolichoptera* in a lake so heavily polluted.

Included in ecological group II were species which occurred most often and in the largest numbers in lakes at a considerable stage of eutrophication, whereas their dominance in the rotifer biomass increased with the rising of the trophic state. This is

a relatively numerous group consisting of: *Keratella cochlearis* forma *tecta* (Gosse), *K. quadrata* (Müller), *Pompholyx sulcata* Hudson, *Filinia longiseta* (Ehrenberg), *Anuraeopsis fissa* (Gosse), *Trichocerca pusilla* (Lauterborn), *Brachionus angularis* Gosse and other species of the genus *Brachionus*, as well as *Proales micropus* (Gosse) and Bdelloidae (Fig. 2). The above-listed species are commonly considered indicative of the pelagic zone of highly eutrophic lakes (Berzins 1949, Järnefelt 1952, Pejler 1957, 1965, Radwan 1973, Hakkarri 1978, Mäemets 1983). An exception is *P. micropus*, occurring in overgrown water bodies (Kutikova 1970) and Bdelloidae, mostly littoral organisms, many of which are typical of heavily polluted waters. According to Čujkovič (1975), water pollution causes littoral species to move to the pelagic zone. This has also been found to occur in the polluted lakes under study, in whose pelagic zone 1 up to 4 littoral species were found. However, at least 2/3 of the rotifer communities found in the polluted lakes consisted of the same species as those in the "clean" eutrophic lakes, and it was on these species that the rotifer biomass depended.

The nature of the relationship between the lake trophic state and the level of dominance of the above-discussed ecological groups in the rotifer biomass makes them indicative. It is thus possible to consider ecological group I indicative of low trophic states (mesotrophy), and group II – indicative of high trophic-state lakes (eutrophy and polytropy).

Species making up group III are characterized by the lack of a relationship between their presence and dominance in the community, and the lake trophic state. The number of these species is large, but they occur sporadically and in small numbers. The abundance of this ecological group depends mainly on widely distributed eurytopic rotifer species. A rise of the trophic state was not followed by any significant changes in their proportion in the rotifer biomass, e.g., *Trichocerca birostris* (Minkiewicz), *Keratella cochlearis* f. *typica* (Gosse), *Collotheca mutabilis* (Hudson), or very wide variation in the biomass of these organisms was independent of the trophic state (*Conochilus unicornis* Rousselet, *Polyarthra vulgaris* Carlin).

Therefore in most lakes species of ecological group III account for over 50% of the rotifer community biomass. At the same time considerable variation, independent of the trophic states of the biomass of this group, significantly affects the dominance, of indicative nature, of ecological groups I and II (Fig. 2). Because of this, ecological group III was left out in further analyses, and the measure finally adopted of the structure-changing effect of the trophic state on the rotifer community was only the ratios of the biomass of both indicator groups, expressed as the percentage of each of these groups in their total biomass (Fig. 3).

Attention is attracted by the nature of changes in the structure of the rotifer communities against rising lake trophic states. At first, with a TSI_{SD} increase from 32.2 to 45.0 (which corresponds to a considerable decrease of disc visibility, from 6.9 to 2.8 m), the species structure of the community does not practically change. But a TSI_{SD} increase from 45 to 55 (meso-eutrophic lakes) already disturbs the species structure stability. In this lake group there are, in addition to water bodies still with a strong

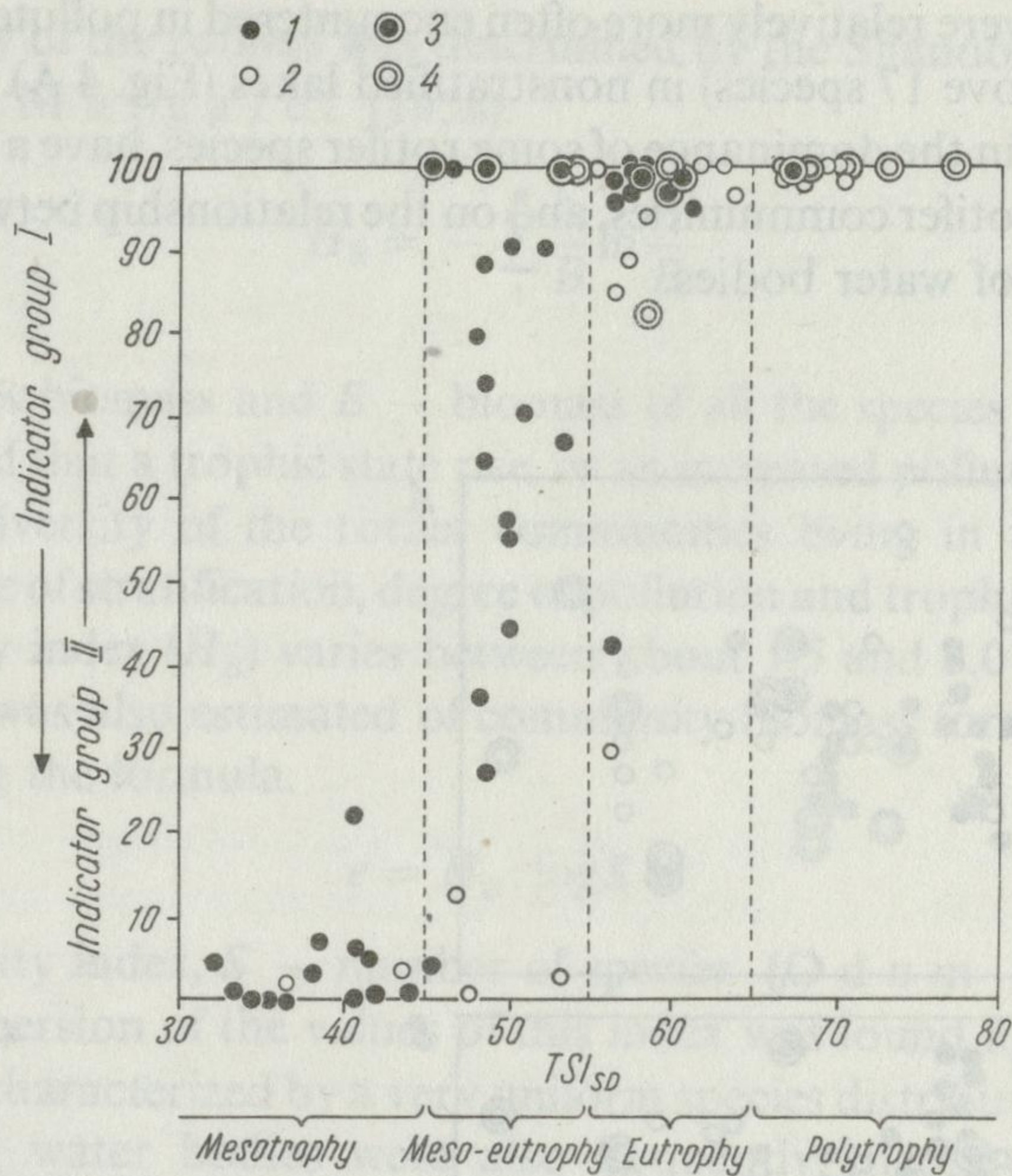


Fig. 3. Relationship between the proportion (%) of the indicator rotifer groups distinguished (I, II) in their total biomass and the TSI_{SD} of the lakes under study

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

dominance of ecological group I, also lakes where species indicative of eutrophy already represent about 90% of the biomass of all indicator organisms. In eutrophic lakes the species structure of the rotifers becomes stabilized again, but at a different quantitative level — there is a positive dominance of the species that make up indicator group II, while organisms indicative of mesotrophy occur in small numbers. In polytrophic lakes the latter were not practically encountered any more.

Thus the change of the specific structure of the rotifer community does not proceed gradually, but in steps. This is true of all unpolluted lakes: both stratified and nonstratified. In the polluted lakes, irrespective of the TSI_{SD} value, ecological group II (indicative) was clearly dominant, to a degree typical of eutrophic and polytrophic lakes.

4.1.1.3. Species diversity

A change of the species structure of the rotifer communities was not, however, accompanied by directional changes in the number of species making up these communities. In most of the lakes, in over 80% of them, under study pelagic rotifer communities are composed of 10 up to 17 species, the number of species showing no relationship to the trophic state of lakes. It may only be stated that communities poor in

species (below 10) were relatively more often encountered in polluted lakes, whereas the richest of them (above 17 species) in nonstratified lakes (Fig. 4 A). This fact, as well as the great variation in the dominance of some rotifer species, have a significant influence on the diversity of rotifer communities, and on the relationship between this feature and the trophic status of water bodies.

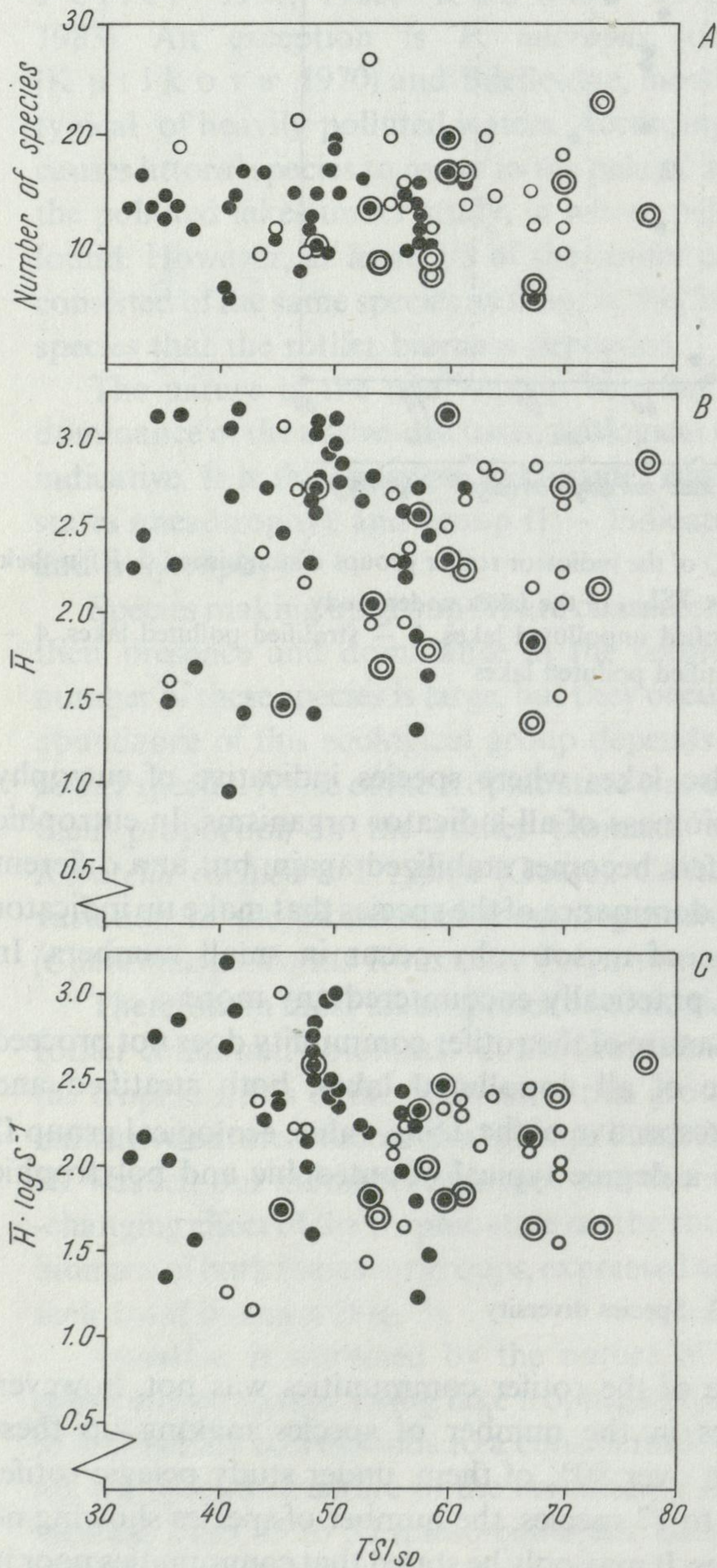


Fig. 4. Relationship between the lake TSI_{SD} and the number of species (A), general diversity index (B) and uniformity index (C) of the rotifer zooplankton community

Lake denotations as in Figure 3

Specific diversity of the rotifers was determined by the Shannon-Weaver diversity index, modified by Margalef (1958):

$$\bar{H}_B = - \sum_1^n \frac{b_i}{B} \ln \frac{b_i}{B}$$

where: b_i — i species biomass and B — biomass of all the species of the community.

It has been found that a trophic state rise, or an increased pollution of lakes do not affect the species diversity of the rotifer communities living in them. In all lakes, regardless of the type of stratification, degree of pollution and trophic state, the value of the general diversity index (\bar{H}_B) varies between about 1.5 and 3.0 (Fig. 4 B).

The uniformity was also estimated of community biomass formation by different rotifer species, using the formula:

$$e = \bar{H}_B : \log S$$

where: \bar{H}_B — diversity index, S — number of species (O d u m 1977).

The greatest dispersion of the values of this index was found for the mesotrophic lakes. Besides lakes characterized by a very uniform species distribution in the biomass (high index values), water bodies were also frequently encountered with a high dominance of several species. In the eutrophic, polytrophic, and in most of the polluted lakes the highest values of the index in question do not exceed 2.5, hence the dispersion of the values of the index is also narrower (Fig. 4 C). Along with a rising trophic state and level of pollution of lakes there thus occurs a tendency of these lakes to become similar with respect to the degree of species uniformity, manifested by an increased role of the dominant species — with the following remaining, however, unchanged: number of species and species diversity of the rotifer communities inhabiting these lakes.

The above-presented nature of the relationship between the lake trophic state and the species diversity index may indicate a relatively low proneness of this structural characteristic of the rotifer community to the action of agents directly connected with the trophic state, both those that can stimulate and those that can limit the diversity of this community.

4.1.1.4. Morphological variation of *Keratella cochlearis* in lakes of different trophic states

Keratella cochlearis is typically an eurytopic species commonly occurring in lakes varying in the trophic state; it is not therefore, an indicative species. A characteristic feature of *K. cochlearis* is its great morphological variation. It is manifested first of all by a variable length of the posterior spine — from a very long spine (forma *macracantha*) to its complete absence (f. *tecta*). In the lakes under study two forms were found in the summer: *K. cochlearis* f. *typica* and *K. cochlearis* f. *tecta*. Many authors (e.g., Carlin 1943, Pejler 1962, Hillbricht-Ilkowska 1972) are of the opinion that the principal factor determining the variation of *K. cochlearis* is, in addition to temperature, the trophic factor. As the species was found in all the lakes

under study, it is possible to follow changes in the proportions of the morphological forms in the total population biomass in relation to the lake trophic state.

The results presented in Figure 5 show that a rising trophic state is accompanied by a growth of the proportion of the *tecta* form in the population. In mesotrophic lakes the *tecta* form occurred sporadically – in all water bodies with a TSI_{SD} below 40 it was entirely absent, in the remaining lakes it represented no more than 10% of the biomass. But in most of the highly eutrophic lakes ($TSI_{SD} > 70$) the *tecta* form is clearly dominant, representing 70–100% of the biomass of *K. cochlearis* population.

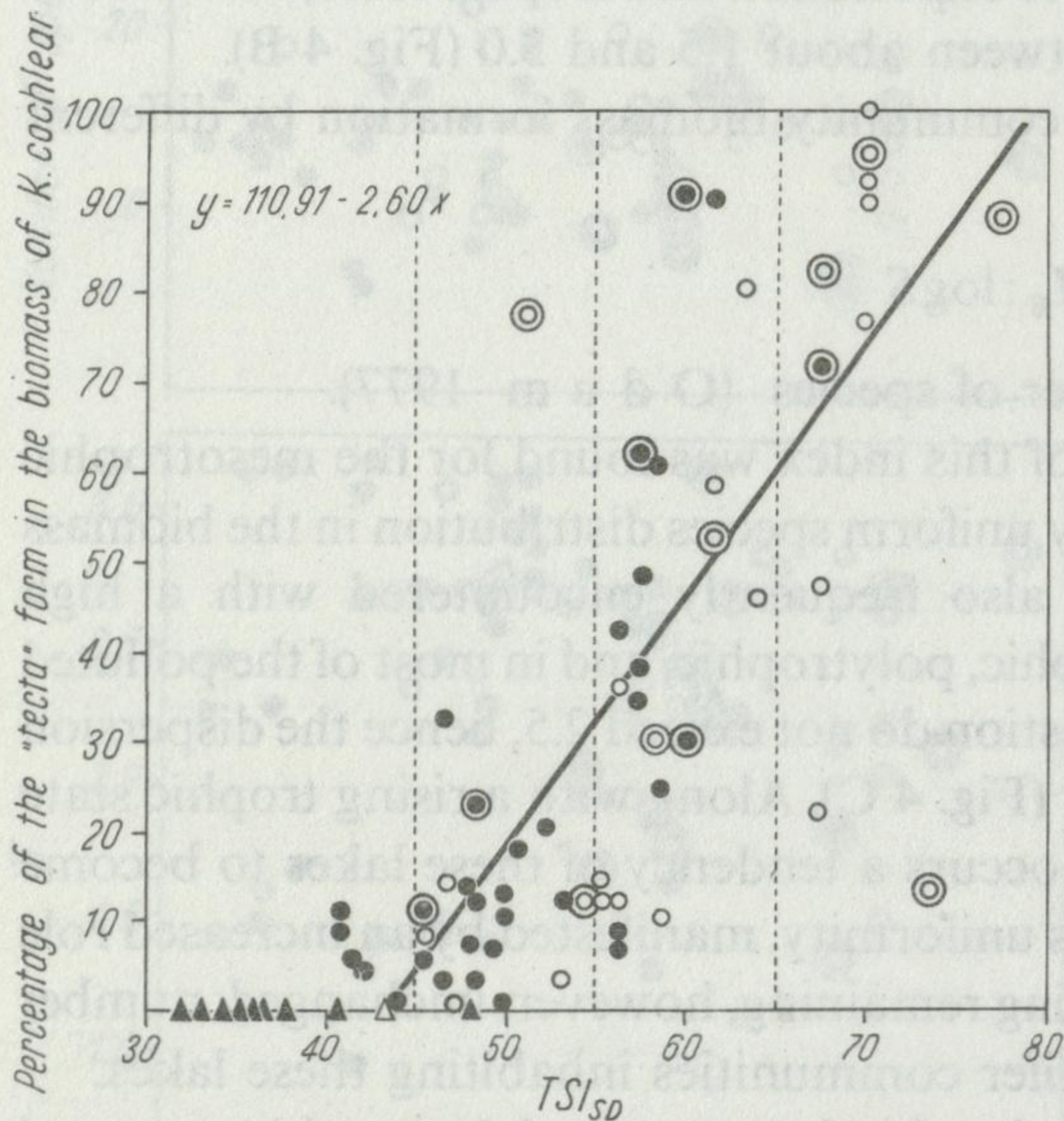


Fig. 5. Relationship between the lake TSI_{SD} and the percentage of the 'tecta' form in the biomass of *Keratella cochlearis*

Triangles – lakes in which "tecta" form was not found: full triangles – stratified lakes, open triangle – nonstratified lake; denotations of other lakes as in Figure 3

The relationship found is rectilinear in nature; the correlation is highly significant, amounting to: $r = 0.81$, $p < 0.001$ for the unpolluted lakes, and $r = 0.74$, $p < 0.001$ for all those lakes in which the *tecta* form was found to be present. Thus the presence and abundance of *K. cochlearis* f. *tecta* in the summer do not depend on the morphological type of the study lakes, or on the direct action of sewage. They do not depend on temperature either, for in the period discussed the temperature of the upper water layers was in all the lakes similar. These results confirm Hillbricht-Ilkowska's (1972) view that morphological changes in *K. cochlearis* are influenced in a decisive way by the food factor – increased concentration, in eutrophic lakes, of the bacteria-detritus suspension, the basic food of *K. cochlearis*.

Erman (1962) found a relationship between food concentration and the length of spines in another rotifer with a variable morphology – *Brachionus calyciflorus* Pallas. This relationship was manifested by a shortening of spines with a growing food concentration. Simultaneously, the same author and Halbach (1971) have demonstrated that *B. calyciflorus* forms with longer spines are characterized by a higher filtering rate. According to Erman (1962), the cause of the occurrence of forms with

longer spines in lakes poor in food is the necessity of a higher filtering rate where there is a food deficit. A converse situation is found in environments rich in food, where even a low rate filtering ensures the intake of a sufficient food ratio. The food factor does not, of course, rule out the effect of other factors, e.g., predation (Gilbert 1967), or temperature (Lindström and Pejler 1975). These authors have demonstrated experimentally that temperature plays a significant role in seasonal morphological changes of *K. cochlearis* (longer spines in winter, shorter ones in summer).

Thus temperature can be the factor which decides whether the *tecta* form will appear or not; this form does not occur at low temperatures. At higher temperatures (summer stagnation period) it appears if there are favourable food conditions — in accordance with the hypothesis concerning the relationship between the length of the spines and the filtering rate. The hypothesis only explains the occurrence of the efficiently filtering form (*typica*) in mesotrophic lakes with a low food content, and the high dominance of the form with a lower filtering efficiency (*tecta*) in polytrophic lakes rich in food.

4.1.1.5. Description of the occurrence of the genus *Asplanchna*

In the lakes under study two species of the genus *Asplanchna* were found to be present. They were: *Asplanchna priodonta* and *A. girodi* Guerne.

Asplanchna priodonta is typically an eurytopic species (Radwan 1973). Its occurrence in the lakes under study is of the same nature, too. The species was not one

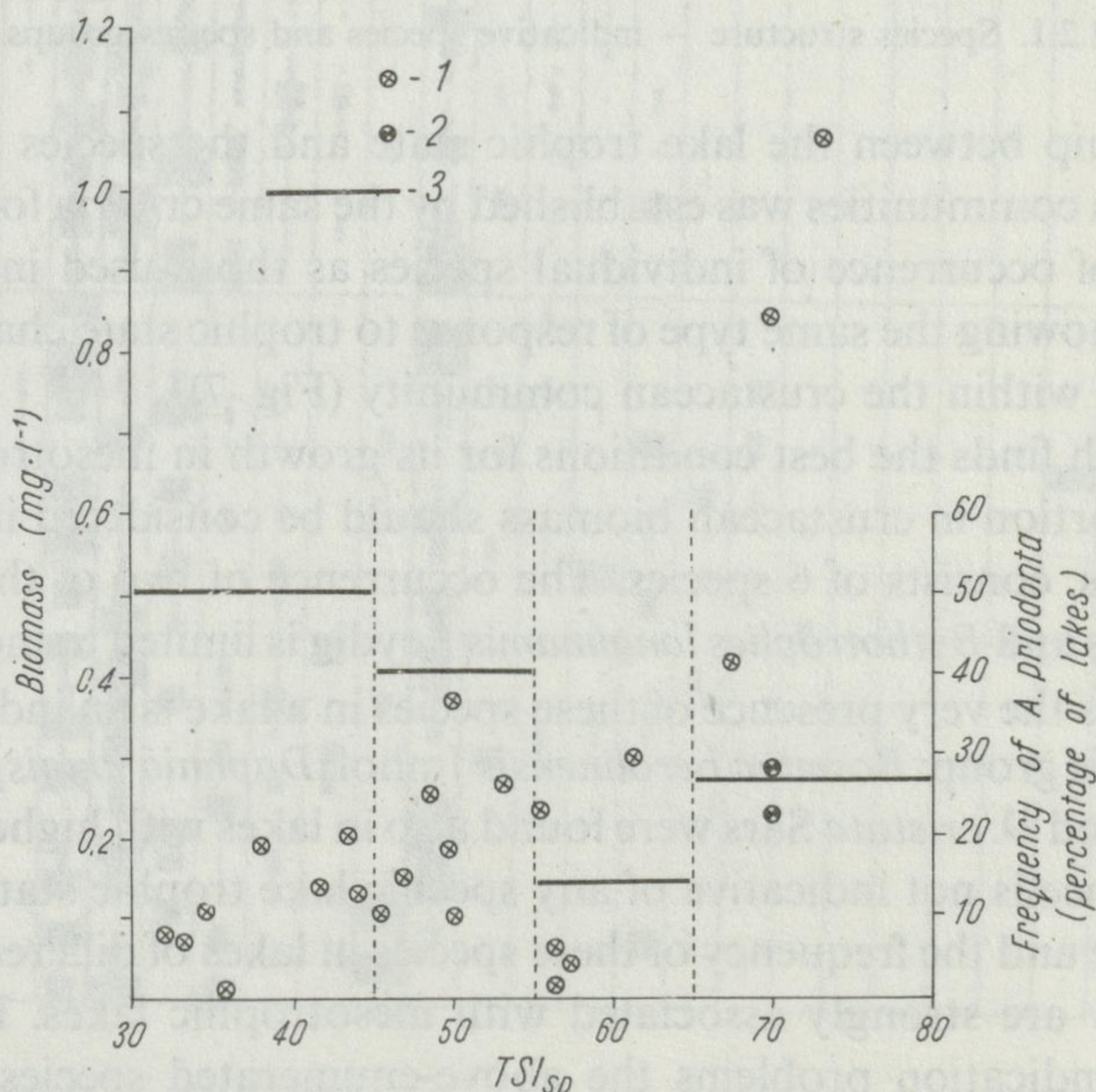


Fig. 6. Relationship between the TSI_{SD} of the study lakes and the biomass of *Asplanchna* sp. and the frequency of *Asplanchna priodonta* in these lakes

1 — biomass of *A. priodonta*, 2 — biomass of *A. girodi*, 3 — frequency

of the frequently-encountered species – it only occurred in the epilimnion of 37% of the lakes. The limited occurrence has not been found to be connected with the morphological lake type. The frequency of *A. priodonta* in the nonstratified and stratified water bodies was similar. The frequency of this species was also estimated in lakes at different trophic state stages (Fig. 6). It occurred relatively frequently in lakes regarded to be mesotrophic (50% of these lakes) and meso-eutrophic (40%), being a rare species in lakes at an advanced stage of eutrophication.

A. priodonta varies in abundance between 0.3 and 168.0 ind.·l⁻¹, and only in 4 nonstratified lakes did it exceed 10.0 ind.·l⁻¹.

The biomass of *A. priodonta* also shows relatively wide variation, although a clear tendency towards biomass growth can be seen as the trophic state rises (Fig. 6). In the lakes studied there exists therefore an inverse relationship between the frequency of occurrence of *A. priodonta* in lakes of a specific trophic state, and the biomass of the species.

The occurrence of the second species – *Asplanchna girodi* is, according to Kutikova (1977), typical of ponds. This rotifer species was found in small numbers (3–6 ind.·l⁻¹) only in two shallow and highly eutrophic lakes (TSI_{SD} = 70), i.e., in water bodies which are in respect of their morphology and trophic state similar to ponds.

4.1.2. Community structure of the crustaceans

4.1.2.1. Species structure – indicative species and species groups

The relationship between the lake trophic state and the species structure of the pelagic crustacean communities was established by the same criteria for the quantification and nature of occurrence of individual species as those used in the case of the rotifers. Species showing the same type of response to trophic state changes form three ecological groups within the crustacean community (Fig. 7).

Group I, which finds the best conditions for its growth in mesotrophic lakes, and whose high proportion in crustacean biomass should be considered indicative of low trophic state lakes, consists of 6 species. The occurrence of two of them: *Heterocope appendiculata* Sars and *Bythotrophes longimanus* Leydig is limited to mesotrophic lakes (TSI_{SD} < 45). Thus the very presence of these species in a lake is an indicator. The next three species of this group: *Bosmina berolinensis* Imhof, *Daphnia longispina hyalina* var. *galeata* (Leydig) and *D. cristata* Sars were found also in lakes with higher trophic states, hence their presence is not indicative of any specific lake trophic state. However, the dominance degree and the frequency of these species in lakes of different trophic states indicate that they are strongly associated with mesotrophic lakes. In the literature dealing with bioindication problems the above-enumerated species are commonly considered indicator species indicative of low lake trophic states (Litýńskí 1925, Bowkiewicz 1938, Pejler 1965, Patalas and Patalas 1966, Pijanowska 1978).

Included in the group of species characteristic of low trophic states was also *Daphnia cucullata* Sars. This species was found in 90% of the lakes studied, as often in the mesotrophic as in the eutrophic lakes. The presence of *D. cucullata* is not indicative, as has already been noted by P a t a l a s (1954) and G i e y s z t o r (1959). It is, however, generally believed that it is a species characteristic of eutrophic lakes, its importance in the zooplankton grows with a rising trophic state. An analysis of the zooplankton of the study lakes has shown that this relationship is also connected with the lake morphometry and stratification type. In shallow nonstratified water bodies the relative biomass of *D. cucullata* shows considerable variations, independent of the TSI_{SD} value, while in stratified lakes it diminishes if the TSI_{SD} increases. In deep, mesotrophic lakes *D. cucullata* may account for 90% of the crustacean biomass, whereas in eutrophic lakes it does not exceed 30% of the biomass (Fig. 7). On account of this, *D. cucullata* has been included in the group of organisms indicative of a low trophic state, with the reservation that such a community of organisms is characteristic primarily of deep, stratified lakes.

D. cucullata is sometimes absent or occurs in small numbers also in mesotrophic lakes, but only when *Daphnia longispina hyalina* var. *galeata* is dominant in the epilimnion of these lakes. Both species have similar food requirements, and according to the principle of competitive mutual exclusion, two related species occurring together cannot occupy the same ecological niche (e.g., H a r d i n 1960, H u t c h i n s o n 1967). In the case of the two species discussed, the diversification of their niches is realized among other things through individual body size differences, and differences in their vertical distribution (M a t v e e v 1973) — in most of the lakes under study *D. cucullata* occurred most abundantly in the epilimnion, and *D. longispina hyalina* var. *galeata* in the metalimnion and upper layers of the hypolimnion.

Ecological group II consists of species whose high percentage in the biomass of the crustacean community may be a trophic state index for lakes at a high eutrophication stage. Similarly to group I, this group also includes few species that could be considered index species, as understood traditionally, i.e., ones whose presence is limited to eutrophic water bodies. Most of them can be considered eurytopic, as they were found in lakes of all trophic types (Fig. 7). This particularly applies to both the *Mesocyclops* species, which were equally often caught in the epilimnion of the mesotrophic and eutrophic lakes. A very clear relationship was, however, found between the trophic state and the percentage of these species in the biomass of the crustacean community. With a rise in the trophic state the relative biomass of *Mesocyclops leuckarti* (Claus) and *M. (Th.) oithonoides* (Sars) increased from 1 – 10% in the mesotrophic lakes to 20 – 40% in the eutrophic lakes.

One of the frequently-encountered species (65% of lakes) is also *Chydorus sphaericus* (O. F. Müller). 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) relate the increase in the proportion of this species in the crustacean community to the process of eutrophication. In the mesotrophic lakes under study *Ch. sphaericus* was encountered sporadically and in small numbers, but with a rising trophic state the frequency and dominance of this

species increased to attain the maximum levels in the eutrophic lakes. However, as the trophic state continues to rise, the role of *Ch. sphaericus* in the zooplankton decreases — only in 3 out of 11 polytrophic lakes (TSI_{SD} above 65) was this cladoceran species found to occur.

Diaphanosoma brachyurum (Lievin) occurred yet more often (in 75% of the lakes under study). In most lakes this species was found in small numbers; larger numbers of this cladoceran were found only in highly eutrophic lakes, where it often represented over 20% of the biomass of the crustacean community.

The remaining species included in index group II occurred far less often. In lakes of different trophic states *Bosmina longirostris* (O. F. Müller) occurred in small numbers, and only in two shallow and polytrophic lakes did it form abundant populations, accounting then for over 75% of the crustacean community biomass. Such occurrence of this species agrees with the data found in the literature. According to Patals and Patals (1966), during the summer stagnation *B. longirostris* is found to occur most often and in the largest numbers in pond-type water bodies, i.e., usually highly eutrophic. Litýnski (1925), too, considers the summer growth of *B. longirostris* to be typical of small lakes. Thus although the presence of *B. longirostris* in the pelagic zone is not in itself an index, a growth of the dominance of this species should be attributed to an advancing lake eutrophication, which agrees with the views held by Brooks (1969).

The fact must also be stressed that the crustacean communities of two lakes with a very high dominance of *B. longirostris* were very poor in species, and lacked *Daphnia* sp.

Bosmina coregoni Baird is characterized by great morphological variation — Manuilova (1964) distinguishes 4 subspecies. All of them were found in the lakes under study. However, since the subspecies occur sporadically, it is not possible to unequivocally relate them to a specific trophic state of the lakes studied. Only in the case of the most frequent subspecies, *B. c. thersites*, was a tendency found towards a more frequent and abundant occurrence in high-trophic-state lakes, due to which the subspecies has been included in index group II. Pijanowska (1978) is also of the opinion that *B. c. thersites* occurs in largest numbers and attains the highest fecundity in lakes with high TSI_{SD} values.

Cyclops kolensis Lilljeborg was found in 5 lakes; they are all eutrophic lakes, and at the same time polluted with sewage, sometimes very heavily. Ivanova (1977) has reported that this species is a planktonic form of the littoral and pelagic zone of lakes “subjected to eutrophication”, which term should be understood as defining lakes undergoing rapid eutrophication under the influence of anthropopression, and not due to natural factors. In this situation the presence of *C. kolensis* in the lake pelagic zone in summer indicates its importance as an index for both the lake trophic state and pollution.

Group III includes species, the presence of which does not, for various reasons, show any relationship to a specific trophic state (Fig. 7). There are among them crustaceans whose relationship to the lake trophic state cannot be established because their occurrence is sporadic (*Acanthocyclops viridis* Jurine, *Polyphemus pediculus*

(Linné), three subspecies of *Bosmina coregoni*). Included in this group have also been high frequency species: *Bosmina crassicornis* (P. E. Müller), *Leptodora kindtii* (Focke). These cladocerans were also often present in the mesotrophic and eutrophic lakes, where their proportion in the community biomass remained at a relatively stable level, regardless of the trophic state. For the same reasons, *Mesocyclops (Th.) hyalinus* (Rehberg) and *Daphnia longispina hyalina* var. *pellucida* (Leydig) have been included in group III.

Among the most frequently-encountered species in the pelagic zone of the study lakes is *Eudiaptomus graciloides* (Lilljeborg) – in 87% of the lakes. It was common in lakes varying in the trophic state, sometimes accounting for over 40–50% of the community biomass; variation in the biomass and dominance of this species is not, however, correlated with the trophic state of a lake. *Eudiaptomus gracilis* (Sars) occurred far less often (in 21% of the lakes). Due to the nature of its occurrence, this species (great variations in the biomass, not related to the trophic state) cannot be recognized, as cannot the preceding species, as an organism useful in the lake trophic state bioindication.

Limnocalanus macrurus Sars has been included in ecological group III for a different reason. This species is commonly regarded to be an index organism, indicative of oligo- and mesotrophy. But W i e r z b i c k a (1953), and then P a t a l a s and P a t a l a s (1966) have found that the occurrence of *L. macrurus* in Poland is limited to 11 comparatively large and deep lakes near Giżycko and Mikołajki, so it cannot be used for the bioindication of lakes located outside this limited area of its occurrence.

To sum up, ecological group I which consists of: *Heterocope appendiculata*, *Bosmina berolinensis*, *Bythotrephes longimanus*, *Daphnia longispina hyalina* v. *galeata*, *D. cristata* and *D. cucullata* has been recognized as an indicator group indicative of low-trophic-state lakes (mesotrophy), and group II, consisting of: *Mesocyclops leuckarti* and *M. (Th.) oithonoides*, *Diaphanosoma brachyurum*, *Bosmina coregoni thersites*, *Chydorus sphaericus*, *Bosmina longirostris* and *Cyclops kolensis* has been recognized as a group indicative of high-trophic-state lakes (eutrophy and polytropy).

The adopted measure of the effect of the trophic state on the species structure of the crustacean community, as in the case of the rotifers, was the relationship only between both index groups, and expressed by the percentage of either of the groups in their total biomass (Fig. 8).

For the stratified lakes a high and statistically significant relationship was found between the TSI_{SD} and the dominance of index groups in their joint biomass (for group II: $r = 0.84$, $p < 0.001$).

In all the stratified mesotrophic lakes species indicative of eutrophy were found, but their proportion in the biomass of all the index organisms does not exceed 25%. Although the TSI_{SD} range of these lakes is fairly wide, the relationships between both crustacean index groups, as in the case of rotifers, are not subject to directional changes. The mesotrophic nature of these lakes is also confirmed by a specific nature of the species composition – the occurrence of most ecological group I species is virtually

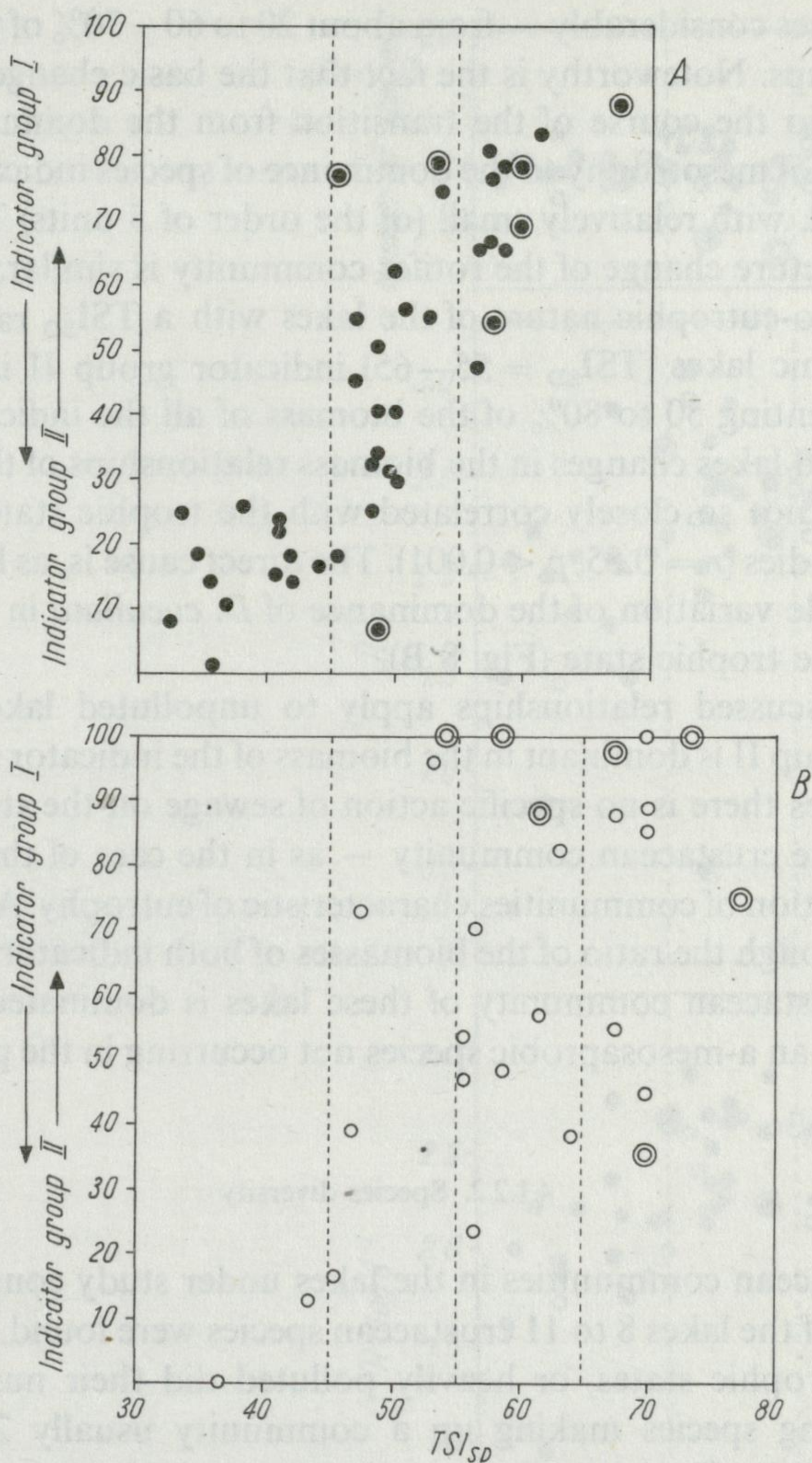


Fig. 8. Relationship between the percentage of indicator groups of crustaceans (I, II) in their total biomass and the TSI_{SD} of stratified (A) and nonstratified (B) lakes
Lake denotations as in Figure 3

limited to these lakes. At the same time, many species typical of eutrophy were found in them sporadically.

The species composition of the communities inhabiting lakes of the remaining two trophic types does not show such clear difference. In both the meso-eutrophic and eutrophic lakes group I is poor, limited to 1–2 species, while the species composition of indicator group II is in both trophic types of lake already fully established.

What makes the meso-eutrophic lakes clearly different from the stratified eutrophic lakes is the degree of dominance of index groups, and especially the nature of dominance changes as the TSI_{SD} increases. In the meso-eutrophic lakes the dominance

of group II increases considerably – from about 20 to 60–70% of the total biomass of the indicator groups. Noteworthy is the fact that the basic change of the community species structure in the course of the transition from the dominance of a group of organisms typical of mesotrophy to the dominance of species indicating a high trophic state is very rapid, with relatively small (of the order of 5 units) TSI_{SD} changes. The course of the structure change of the rotifer community is similar, which confirms an intermediate, meso-eutrophic nature of the lakes with a TSI_{SD} range of 45–55.

In the eutrophic lakes ($TSI_{SD} = 55–65$) indicator group II is already definitely dominant, representing 50 to 80% of the biomass of all the indicator species.

In nonstratified lakes changes in the biomass relationships of the indicator groups distinguished are not so closely correlated with the trophic state, as in the case of stratified water bodies ($r = 0.55, p < 0.001$). The direct cause is, as has been mentioned earlier on, the wide variation of the dominance of *D. cucullata* in nonstratified lakes, independent of the trophic state (Fig. 8 B).

The above-discussed relationships apply to unpolluted lakes. In most of the polluted lakes group II is dominant in the biomass of the indicator species (Fig. 8 A, B). Thus in these lakes there is no specific action of sewage on the structure and species composition of the crustacean community – as in the case of the rotifers, pollution leads to the formation of communities characteristic of eutrophy. An exception is Lake Kraksy Duże. Though the ratio of the biomasses of both indicator groups is typical of eutrophy, the crustacean community of these lakes is dominated by *Daphnia pulex* (99% of biomass), an a-mesosaprobic species not occurring in the pelagic zone of lakes of our latitude.

4.1.2.2. Species diversity

Pelagic crustacean communities in the lakes under study consist of relatively few species. In most of the lakes 8 to 11 crustacean species were found, and only in lakes of extremely high trophic states, or heavily polluted did their number drop to 3–6 (Fig. 9 A). Among species making up a community usually 2–4 species clearly dominate, determining the level of community biomass (Fig. 9 A), while the remaining species mainly cause species diversity of that community. This character of the structure has been described on the basis of selected species diversity indices.

The value of the diversity index, calculated according to the biomass (\bar{H}_B), has been presented in Figure 9 B. In the mesotrophic lakes, the crustacean community diversity is comparatively low, the index value does not exceed 2.2 bits (except Lake Ołów). A trophic state rise is followed by a clear increase in the species diversity, the number of species remaining unchanged, to attain the highest values (2.4–3.0 bits) in eutrophic lakes, and in those close to eutrophy (for phyto- and zooplankton communities the maximum value of this index does not probably exceed 3.5–4.5 bits – Giljarov 1973). The increase in the species diversity that accompanies the rise of the trophic state is not, however, continuous; in the lakes under study diversity increases only within the range of TSI_{SD} changes from 30 to about 60. For this lake group a statistically significant correlation has been found between the TSI_{SD} and \bar{H}_B : $r = 0.60, p < 0.001$

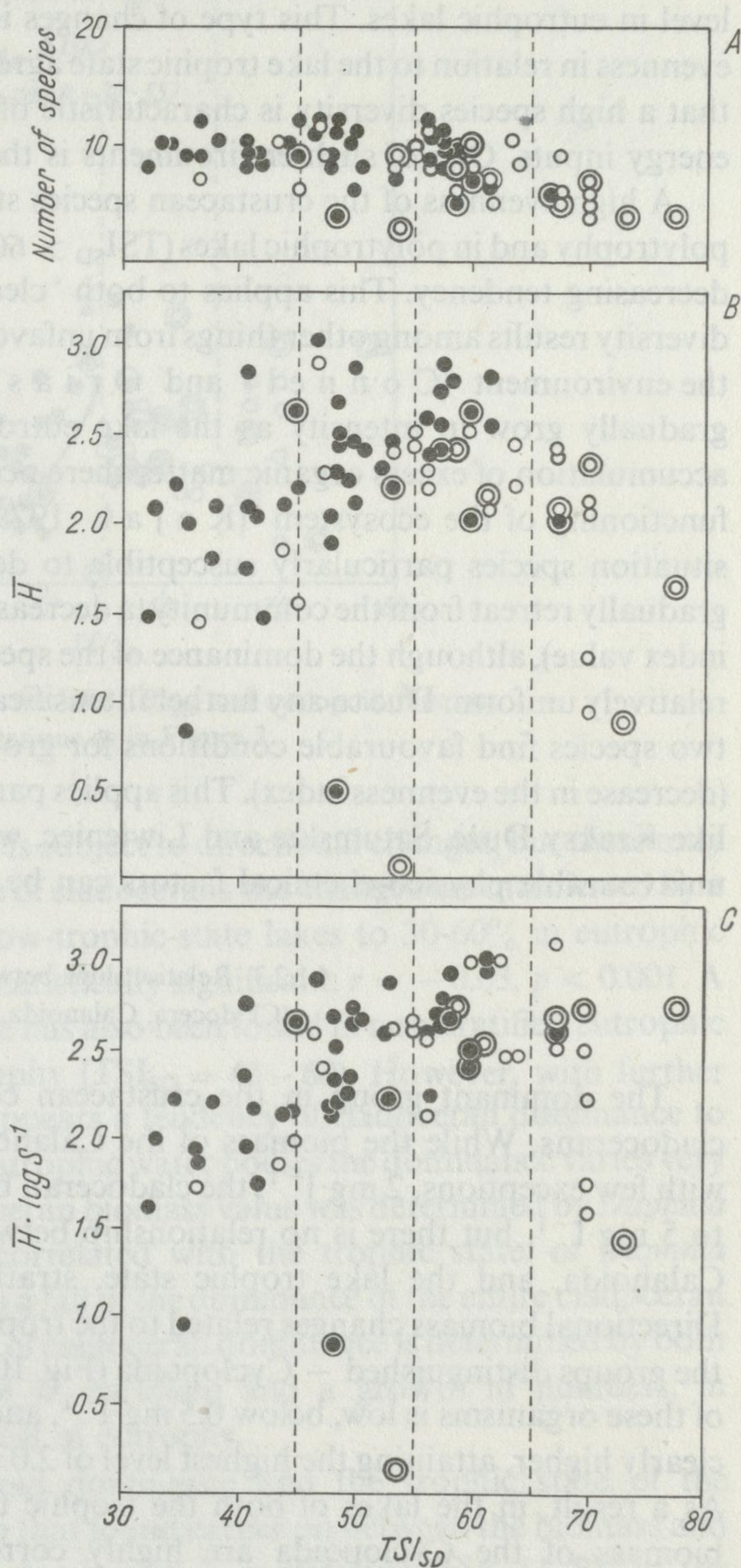


Fig. 9. Relationship between the lake TSI_{SD} and the number of species (A), general diversity index (B) and uniformity index (C) of crustacean zooplankton communities

Lake denotations as in Figure 3

(the heavily polluted lakes Sztumskie and Kraksy Duże have not been taken into account).

Species diversity increase in the course of eutrophication leads on to a more even contribution of all crustacean species to the community biomass. This phenomenon is well illustrated by the evenness "e" index (Fig. 9 C). As in the case of the diversity index, the growth of the evenness index is correlated, in a statistically significant way, with the growth of the TSI_{SD} from 30 to 65 units ($r = 0.69$, $p < 0.001$), and it attains the highest

level in eutrophic lakes. This type of changes in the crustacean species diversity and evenness in relation to the lake trophic state agrees with O d u m ' s (1975, 1977) view that a high species diversity is characteristic of environments with high nutrient and energy inputs. One of such environments is the eutrophic lakes.

A high evenness of the crustacean species structure persists in most lakes close to polytropy and in polytrophic lakes ($TSI_{SD} > 60$) in which the species diversity shows a decreasing tendency. This applies to both "clean" and polluted lakes. A low species diversity results among other things from unfavourable physico-chemical conditions in the environment (C o n n e l l and O r i a s 1964). The action of such factors may gradually grow in intensity as the lake eutrophication increases when due to the accumulation of excess organic matter there occur ever-increasing disturbances in the functioning of the ecosystem (K a j a k 1979). In the lakes under study in such a situation species particularly susceptible to deteriorating environmental conditions gradually retreat from the community (a decrease in the number of species and diversity index value), although the dominance of the species remaining in the community is still relatively uniform. Due to any further intensification of the limiting factors, only one or two species find favourable conditions for growth and begin to be clearly dominant (decrease in the evenness index). This applies particularly to very heavily polluted lakes, like Kraksy Duże, Sztumskie and Liwieniec, where an exceptionally strong action of unfavourable physico-chemical factors can be expected.

4.1.2.3. Relationships between higher taxa (Cladocera, Calanoida, Cyclopoida)

The dominant group in the crustacean communities of the study lakes is the cladocerans. While the biomass of the Calanoida and Cyclopoida does not exceed, with few exceptions, $2 \text{ mg} \cdot \text{l}^{-1}$, the cladoceran biomass in many lakes amounts to 3 up to $5 \text{ mg} \cdot \text{l}^{-1}$, but there is no relationship between the biomass of this group, and of Calanoida, and the lake trophic state, stratification type or degree of pollution. Directional biomass changes related to the trophic state have been found in the third of the groups distinguished – Cyclopoida (Fig. 10). In the mesotrophic lakes the biomass of these organisms is low, below $0.5 \text{ mg} \cdot \text{l}^{-1}$, and in the meso-eutrophic lakes it is fairly clearly higher, attaining the highest level of $2.0 \text{ mg} \cdot \text{l}^{-1}$ in lakes approaching eutrophy. As a result, in the lakes of both the trophic types mentioned above changes in the biomass of the Cyclopoida are highly correlated with TSI_{SD} changes ($r = 0.74$, $p < 0.001$). However, already in the eutrophic lakes the growth of the biomass of these organisms is impeded, and there is even a certain tendency to decrease. In those lakes, as in the polytrophic lakes, the biomass of the Cyclopoida remains at the level of $0.4 - 1.8 \text{ mg} \cdot \text{l}^{-1}$. The above-discussed relationships concern "clean" lakes. In polluted lakes cyclopoid biomass is not correlated with the TSI_{SD} .

The contribution has also been assessed of the above-mentioned taxonomic groups to the total crustacean zooplankton biomass of the unpolluted lakes (Fig. 11). It has been found that as the lake trophic state rises, the proportion of cyclopoids and

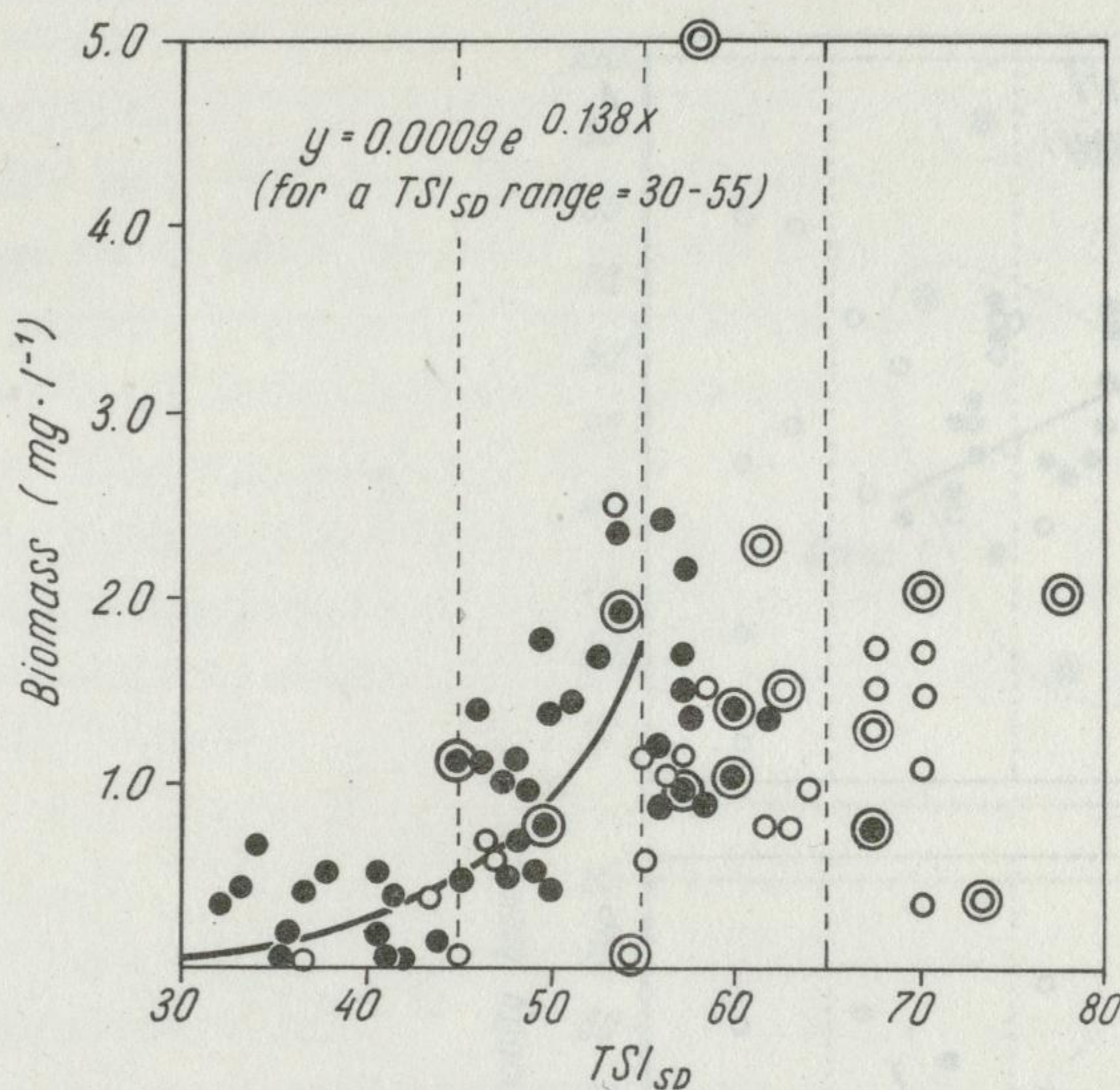


Fig. 10. Relationship between the lake TSI_{SD} and cyclopoid biomass
Lake denotations as in Figure 3

cladocerans in the community biomass is subject to directional changes, but these only take place in stratified lakes. In the case of cladocerans the changes are manifested by a dominance fall – from 60–90% in low-trophic-state lakes to 30–60% in eutrophic lakes (Fig. 11 A). This relationship is statistically significant: $r = -0.63$, $p < 0.001$. A similar degree of cladoceran dominance has also been found in nonstratified eutrophic lakes and in those approaching eutrophy ($TSI_{SD} = 45 - 60$). However, with further trophic state rise in these lakes there appears a tendency of cladoceran dominance to increase anew, although in extremely eutrophic water bodies the dominance varies very greatly. In the stratified lakes the cladoceran biomass value was determined by *Daphnia* sp. (Fig. 7). For this reason, a fall, correlated with the trophic state, of *Daphnia* dominance is practically tantamount to a fall of the dominance of the entire cladoceran group. In nonstratified lakes the nature of cladoceran dominance is determined by both great variations in the dominance of *D. cucullata* and a growth in numbers, in polytrophic lakes, of cladocerans typical of eutrophy.

The relationship between cyclopoid dominance and the trophic state of the stratified lakes is in its nature similar to that found earlier on between the biomass and the trophic state, but the growth of dominance is continuous (Fig. 11 B). In the eutrophic lakes cyclopoids already constitute almost half the pelagic zooplankton biomass. The relationship found is highly statistically significant ($r = 0.80$, $p < 0.001$). Also in the nonstratified lakes cyclopoid dominance increased at first, but in most of the eu- and polytrophic lakes it was maintained at a comparatively low level – from 20 to 35% of the community biomass.

No directional changes could be seen in the dominance of the last group – the calanoids (Fig. 11 C). Regardless of the lake trophic state and morphometry, they

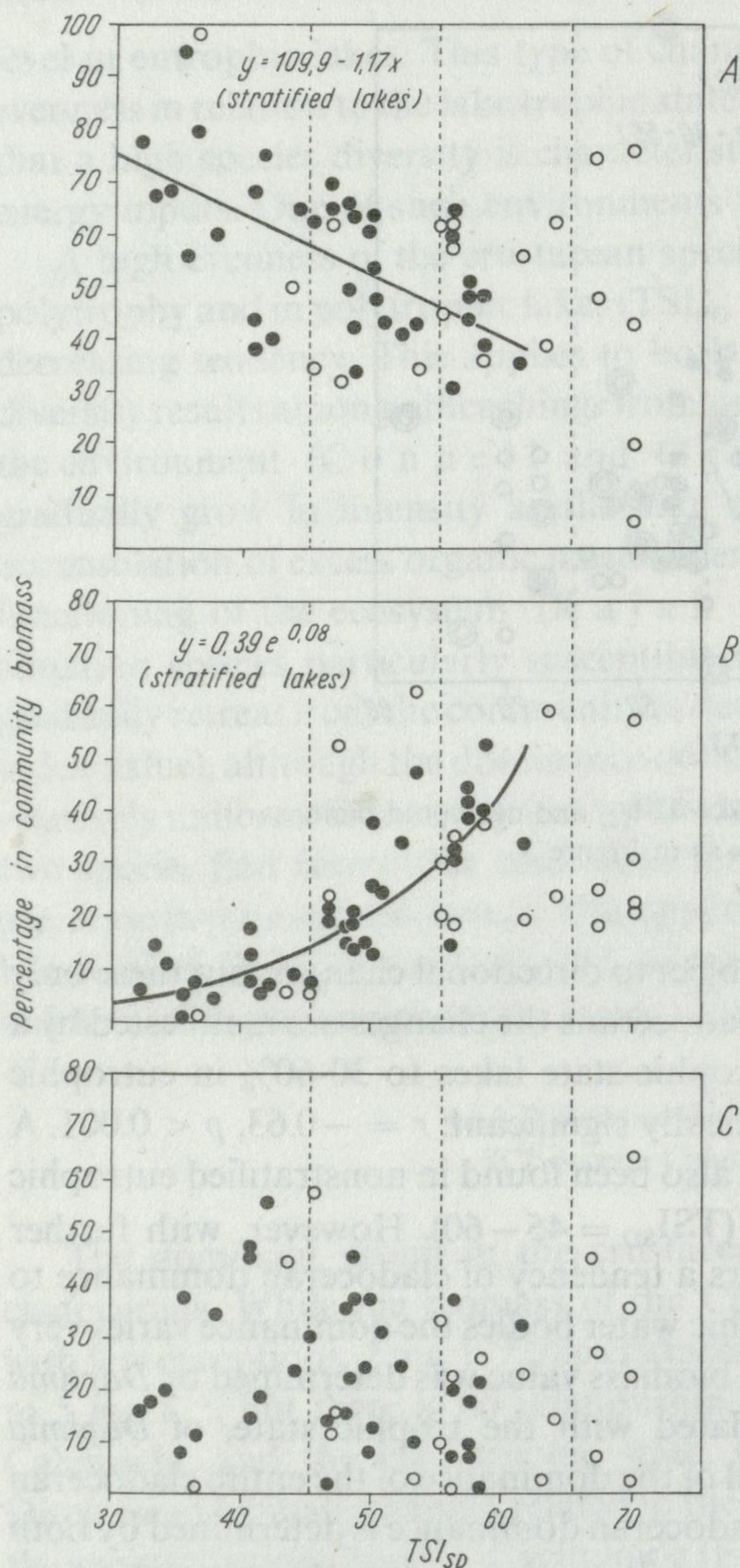


Fig. 11. Relationship between the percentage of Cladocera (A), Cyclopoida (B) and Calanoida (C) in crustacean community biomass and the TSI_{SD} of unpolluted lakes
Lake denotations as in Figure 3

represented from 1 to 60% of the crustacean biomass. For the abundance of this group depended on species of the genus *Eudiaptomus*, whose presence is in no relationship to the trophic state.

In the group of 14 polluted lakes there is no correlation between the trophic state index based on Secchi's disc visibility and the dominance of the taxonomic groups distinguished. In this lake group, however, the gradient analysis is most difficult. Trophic state indices calculated on the basis of phosphorus concentration, amount of chlorophyll, or Secchi's disc visibility do not always correctly describe the situation prevailing in lakes under the pressure of point pollution. Nevertheless, taking into account all available data describing each of the lakes, it is possible to identify three

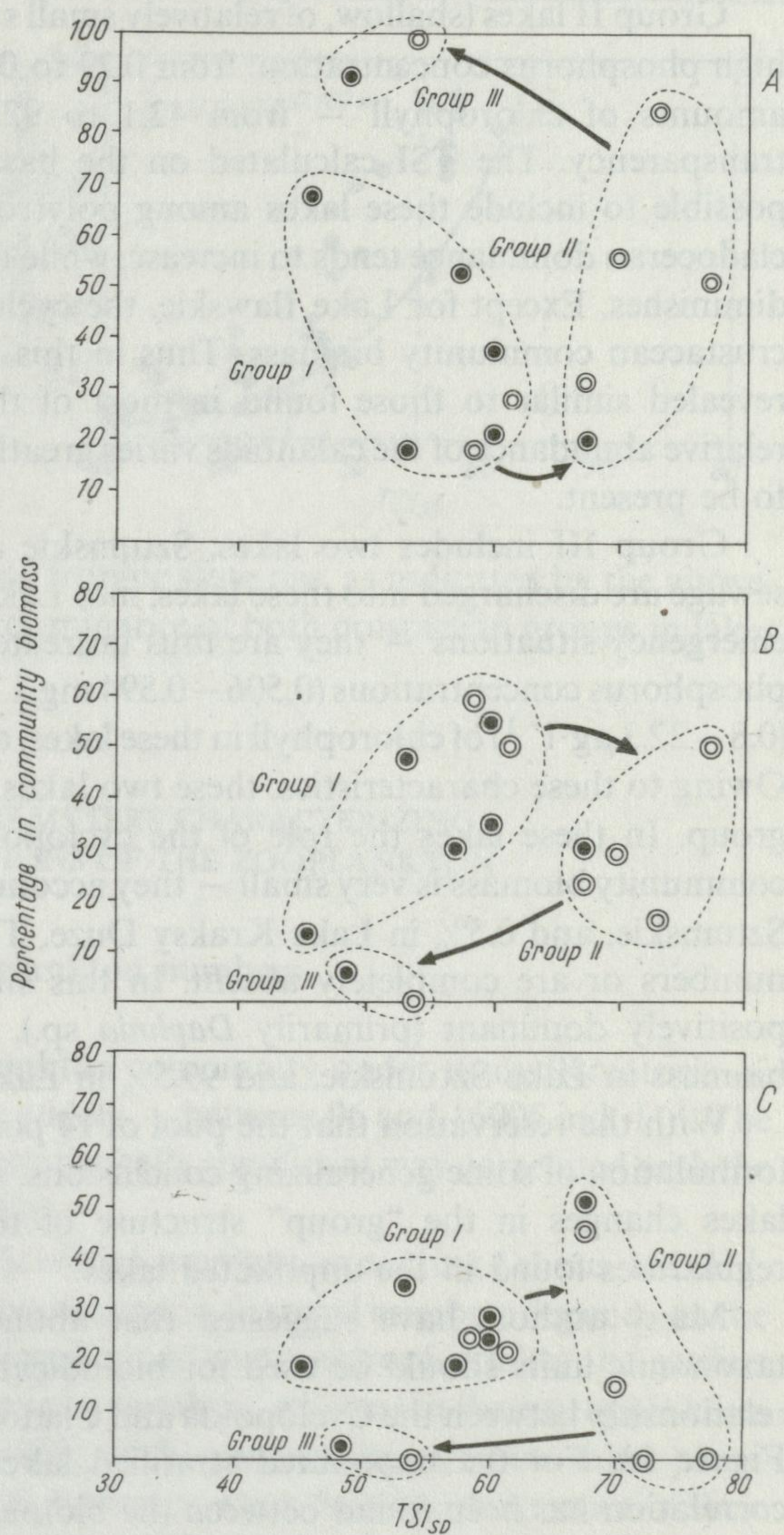


Fig. 12. Relationship between the percentage of Cladocera (A), Cyclopoida (B) and Calanoida (C) in crustacean community biomass and the TSI_{SD} of the three (I, II, III) polluted lake groups distinguished.

Lake denotations as in Figure 3

groups of polluted lakes, each of which is characterized by a different type of dominance of the cladocerans, calanoids and cyclopoids (Fig. 12).

Group I comprises 6, mostly stratified, lakes with a moderate, for polluted lakes, concentration of total phosphorus ($0.17-0.28 \text{ mg}\cdot\text{l}^{-1}$) and TSI_{SD} values typical of eutrophy (53.2–61.5). Included in this group was also Lake Niegoçin – with a relatively low phosphorus concentration ($0.10 \text{ mg}\cdot\text{l}^{-1}$) and a TSI_{SD} approaching mesotrophy. With an increasing TSI_{SD} in these lakes, the cladoceran dominance diminishes, but there occurs a clear dominance of cyclopoids typical of eutrophy, coming up to 50–60% of the crustacean biomass. The changes are thus of the same nature as those in the unpolluted eutrophic lakes.

Group II lakes (shallow, of relatively small surface area) are characterized by a very high phosphorus concentration: from 0.29 to 0.98 mg·l⁻¹, and proportionately large amounts of chlorophyll — from 42.1 to 92.4 μg·l⁻¹, and thereby a low water transparency. The TSI calculated on the basis of these three parameters makes it possible to include these lakes among polytrophic water bodies. In these lakes the cladoceran dominance tends to increase, while the dominance of the cyclopoids clearly diminishes. Except for Lake Iławskie, the cyclopoids represent only 16–29% of the crustacean community biomass. Thus in this lake group also some regularities are revealed similar to those found in most of the unpolluted polytrophic lakes. The relative abundance of the calanoids varies greatly, and in two lakes they were not found to be present.

Group III includes two lakes: Sztumskie and Kraksy Duże. Large amounts of sewage are discharged into these lakes; into Lake Sztumskie effluents are discharged in emergency situations — they are thus untreated and unpurified effluents. With high phosphorus concentrations (0.506–0.594 mg·l⁻¹), there were relatively small amounts (0.8–22.3 μg·l⁻¹) of chlorophyll in these lakes, and thereby relatively low TSI_{SD} values. Owing to these characteristics, these two lakes have been distinguished as a separate group. In these lakes the role of the cyclopoids in contributing to the crustacean community biomass is very small — they account for only 6.5% of this biomass in Lake Sztumskie, and 0.5% in Lake Kraksy Duże. The calanoids, too, occur in very small numbers or are completely absent. In this situation it is the cladocerans that are positively dominant (primarily *Daphnia* sp.), representing 91% of the community biomass in Lake Sztumskie, and 99.5% in Lake Kraksy Duże.

With the reservation that the pool of 14 polluted lakes is maybe too small for the formulation of some generalizing conclusions, it may be accepted that in the polluted lakes changes in the “group” structure of the crustacean community follow the regularities found in the unpolluted lakes.

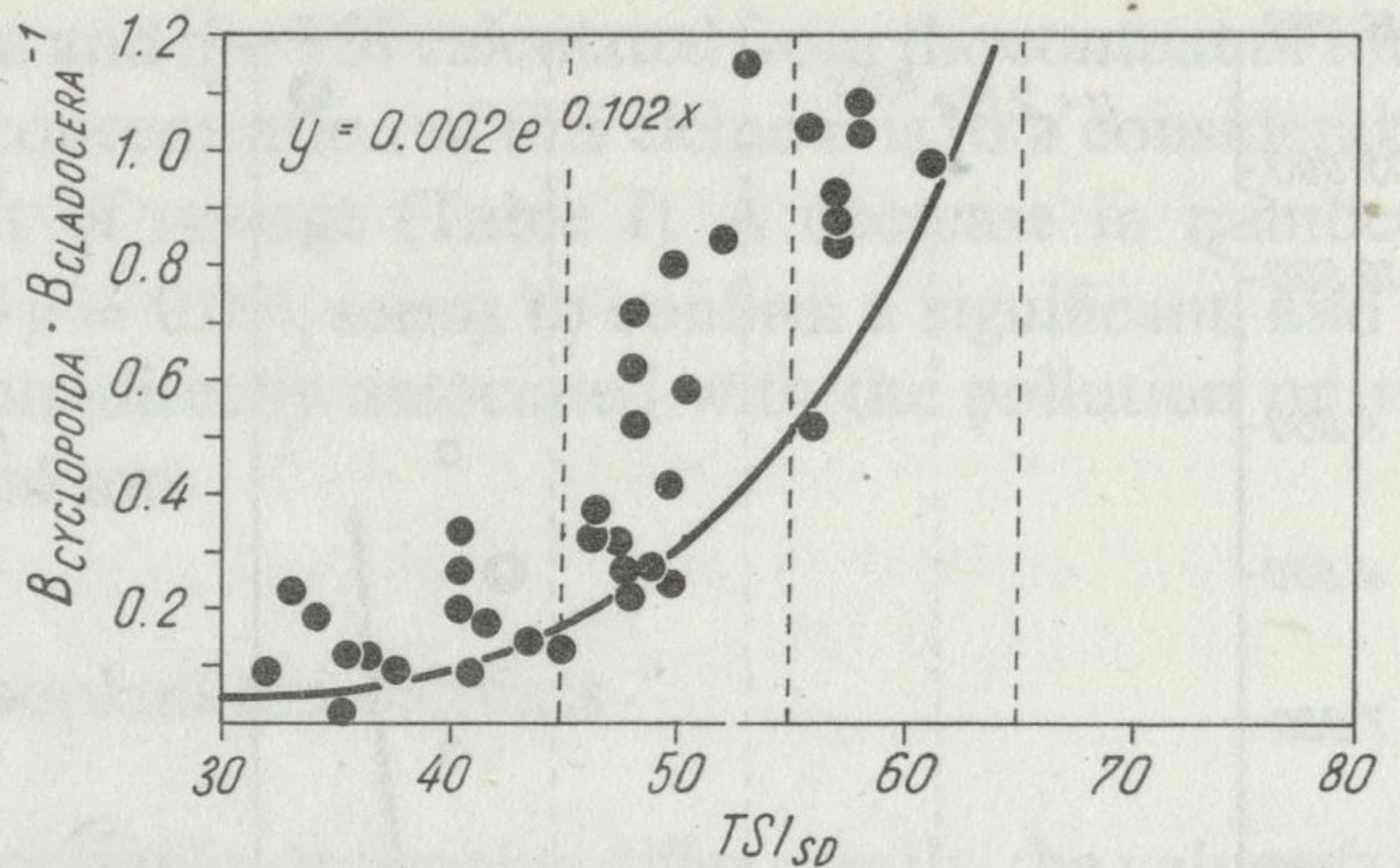
Many authors have suggested that abundance relationships between selected taxonomic units should be used for bioindication. In the present study the biomass relationship between the Cyclopoida and Cladocera ($B_{Cycl.}:B_{Clad.}$) has been evaluated — Figure 13. For the unpolluted stratified lakes a very high, statistically significant correlation has been found between the biomass ratio of these groups and the TSI_{SD} ($r = 0.82, p < 0.001$). This relationship is described by the curvilinear regression:

$$y = 0.003 e^{0.098x}$$

where: $y = B_{Cycl.}:B_{Clad.}$, $x = TSI_{SD}$. The range of variation of the index varies between about 0.1 for the mesotrophic lakes and over 1.0 for the eutrophic lakes.

No statistically significant relationship has been found between the biomass ratio discussed and the TSI_{SD} in the nonstratified and in the polluted lakes. This does not, however, indicate that these lakes lack specific regularities of changes in the biomass relationship between both crustacean groups. For over the range from mesotrophy to eutrophy (TSI_{SD} < 65) in most of the nonstratified and polluted lakes changes in the biomass ratio Cyclopoida:Cladocera follow the regularities specific to the stratified lakes. The lack of correlation between the index considered and the trophic state is the

Fig. 13. Variation of the Cyclopoida:Cladocera biomass ratio in relationship to the TSI_{SD} of unpolluted stratified lakes
Lake denotations as in Figure 3



result of its decrease with the progressing trophic state rise, as indicated by the above-discussed changes in the biomass and dominance of both crustacean groups in lakes characterized by high TSI_{SD} values.

4.2. ANALYSIS OF PARAMETERS CHARACTERIZING QUANTITATIVE RELATIONS OF THE ZOOPLANKTON

4.2.1. Zooplankton numbers

The abundance of the whole zooplankton community under study (Rotatoria + Crustacea) varies in the study lakes very widely — between 96 and 16005 ind. · l⁻¹. The changes in numbers are highly, and in a statistically significant way correlated with the increase of the TSI_{SD} ($r = 0.80$, $p < 0.001$).

The level of numbers, and particularly of high numbers, exceeding 1 thous. ind. · l⁻¹, depends primarily on the rotifers. Their percentage in the total numbers depends on the lake trophic state. In most of the mesotrophic and meso-eutrophic lakes the rotifers represent less than 50–60% of the community numbers, whereas in the eutrophic lakes a rapid growth of rotifers — up to 80–95% of the community numbers takes place. Consequently, in practically all eu- and polytrophic water bodies, irrespective of their morphometry and degree of pollution, the zooplankton community abundance is determined by the rotifers.

The numbers of rotifers (without *Asplanchna*) increased continuously over the whole trophic state gradient studied (Fig. 14 A). A high statistically significant relationship has been found between the abundance of rotifers and the TSI_{SD} ($r = 0.79$, $p < 0.001$), and over the range of TSI_{SD} variation the increase in numbers was exponential: $y = 2.19 e^{0.11x}$, where: y — rotifer numbers (ind. · l⁻¹), x — TSI_{SD} .

In low-trophic-state lakes ($TSI_{SD} = 32 - 55$) the number of rotifers is small, of the range 20–400 ind. · l⁻¹, and the tendency to increase with a rising trophic state is weak. An exception was 4 lakes, therein two stratified water bodies with a shallow hypolimnion (Jańkowskie, Bartąg), and one heavily polluted lake (Elckie). A clear growth in numbers is only found in eutrophic lakes, and in polytrophic lakes the level of numbers does not practically fall below 2–3 thous. ind. · l⁻¹. This does not apply to two

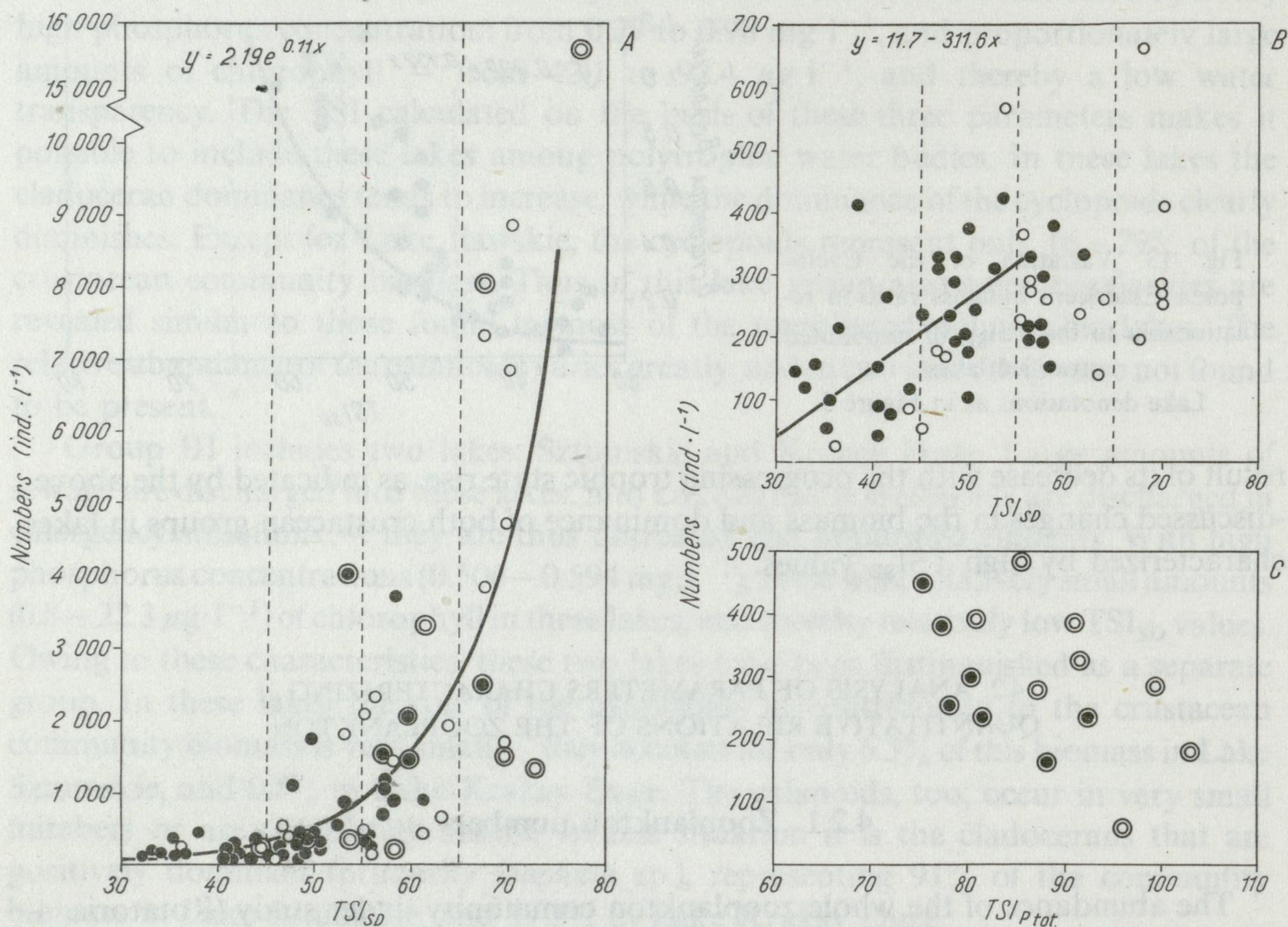


Fig. 14. Relationship between the numbers of rotifers (without *Asplanchna* sp.) and the TSI_{SD} (A), and between the numbers of crustaceans and the TSI_{SD} in unpolluted lakes (B) and the TSI_{Ptot.} in polluted lakes (C)

Lake denotations as in Figure 3

polluted lakes. Great variations in numbers, often independent of the TSI_{SD} values, in the polluted lakes seem to indicate that in many of these lakes the density of rotifers is limited by factors that are not directly related to the trophic state.

A different relationship between the abundance and the trophic state is found for the crustacean community. The abundance of rotifers increases over the whole trophic state gradient studied, whereas for the crustaceans such a regularity was only found over the TSI_{SD} variation range of 30 to 55; i.e., within the range mesotrophy – meso-eutrophy (Fig. 14 B). This relationship, although not very high ($r = 0.56$), is statistically significant ($p < 0.001$) and is of the linear function type: $y = 11.7 - 311.6x$, where: y – crustacean numbers, x – TSI_{SD} of the range 30 – 55. In the eutrophic lakes the tendency to increase is impeded, and even a certain fall of crustacean numbers is seen as the TSI_{SD} increases. In the polytrophic lakes the crustacean abundance does not tend to grow either, instead, it remains at a level specific to eutrophy.

The above-discussed regularities apply to the “clean” lakes. In the polluted lakes there is no relationship between numbers and the TSI_{SD}. As there are certain grounds to believe that the abundance of crustaceans (like that of rotifers) may be affected by factors directly connected with the pollution a study was carried out on the relationship

between the abundance of crustaceans and the TSI calculated from the content of total phosphorus (Fig. 14 C), because the concentration of this element is to a considerable extent proportionate to the amount of sewage (Table I). A decrease in numbers, correlated with the TSI_P ($r = -0.56$, $p = 0.05$), seems to confirm a significant, and at the same time limiting effect of factors directly associated with the pollution on the abundance of the crustacean zooplankton.

4.2.2. Zooplankton biomass

As the rotifer and crustacean individual body weights differ greatly, the value of the biomass of the whole pelagic zooplankton community mainly depended on the crustaceans. In all the lakes, regardless of their trophic state and morphometry, the crustaceans represented over 90% of the zooplankton biomass.

Changes in the rotifer biomass against the TSI_{SD} have been presented in Figure 15 A. The range of variation was: from $0.007 \text{ mg}\cdot\text{l}^{-1}$ in Lake Łabab to $1.291 \text{ mg}\cdot\text{l}^{-1}$ in Lake Sambród. Although the biomass tends to increase as the trophic state of lakes rises, this takes place only in the most eutrophic lakes – the polytrophic lakes. In the

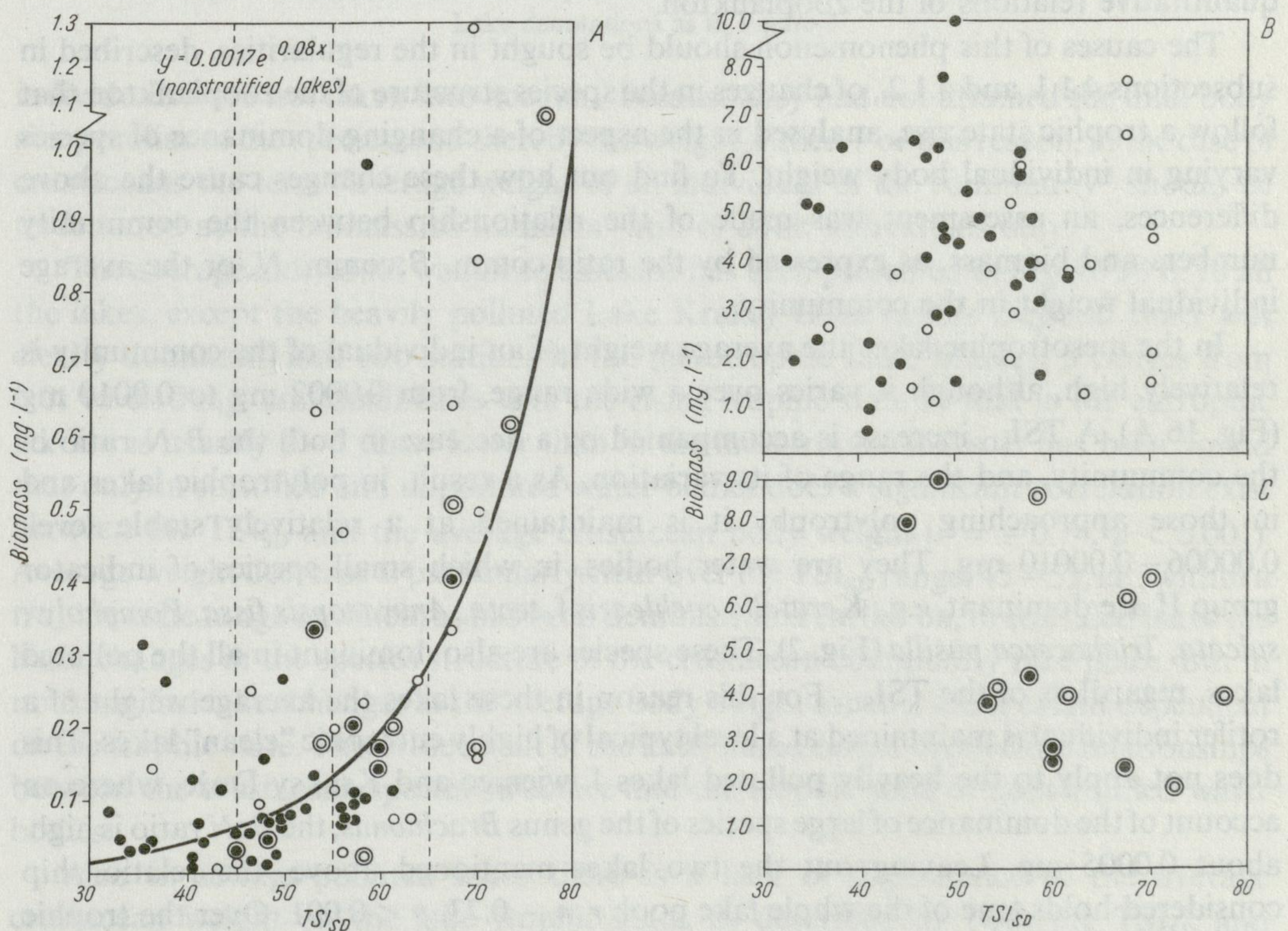


Fig. 15. Relationship between rotifer (without *Asplanchna* sp.) community biomass and the TSI_{SD} (A), and between crustacean biomass and the TSI_{SD} in unpolluted (B) and polluted (C) lakes
Lake denotations as in Figure 3

remaining lakes, irrespective of their trophic state, the biomass varies between 0.01 and 0.3 mg·l⁻¹.

A yet lower degree of the relationship biomass : trophic state of lakes was found for the crustaceans, the range of variation being: from 0.40 mg·l⁻¹ in Lake Ołów to 10.15 mg·l⁻¹ in Lake Guzianka Duża (Fig. 15 B). These changes are not correlated with the trophic state – neither in the whole unpolluted lake pool ($r = 0.10$) nor in the dimictic and polymictic lakes considered separately ($r = 0.13$, $r = 0.28$, respectively). But it was possible to find directional changes (decrease) in the crustacean biomass, following the increase of the TSI_{SD} in the polluted lakes (Fig. 15 C). On the other hand, a relationship like that found in the case of numbers is not found to occur between the crustacean biomass and the TSI_P of these lakes.

4.2.3. Relationship between community biomass and numbers – average individual body weight in communities

The results presented in the two preceding subsections indicate a different, sometimes opposite nature of the relationship between the trophic state of the study lakes and the numbers and biomass – the basic parameters characterizing the quantitative relations of the zooplankton.

The causes of this phenomenon should be sought in the regularities, described in subsections 4.1.1. and 4.1.2., of changes in the species structure of the zooplankton that follow a trophic state rise, analysed in the aspect of a changing dominance of species varying in individual body weight. To find out how these changes cause the above differences, an assessment was made of the relationship between the community numbers and biomass, as expressed by the ratio comm. B :comm. N , or the average individual weight in the community.

In the mesotrophic lakes the average weight of an individual of the community is relatively high, although it varies over a wide range, from 0.0002 mg to 0.0010 mg (Fig. 16 A). A TSI_{SD} increase is accompanied by a decrease in both the $B:N$ ratio of the community, and the range of its variation. As a result, in polytrophic lakes and in those approaching polytrophy it is maintained at a relatively stable level: 0.00006–0.00010 mg. They are water bodies, in which small species of indicator group II are dominant, e.g., *Keratella cochlearis* f. *tecta*, *Anuraeopsis fissa*, *Pompholyx sulcata*, *Trichocerca pusilla* (Fig. 2). These species are also dominant in all the polluted lakes, regardless of the TSI_{SD}. For this reason in these lakes the average weight of a rotifer individual is maintained at a level typical of highly eutrophic “clean” lakes. This does not apply to the heavily polluted lakes Liwieniec and Kraksy Duże, where on account of the dominance of large species of the genus *Brachionus*, the $B:N$ ratio is high, about 0.0005 mg. Leaving out the two lakes mentioned above, the relationship considered holds true of the whole lake pool: $r = -0.73$, $p < 0.001$. Over the trophic state gradient studied a decrease in average weight is described by the power function: $y = 1.128 x^{-2.21}$, where: y – $B:N$ for the rotifer communities, x – TSI_{SD}.

In the assessment of the average body weight of the crustacean communities young

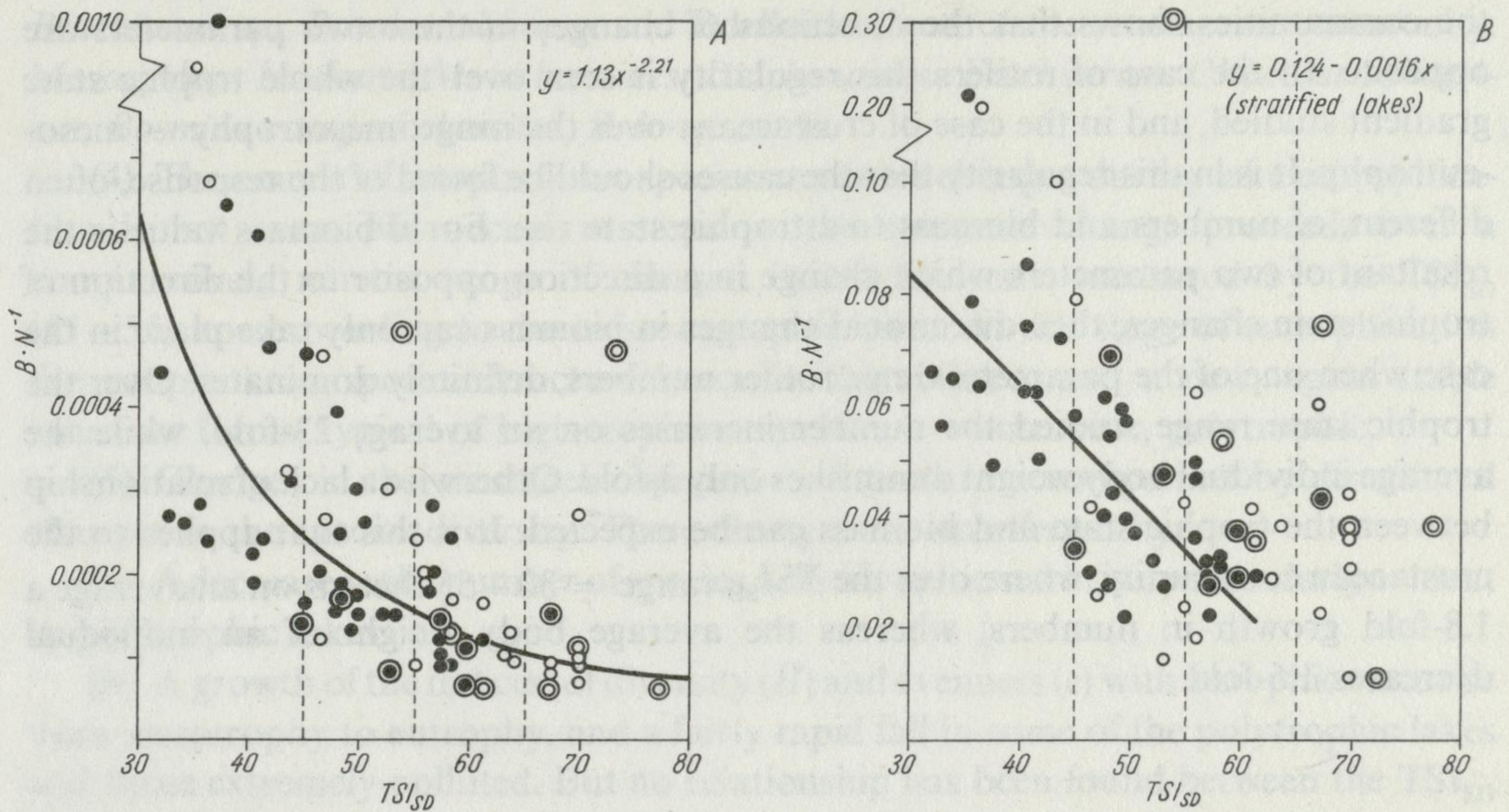


Fig. 16. Variation of the $B:N$ ratio of rotifer (without *Asplanchna* sp.) (A) and crustacean (B) communities in relation to the lake trophic state as expressed by the TSI_{SD}
Lake denotations as in Figure 3

individuals were not taken into account, because they had not attained the final body size peculiar to the species, and thereby the weight, either. For this reason, in the case of crustaceans the term “average weight of an individual of the community” should be understood as the biomass to numbers ratio of adult individuals only.

The average individual weight so assessed has been presented in Figure 16 B. In all the lakes, except the heavily polluted Lake Kraksy Duże (where *Daphnia pulex* was clearly dominant) and two stations in the mesotrophic Lake Mamry, it ranges from 0.01 to 0.10 mg, and diminishes with the rising trophic state so that in the eutrophic lakes it is usually 2–3 times lower than in the mesotrophic lakes. It has been found that only in stratified and unpolluted water bodies does a significant correlation exist between the TSI_{SD} and the average crustacean body weight ($r = -0.74$, $p < 0.001$). Average weight decrease is particularly clear over the TSI_{SD} range: 45–55, i.e., within a trophic state range in which, as has been demonstrated earlier on, in stratified lakes the basic changes in the species structure of the crustacean community take place. But in nonstratified lakes changes in the average body weight are to a lesser extent dependent on the trophic state. This is the result of the lack, stated earlier on, of close relationships between the crustacean species structure and the trophic state of nonstratified water bodies.

Also in sewage-polluted lakes there is a lack of dependence of the average crustacean weight on the lake trophic state, as described by both the TSI_{SD} and $TSI_{P\ total}$.

A comparison of the changes in rotifer and crustacean numbers, taking place during eutrophication, with changes in the average body weight of the individuals making up

the communities shows that the directions of changes in these two parameters are opposite. In the case of rotifers this regularity is seen over the whole trophic state gradient studied, and in the case of crustaceans over the range: mesotrophy – meso-eutrophy. It is in this regularity that the causes should be found of the response, often different, of numbers and biomass to a trophic state rise. For if biomass value is the resultant of two parameters which change in a direction opposite to the direction of trophic state changes, then directional changes in biomass can only take place in the case when one of the parameters, e.g., rotifer numbers, definitely dominates. Over the trophic state range studied the number increases on an average 23-fold, while the average individual body weight diminishes only 3-fold. Otherwise a lack of relationship between the trophic state and biomass can be expected. It is this that applies to the crustacean community, where over the TSI_{SD} range = 30 – 55 there is on an average a 1.8-fold growth in numbers, whereas the average body weight of an individual decreases 1.6-fold.

5. SUMMARY OF RESULTS AND CONCLUSIONS ON THE USEFULNESS OF ZOOPLANKTON STRUCTURAL CHARACTERISTICS AS BIOINDICATORS OF LAKE EUTROPHICATION

An analysis of the parameters characterizing the specific, trophic and quantitative structure of the zooplankton over a trophic state gradient of lakes of different morphometry and degree of pollution permits the following regularities to be stated:

(1) By analysing the percentages of particular species in the community biomass, in the rotifer and crustacean zooplankton three ecological groups of organisms can be distinguished, each characterized by a different type of response to lake trophic state changes:

ecological group I – decrease of dominance with a rising trophic state,
ecological group II – increase of dominance with a rising trophic state,
ecological group III – lack of relationship between the dominance of this group in the community biomass, and the trophic state.

(2) Thus the change of the species structure, taking place during lake eutrophication is determined by a relatively small group of organisms included in ecological groups I and II – in the crustacean community they represent 48%, and in the rotifer community only 28% of all the species found.

(3) Ecological group I consists of: *Chromogaster ovalis*, *Conochilus hippocrepis*, *Ascomorpha ecaudis*, *Gastropus stylifer*, *Polyarthra major* (in the rotifer community), *Heterocope appendiculata*, *Bosmina berolinensis*, *Bythotrephes longimanus*, *Daphnia longispina hyalina* v. *galeata*, *D. cristata* and *D. cucullata* (in the crustacean community), ecological group II of the rotifer community includes: *Keratella cochlearis* f. *tecta*, *K. quadrata*, *Pompholyx sulcata*, *Filinia longiseta*, *Anuraeopsis fissa*, *Trichocerca pusilla*,

Brachionus sp., *Proales micropus* and Bdelloidae, and of the crustacean community: *Mesocyclops leuckarti*, *M. oithonoides*, *Diaphanosoma brachyurum*, *Chydorus sphaericus*, *Bosmina coregoni thersites*, *B. longirostris*.

(4) The course of zooplankton species structure changes during lake eutrophication is not even, but occurs in steps — the structure change proceeds over a comparatively narrow range of changes in trophic state, measured by the TSI_{SD} (45–55), corresponding to the meso-eutrophic lakes. At this stage of eutrophication the zooplankton species structure becomes destabilized, and a new, again stable structure forms, typical of high-trophic-state lakes — eutrophic, polytrophic.

(5) Changes in the crustacean species structure are accompanied by directional changes in the species diversity. These changes are manifested by:

(a) A decrease in the number of species with a trophic state rise, particularly evident in polytrophic lakes.

(b) A growth of the indices: of diversity (\bar{H}) and evenness (e) with a trophic state rise from mesotrophy to eutrophy, and a fairly rapid fall in some of the polytrophic lakes and those extremely polluted. But no relationship has been found between the TSI_{SD} and the number of species and the indices of species diversity of the rotifers.

(6) A lake trophic state rise is accompanied by morphological changes of the individuals of the commonest rotifer species in the lakes under study — *Keratella cochlearis*. In the mesotrophic lakes the “*tecta*” form was found sporadically, and in the polytrophic lakes it represented from 70 to 100% of the *K. cochlearis* biomass. These changes can be related to the food conditions in lakes of different trophic states.

(7) The structure of the crustacean community, understood as a system of three taxonomic groups (Cladocera, Calanoida, Cyclopoida), is determined mainly by two groups: Cyclopoida and Cladocera. Their changes are manifested by an increase of biomass and dominance of the cyclopoids, and a decrease of cladoceran dominance with advancing eutrophication. Consequently, in stratified lakes the $B_{Cycl.}:B_{Clad.}$ ratio increases from 0.1–0.3 in mesotrophic lakes to 1.0 (and more) in eutrophic lakes.

(8) The proportion of rotifers in the abundance of the pelagic zooplankton of the study lakes increases from about 50% (and less) in the mesotrophic lakes to over 90% in the eutrophic lakes.

(9) Over the whole TSI_{SD} range analysed the abundance of rotifers increases along with the rising trophic state — mainly through a growth in numbers of small-bodied species. In the mesotrophic lakes the level of numbers does not exceed $500 \text{ ind.} \cdot \text{l}^{-1}$, while in the polytrophic lakes it varies greatly: $1500 - 16000 \text{ ind.} \cdot \text{l}^{-1}$. The relationship is exponential in nature.

(10) The number of crustaceans grows proportionately to the trophic state only over a TSI_{SD} range of 30–55 (from mesotrophy to meso-eutrophy), the relationship being of the linear type. In the eutrophic lakes the growth in numbers became impeded, and even showed a tendency to fall.

(11) Over the range: mesotrophy-eutrophy the rotifer biomass shows a certain growth tendency, but the growth is accompanied by very great variation in biomass in many of the lakes. A significant biomass growth (above $0.3 \text{ mg} \cdot \text{l}^{-1}$) is seen only in the polytrophic lakes.

(12) No relationship has been found between the crustacean biomass and the trophic state. This applies to both the whole lake pool studied and the morphometric lake groups distinguished.

(13) The biomass to numbers ($B:N$) ratio of the rotifer and crustacean communities, that is, the average individual weights of these communities, decreases as the trophic state rises. This is the result of an increasing dominance of small rotifer and crustacean species in the course of lake eutrophication.

(14) Thus changes in numbers that follow a trophic state rise, and changes in the average individual body weight of the communities considered are opposite.

(15) In the above regularity the direct cause should be found of differences in the response of numbers and biomass of the communities to a trophic state rise. For if biomass is the resultant of two parameters changing in different directions, then only in the case of a definite predominance of one of the parameters can biomass changes be directional.

One of the aims of the study is an evaluation of the usefulness of the pelagic zooplankton as a lake trophic state bioindicator. The above-discussed regularities, as well as a statistical analysis of the relationships between the lake trophic state and the zooplankton structure indicate differences in the usefulness of the rotifer and crustacean communities as bioindicators. Most of the rotifer community structural characteristics analysed show a high correlation with changes in the TSI_{SD} over the whole trophic state gradient, independently of the lake morphometry. But the crustacean community structural parameters are not so versatile — for there is no characteristic among them that would characterize the whole trophic state range of the lakes under study. Directional changes, significantly correlated with the trophic state, of many structure parameters of this community were only found in the stratified lakes (e.g., the percentage of ecological group II in the biomass of the indicator organisms, or the cyclopoid : cladoceran biomass ratio), whereas the course of changes of other parameters, e.g., the species diversity indices or numbers, does not run in one direction. The growth phase in the eu- and polytrophic lakes was followed by a fall of the value of a given character. This limits the usefulness of such a characteristic, as an indicator, to only a narrow range of trophic state variation ($TSI_{SD} = 30 - 55$ or $30 - 65$). Dominant among the lakes that correspond to these TSI_{SD} ranges are stratified lakes. On the other hand, in nonstratified lakes the variation of the parameters analysed is usually greater. Thus in this case also directional changes in the structure of the crustacean community apply primarily to the stratified lakes. The above-presented facts permit the statement that:

(a) Changes in the qualitative and quantitative structure of the rotifer community are practically representative of the whole lake pool under study, while changes in the crustacean community structure — only of stratified water bodies.

(b) Due to the great variation of the crustacean structure in the polytrophic lakes, and in those approaching polytrophy, or the direction of changes in the structure of this community, opposite to that seen in lower trophic state lakes, the structural

Table III. Basic and supplementary lake trophic state indices based on quantitative and qualitative zooplankton structure characteristics

Indices	Characteristics	TSI _{SD}				Applies to:
		< 45	45–55	55–65	> 65	
Basic	1. proportion of indicator community II in total rotifer indicator community biomass (%)	> 10	10–90		< 90	all study lakes
	2. proportion of the “ <i>tecta</i> ” form in the abundance of <i>Keratella cochlearis</i> (%)	0–5	5–20	20–60	< 60	all study lakes
	3. numbers of Rotatoria (ind.·l ⁻¹)		> 400	400–2000	< 2000	all unpolluted lakes
	4. proportion of indicator community II in total crustacean indicator community biomass (%)	> 25	25–60	< 60	–	stratified lakes
	5. proportion of Cyclopoida in crustacean biomass (%)	> 15	15–30	< 30	–	stratified lakes
	6. <i>BCyclopoida:BCladocera</i>	> 0.2	0.2–0.8	< 0.8	–	stratified lakes
Supplementary	7. zooplankton numbers (rotifers + crustaceans) (ind.·l ⁻¹)		–		< 2000	all study lakes
	8. <i>B:N</i> of rotifer community (mg)	–		> 0.00015		all study lakes
	9. numbers of crustaceans (ind.·l ⁻¹)	> 180–200		–		all study lakes
	10. <i>B:N</i> of crustacean community (mg)	> 0.05–0.06		–		mainly stratified lakes
	11. Cyclopoida biomass (mg·l ⁻¹)	> 0.4–0.5		–		mainly stratified lakes
	12. crustacean species diversity indices ($\bar{H}_B, \bar{H}_B:\log S$)	> 2.2–2.3		–		mainly stratified lakes

characteristics of the crustacean community as indicators of high lake trophic states are not very useful.

(c) No specific action has in principle been found of point pollution sources on the pelagic zooplankton structure; in polluted lakes the zooplankton structure change follows the general regularities found for "clean" lakes. Differences between particular lakes, usually greater than between "clean" lakes, or a certain acceleration (relative to the TSI) of the zooplankton structure change can be recognized as characteristic of polluted lakes.

Taking into account all the above regularities, a trial was undertaken for determining the usefulness of particular structure characteristics as lake trophic state bioindicators. On the basis of a statistic analysis 6 characteristics have been distinguished whose specific variation in the course of lake eutrophication makes it possible to determine value ranges characteristic of the lake trophic types distinguished (mesotrophy, meso-eutrophy, eutrophy, polytropy). They have been recognized as the basic lake trophic state indices – Table III. Three indices, based on rotifer community structure comprise the whole lake pool under study. They are:

(1) The degree of dominance of rotifer ecological groups I and II in the total rotifer biomass. A low dominance of ecological group II – below 10% indicates a mesotrophic lake type, whereas values of the range of 11–90% – a meso-eutrophic type. As the type of dominance of group II in eutrophic and polytrophic lakes is similar – above 90% of total biomass, it is impossible to determine a separate value of this index for each of these two lake trophic types. But it is possible to accept dominance differences between the species making up ecological group II as indicators. Characteristic of polytrophic lakes (TSI_{SD} above 70) is a decrease in the dominance of *Keratella cochlearis* f. *tecta* and *Pompholyx sulcata* in favour of the remaining species, primarily *Anuraeopsis fissa* and *Trichocerca pusilla*. In all the polluted lakes, irrespective of the TSI_{SD} values, the index in question attains levels typical of eutrophic and polytrophic lakes.

(2) The proportion of the "tecta" form in the *Keratella cochlearis* population biomass; in most of the mesotrophic lakes the "tecta" form was not present, and its percentage in other lakes clearly tended to increase with a rising trophic state. On the basis of a statistical analysis the index values, characteristic of the lake trophic types distinguished, have been determined. They are as follows – mesotrophy: below 5% of *Keratella cochlearis* biomass, meso-eutrophy: 5–20%, eutrophy: 21–60%, polytropy: above 60%.

(3) Rotifer numbers. A slight, relative to the mesotrophic lakes, growth in numbers of the rotifers in meso-eutrophic lakes does not make it possible to determine separate index values of abundance for these lake trophic types. It has, therefore, been assumed that an abundance level below 400 ind.·l⁻¹ is characteristic of both mesotrophic and meso-eutrophic lakes, abundance levels of the range of 400–2000 ind.·l⁻¹ – for eutrophic lakes, and higher ones indicate polytropy.

The remaining basic indices based on structural characteristics of the crustacean community are applicable only to the stratified lakes:

(4) Dominance degree of crustacean ecological groups I and II in total crustacean biomass. In the mesotrophic lakes the proportion of ecological group II does not exceed 25% of the biomass of the indicator species. The dominance of group II, varying between 25 and 60%, indicates a meso-eutrophic, and above 60% — a eutrophic lake type.

(5) The contribution of cyclopoids to the crustacean biomass. Mesotrophic lakes are characterized by a low, below 15%, proportion of cyclopoids in the crustacean biomass. Values of this index ranging from 15 to 30% have been accepted as characteristic of the meso-eutrophic lakes, and ones above 30% of the crustacean biomass — as characteristic of eutrophic water bodies.

(6) The $B_{Cyclop.} : B_{Cladoc.}$ ratio. Values below 0.2 have been accepted as the upper limit of this index mesotrophic lakes. A value of the biomass ratio varying between 0.2 and 0.8 indicates a meso-eutrophic lake type, whereas higher values indicate eutrophy.

The remaining elements of the pelagic zooplankton structure are not so fully characteristic and useful as indicators. However, they include characteristics which can, to a limited extent, serve as indicators of certain eutrophication stages. These can be termed the “auxiliary” indices. The following have been included among them:

(7) Zooplankton abundance. Above 2000 ind. · l⁻¹ (Rotatoria + Crustacea) it is typical of polytrophic lakes.

(8) The $B : N$ ratio of the rotifer community. Low values of the average individual body weight of a rotifer, below 0.00015 mg, indicate a high lake eutrophication — polytropy and advanced stages of eutrophy.

(9) Crustacean abundance. Below 150–180 ind. · l⁻¹ it is characteristic of mesotrophic lakes.

(10) The $B : N$ ratio of the crustacean community. In mesotrophic lakes and in ones approaching mesotrophy it is greater than 0.05–0.06 mg.

(11) Cyclopoid biomass. Its level below 0.4–0.5 mg · l⁻¹ indicates mesotrophy.

(12) Crustacean species diversity indices. In the case of unpolluted stratified lakes the values of the indices of diversity (\bar{H}_B) and evenness (e_B) below 2.2–2.3 characterize a low trophic state (mesotrophy).

Though the lakes analysed differ from each other in morphometry, mictic state and trophic state, no basic differences have been found between them as regards the species composition of the zooplankton communities in their pelagic zone. The number of species occurring over a narrow range of TSI variation (indicator species sensu stricto) was small. However, the short list of indicator species, with their numbers often being small and limiting their catchability, as well as the alternate nature of these indicators (present or absent), significantly restrict their usefulness as bioindicators. Supported by literature data, these facts indicate that the separation of high-value biological indicators should be based on the principle of broadly understood indicator communities, and not on species considered separately. It has been found that of high bioindicative values are first of all group parameters of the zooplankton structure (Table III). Their value as indicators is the result of a variable percentage of these groups in the community biomass, or a variable relationship between the biomasses of

the groups distinguished, that is to say, is based on the relative biomass of these groups. But considerably limited is the usefulness as indicators of strictly quantifiable structural characteristics, based on absolute numbers or biomass of a community. Due to variable, and often opposite changes in numbers of the particular species following a trophic state rise, and related changes in the average body weight of the individuals making up the plankton communities, the values of the quantifiable structure parameters vary considerably. For this reason, in the case of a gradient lake analysis based on studies of the "monitoring" type the zooplankton numbers, and even more zooplankton biomass, are of no indicative value of trophic state, or their usefulness as indicators is limited to the extreme lake trophic types.

The main object of analysis in the present paper is the community structure. It seems, however, that many species population structure elements such as morphological changes or individual size, may also be of great importance as lake trophic state indicators.

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6. SUMMARY

The study covered 67 lakes of different trophic states, water stability types and intensity of pollution (Fig. 1, Tables I, II). An analysis of the parameters characterizing the zooplankton abundance and structure in lakes lined up in a gradient in ascending order of rising trophic state has shown that:

(1) During the summer stagnation 3 ecological groups of species can be distinguished in the rotifer and crustacean communities. The groups are characterized by different types of response to a lake trophic state rise. A trophic state rise is followed by a decrease of the dominance of group I in the community biomass, and an increase of that of group II (Figs. 2, 7). This makes it possible to accept these groups as low- and high-trophic-state indicator communities. Ecological group III includes eurytopic species.

(2) The course of changes in the species structure during lake eutrophication is not even, but step-like in nature (Figs. 3, 8) – the change of structure occurs over a narrow range of TSI_{SD} variation (45–55).

(3) Changes in the crustacean species structure are accompanied by directional changes in the species diversity of the community (Fig. 9). But no correlation has been found between the TSI_{SD} and the species diversity of the rotifers (Fig. 4).

(4) A trophic state rise is accompanied by an increase in the proportion of the "tecta" form in the population of *Keratella cochlearis* – by from 0.5% in the mesotrophic lakes to over 70% in the polytrophic lakes.

(5) The growth of the rotifer numbers and biomass is exponential throughout the TSI_{SD} range analysed (Figs. 14, 15). Crustacean growth in number is proportionate to the trophic state only over a TSI_{SD} range of 30–55, this relationship being of the linear regression type (Fig. 14). No relationship has been found between the trophic type and the biomass of the crustaceans (Fig. 15).

(6) As a result of an increasing dominance of small species, the individual weight of rotifers and crustaceans decreases ($B:N$) as the trophic state rises (Fig. 16).

(7) Changes in numbers and average individual weight of the rotifer and crustacean communities following a trophic state rise are thus opposite. This regularity is the direct cause of differences in the response of the zooplankton numbers and biomass to a trophic state rise.

A statistical analysis has been carried out of the relationship between the lake trophic state and the zooplankton structure parameters studied in an attempt to determine the usefulness of these parameters as lake trophic state bioindicators. A high indicative value has been found first of all for group structure parameters based on the relative biomass of these groups. There is little possibility of using, for this purpose, indices based on absolute numbers, or biomass of communities. The rotifer community has been found to be more useful in bioindication, for rotifer structure changes are practically representative of the whole lake pool under study, whereas structure changes in the crustacean community — only of stratified lakes. Taking into account the above-discussed regularities, 6 zooplankton structure characteristics have been distinguished which change in the course of lake eutrophication in a specific way and make it possible to determine value ranges characteristic of the lake trophic types considered (Table III).

7. POLISH SUMMARY

Badaniami objęto 67 jezior o różnej trofii, typie statyczności wód i natężeniu oddziaływania zanieczyszczeń (rys. 1, tab. I, II). Analizując parametry charakteryzujące obfitość i strukturę zooplanktonu w jeziorach uszeregowanych w gradiencie wzrastającej trofii stwierdzono, że:

1. W okresie stagnacji letniej w zespołach *Rotatoria* i *Crustacea* wyróżnić można 3 ekologiczne grupy gatunków, charakteryzujące się odmiennym typem reakcji na wzrost trofii jezior. Dominacja I grupy w biomase zespołu zmniejsza się wraz ze wzrostem trofii, gdy grupy II wzrasta (rys. 2, 7). Pozwala to na uznanie tych grup za zespoły wskaźnikowe niskiej i wysokiej trofii. Natomiast III grupę ekologiczną tworzą gatunki eurytopowe.

2. Zmiany struktury gatunkowej w procesie eutrofizacji nie przebiegają równomiernie, lecz mają charakter zmiany skokowej (rys. 3, 8) — przebudowa struktury odbywa się w stosunkowo wąskim zakresie zmian TSI_{SD} (45–55).

3. Przebudowie struktury gatunkowej *Crustacea* towarzyszą kierunkowe zmiany zróżnicowania gatunkowego zespołu (rys. 9). Nie stwierdzono natomiast korelacji między TSI_{SD} a zróżnicowaniem gatunkowym *Rotatoria* (rys. 4).

4. Wraz ze wzrostem trofii rośnie udział formy „*tecta*” w populacji *Keratella cochlearis* — od 0–5% w jeziorach mezotroficznych do ponad 70% w jeziorach politroficznych.

5. Liczebność i biomasa *Rotatoria* wzrastają w sposób wykładniczy w całym analizowanym zakresie TSI_{SD} (rys. 14, 15). Liczebność *Crustacea* wzrasta proporcjonalnie do trofii jedynie w zakresie $TSI_{SD} = 30–55$, a zależność ta ma charakter regresji liniowej (rys. 14). Natomiast nie stwierdzono zależności między trofią jezior a biomasa *Crustacea* (rys. 15).

6. W wyniku wzrostu dominacji gatunków drobnych, średni ciężar osobników zespołów *Rotatoria* i *Crustacea* ($B:N$) zmniejsza się wraz ze wzrostem trofii (rys. 16).

7. Towarzyszące wzrostowi trofii zmiany liczebności i średniego ciężaru ciała osobników zespołów *Rotatoria* i *Crustacea* mają zatem przeciwny charakter. Prawidłowość ta jest bezpośrednią przyczyną zróżnicowanej reakcji liczebności i biomasy zooplanktonu na wzrost trofii.

Opierając się na statystycznej analizie zależności między trofią jezior a badanymi parametrami struktury zooplanktonu podjęto próbę określenia przydatności tych parametrów dla bioindykacji stanu trofii jezior. Stwierdzono, że dużą przydatnością wskaźnikową charakteryzują się przede wszystkim grupowe parametry struktury, oparte na względnej biomase tych grup. Natomiast ograniczona jest możliwość wykorzystania do tych celów wskaźników opartych na bezwzględnej liczebności, a szczególnie biomase zespołów. Ponadto stwierdzono większą przydatność zespołu *Rotatoria* dla potrzeb indykacji. Zmiany struktury *Rotatoria* są bowiem praktycznie reprezentatywne dla całej puli badanych jezior, gdy zmiany struktury zespołu *Crustacea* — jedynie dla jezior stratyfikowanych. Uwzględniając omówione prawidłowości wyróżniono 6 cech struktury zooplanktonu, których specyficzny typ zmian w trakcie eutrofizacji pozwala na określenie zakresów wartości charakterystycznych dla rozpatrywanych typów troficznych jezior (tab. III).

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