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

XII. DEPENDENCE OF CHOSEN INDICES OF STRUCTURE AND FUNCTIONING OF ECOSYSTEMS ON TROPHIC STATUS AND MICTIC TYPE OF 42 LAKES*

ABSTRACT: Polymictic lakes have a higher trophic state than dimictic ones, mainly because more nutrients are returned from the bottom sediments to the water. Biomass of phytoplankton (mainly blue-green algae) and of rotifers increase to the highest phosphorus concentrations in polymictic lakes, and reach much higher values than in dimictic ones. Regular changes of 42 indices of lake ecosystem structure and functioning versus their trophic state have been characterized. However, the scatter of values of indices is great, especially in the most hypertrophic lakes, having frequently unexpected characters for so high trophic state.

KEY WORDS: Lakes, trophic state, mixis, structure and functioning of ecosystems.

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1. INTRODUCTION

The paper attempts to compile the results of complex studies on 42 lakes[1] representative for lakelands in north-eastern Poland (Kajak and Zdanowski 1983). The studies include the characteristics of drainage basin (Bajkiewicz-Grabowska 1983), physical and chemical characteristics of lakes (Zdanowski 1983a, 1983b, 1983c), phytoplankton (Spodniewska 1983), zooplankton and its role in phosphorus and nitrogen circulation (Ejsmont-Karabin 1983, Karabin 1983), macrobenthos (Wiśniewski and Dusoge 1983, Stańczykowska, Jurkiewicz-Karnkowska and Lewandowski 1983), and meiobenthos (Prejs and Papińska 1983). In some dimictic lakes the processes of sedimentation have been analysed (Gliwicz 1979).

The aim of the present paper is a characteristic of the structure and of the elements of functioning of lake ecosystems depending on the trophic state, mixis and pollution.

Lakes differing extremely as to their trophic state were cho-

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[1] Some of the detailed papers cover a greater (maximum 46) or smaller number of lakes.

sen - from meso- to hypertrophic ones - a similar number of dimictic and polymictic lakes.

Material from dimictic lakes was taken in 1977, whereas from polymictic lakes - in 1978. Samples from each lake were taken twice - during spring circulation (April-May) and at the height of summer stagnation (July-August).

All lakes examined are in the same geographical region of a similar landscape differentiation and character of soils. Individual differences are described by Bajkiewicz-Grabowska (1983). The lakes vary of course in the size of their drainage basins, character of vegetational cover in that area, the absence or presence and also in the size of point sewage sources (Kajak and Zdanowski 1983).

The list of lakes examined in the order of their increasing trophic state (on the basis of total phosphorus concentration in summer in the epilimnion) and chosen information on these lakes are given in the paper by Kajak and Zdanowski (1983).

Lakes within the dimictic and polymictic type have been divided into 3 groups, according to total phosphorus concentration in summer as a measure of trophic state (Table I); in dividing lakes into groups on one hand, the course of dependences of various parameters on phosphorus concentration (in material examined and in literature), on the other hand the "gaps" in phosphorus concentration within its range for all lakes examined have been taken into account. Thus following groups were distinguished: up to about 50 $\mu g\ P \cdot l^{-1}$, about 50-100 and more than 100 $\mu g\ P \cdot l^{-1}$ (there were no lakes with phosphorus concentrations in summer between 44 and 53 $\mu g\ P \cdot l^{-1}$ and 87-134 $\mu g\ P \cdot l^{-1}$). Polymictic lakes of phosphorus concentration higher than 100 $\mu g \cdot l^{-1}$ were divided additionally into two groups (<300 and $>300\ \mu g\ P \cdot l^{-1}$). Only in two dimictic lakes the phosphorus concentration exceeded 300 $\mu g \cdot l^{-1}$ (being 464 and 506 $\mu g \cdot l^{-1}$) so it was pointless to distinguish a separate group $>300\ \mu g\ P \cdot l^{-1}$.

Group D_I, among the trophic groups distinguished, does not have an equivalent in polymictic lakes (there were no polymictic lakes with such low phosphorus concentration in summer), group D_{II} corresponds approximately to group P_I as regards the range and mean values of phosphorus concentrations, remaining groups (D_{III}, P_{II}, P_{III}) have no equivalents - the range of phosphorus concentrations in group D_{III} is broader than in group P_{II}.

Table I. Concentration of P_{tot} and N_{tot} and their quantitative relations in spring and summer in trophic groups of lakes (D_I, D_{II}, D_{III} and P_I, P_{II}, P_{III}) within two mictic types[1] (number of lakes in brackets)

Parameters	Trophic groups within the mictic types of lakes					
	dimictic lakes			polymictic lakes		
	D_I (10)	D_{II} (6)	D_{III} (7)	P_I (6)	P_{II} (8)	P_{III} (5)
P_{tot} in summer $\mu g \cdot l^{-1}$	36.3 20-44	70.2 59-87	284.0 137-506	78.8 53-92	169.5 134-285	508.4 321-940
P_{tot} spring $\mu g \cdot l^{-1}$	37.5 20-62	82.0 39-131	437.7 58-899	48.7 27-66	116.1 58-212	312.8 74-823
$\frac{P_{tot} \text{ in summer}}{P_{tot} \text{ in spring}}$	1.1 0.6-1.9	1.1 0.7-1.7	1.0 0.5-2.4	1.7 1.2-2.7	1.7 0.7-2.8	2.4 1.1-4.8
N_{tot} in summer mg l^{-1}	1.3 1.0-1.7	1.4 1.0-2.0	2.0 1.4-2.7	1.4 0.6-1.7	2.0 1.1-3.3	2.9 1.8-3.8
N_{tot} in spring mg l^{-1}	1.1 0.6-2.1	1.9 0.8-3.9	1.8 1.1-2.7	1.8 1.0-3.1	1.7 0.7-2.8	2.0 1.8-2.5
$\frac{N_{tot} \text{ in summer}}{N_{tot} \text{ in spring}}$	1.3 0.7-2.1	0.9 0.4-1.6	1.2 1.0-1.6	0.9 0.4-1.2	1.2 0.6-2.0	1.4 1.0-2.1
$\frac{N_{tot} \text{ in summer}}{P_{tot} \text{ in summer}}$	37.9 22-62	21.7 16-33	8.0 5-11	17.2 12-22	12.1 7-23	6.0 3-8
$\frac{N_{tot} \text{ in spring}}{P_{tot} \text{ in spring}}$	32.9 14-71	25.0 8-36	7.7 3-12	39.0 20-64	18.9 8-35	11.6 3-25

[1] Here and in other tables the values of indices being ratios of some values are the means of quotients $\left(\frac{a_1}{b_1} + \ldots \frac{a_n}{b_n}\right)$: n, thus allowing to give the range of index fluctuations, and not the quotient of mean values - $\frac{a_1 + \ldots a_n}{b_1 + \ldots b_n}$.

Together with the increase in concentrations of phosphorus and nitrogen in the epilimnion the values of other factors also increase, namely: conductivity, Ca, Na, K, HCO_3, oxidability (Zdanowski 1983a).

External loads of phosphorus reaching the lakes are discussed in the paper by Kajak and Zdanowski (1983). Here, dependences on mixis and trophic state, apart from the sources and causes of the latter, are the main object. A detailed environmental characteristic of these lakes and the discussion of current problems concerning eutrophication are given by Zdanowski (1982, 1983a).

2. DEPENDENCE OF TROPHIC STATE ON THE MICTIC TYPE OF LAKES

2.1. Total phosphorus and total nitrogen in surface water

Concentration of total phosphorus in the epilimnion in spring and in summer shows a strong positive correlation in both mictic types of lakes (Fig. 1). But the ratio of total phosphorus concentration in the epilimnion during summer stagnation to that during spring circulation in dimictic lakes is usually lower than in polymictic lakes (having a decreasing tendency with the increasing trophic state in dimictic lakes, whereas in case of polymictic lakes there was an increasing tendency) (Table I). This re-

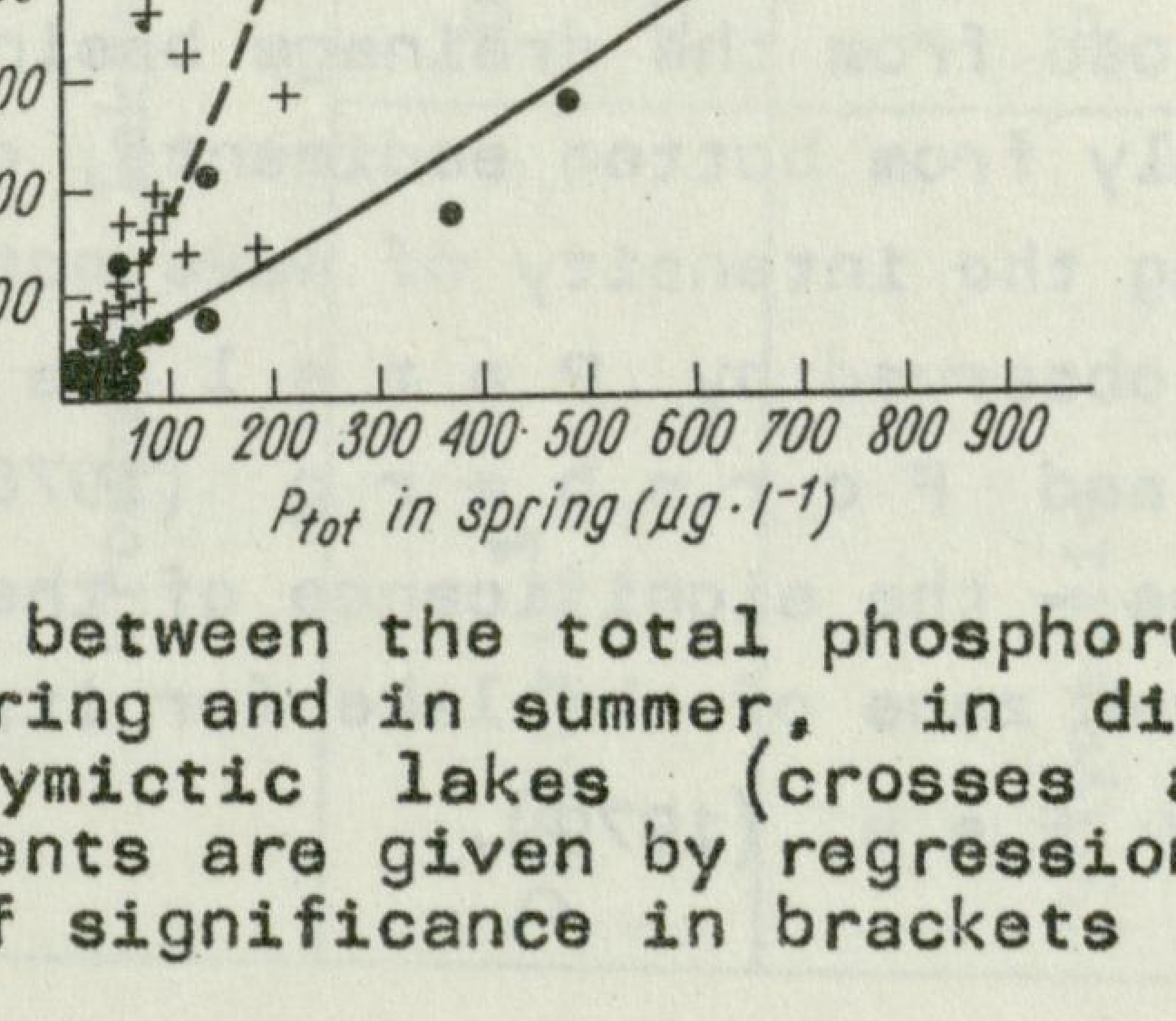

Fig. 1. Relationship between the total phosphorus concentration in the epilimnion in spring and in summer, in dimictic (dots and full line) and polymictic lakes (crosses and broken line) Correlation coefficients are given by regression curves, the level of significance in brackets

gularity is more distinct when calculating this coefficient as a ratio of the sum of total phosphorus concentrations in lakes of a given trophic group in summer to the sum of spring concentrations being for consecutive groups of dimictic lakes 1.1, 0.9 and 0.7. Thus, the greater the fertility of dimictic lakes the greater part of phosphorus resources gets out of circulation in the epilimnion till summer stagnation.

Absolute values of phosphorus concentration in spring are much higher in dimictic lakes than in polymictic ones of a similar trophic state in summer (Table I, group D_{II} and P_I). This is undoubtedly due to the fact that surface waters of dimictic lakes are enriched during the spring circulation with phosphorus, which had cumulated in the hypolimnion during the winter. But this phosphorus, in its large part, gets out of the epilimnion in the period preceding summer stagnation.

The ratio of nitrogen to phosphorus concentration in the epilimnion of both mictic types of lakes decreases with the increasing trophic state in spring and in summer (Table I). The ratio of total nitrogen concentration in summer to that in winter does not depend on the trophic state of dimictic lakes, but shows an analogous dependence as in the case of phosphorus, i.e., an increase with the increasing trophic state of polymictic lakes (Table I).

2.2. Phosphorus and nitrogen in bottom sediments and the transfer of these elements to surface water

Higher concentrations of nitrogen and phosphorus, in summer than in spring, in epilimnion of polymictic lakes, are undoubtedly due to greater amount of nutrients, and especially phosphorus, provided by bottom sediments and their interstitial waters due to wave motion. Fertility, especially in these lakes, depends not only on the load from the drainage basin, but also on the internal load, mainly from bottom sediments, due to a number of factors, including the intensity of wave motion. Such dependence has been already observed by Patalas (1960), and lately by Ryding and Forsberg (1976). The other aspect of this dependence - the significance of the percentage of the bottom in the mixed zone of the lake for its trophic state - has been confirmed by Fee (1979).

Table II. The ratio of phosphorus concentration in bottom sediments in spring and in summer, in water and in bottom sediments in summer, in trophic groups of lakes
5-12 lakes in particular groups, altogether 37 lakes (acc. to data of Zdanowski 1983a, 1983b)

Groups of lakes		P_{tot} in the epilimnion in summer µg · l^{-1} a	P_{tot} in bottom sediments[2] per cent d. wt		c : b	a : c · 100
			spring b	summer c		
Dimictic[1]	$D_I + D_{II}$	46.4 20-87	0.46 0.21-1.28	0.40 0.15-1.11	0.91 0.54-1.46	1.72 0.23-4.87
	D_{III}	284.0 137-506	0.43 0.22-0.89	0.45 0.18-0.93	1.12 0.75-1.54	7.48 3.65-14.88
Polymictic	P_I	78.8 53-92	0.20 0.12-0.25	0.17 0.12-0.23	0.85 0.60-1.04	5.06 2.30-6.17
	P_{II}	169.9 134-285	0.28 0.15-0.47	0.24 0.15-0.33	0.92 0.69-1.53	7.42 4.90-10.66
	P_{III}	508.4 321-940	0.37 0.18-0.58	0.39 0.14-0.57	1.27 0.48-3.17	14.91 7.37-25.50

[1] Group D_I and D_{II} are taken together because of a small number of lakes. [2] In the surface 2 cm layer.

The ratio of phosphorus concentration in summer to that in spring (Table I) shows that the phosphorus load from bottom sediments in polymictic lakes increases with the trophic state, which is undoubtedly due to the simultaneously increasing phosphorus content in bottom sediments of these lakes (Table II). There were very few exceptions from this rule, i.e., polymictic lakes of a summer/spring phosphorus concentration in the epilimnion below 1.0. Within dimictic lakes (which essentially had the opposite regularity - lower or similar epilimnetic P_{tot} concentration in summer than in spring) the exceptions are quite numerous (Table I).

In both mictic types of lakes analysed the phosphorus content in bottom sediments in summer, and the ratio of phosphorus concentration in epilimnion to that in bottom sediments in summer, increase significantly with the increasing trophic state (Table II). Thus, phosphorus concentration in lake epilimnion increases together with increase of the trophic state at a higher rate than its concentration in bottom sediments. One must, however, remember that the majority of phosphorus resources in the lake are cumulated in bottom sediments (Kajak 1978, 1979, 1981).

The phosphorus content in bottom sediments of dimictic lakes is on the average higher than in sediments of polymictic lakes (Table II). This would point to better defence mechanisms against eutrophication - more phosphorus leaves the surface waters for bottom sediments in dimictic lakes than in polymictic ones (which is correct, assuming that sediment samples taken at maximal depth of the lake are representative for sediments in the whole lake). High phosphorus concentrations are recorded in bottom sediments of lakes of both low and very high trophic state (Table II, Zdanowski 1983b). In the former, it is probably due to effective transfer of phosphorus from the epilimnion to bottom sediments, where it remains.

In surface sediment layers of less fertile lakes of both mictic types there is slightly less phosphorus in summer than in spring (probably more goes into the water), whereas in the most fertile lakes there is more phosphorus in sediments in summer (Table II). However, this defence mechanism against excessive fertility of surface waters in summer (by means of phosphorus transfer to bottom sediments) is weak as the differences in concentrations in bottom sediments in spring and in summer are slight. This fact (that differences are small) may, however, be due to other mechanisms; for example, nothing is known about possible phosphorus movements within the bottom sediments.

The main mechanisms of the transfer of phosphorus from bottom sediments to water in both mictic types of lakes differ: in dimictic lakes phosphates are released mostly chemically under oxygen deficit, in polymictic lakes the phosphorus is released mainly by decomposition of organic matter. This is proved by the fact that between spring and summer in bottom sediments of dimictic lakes mainly the amount of mineral phosphorus, whereas in polymictic lakes - of organic phosphorus decreases (Zdanowski 1983b). In dimictic lakes the phosphorus from bottom deposits reaches the surface layers during the circulation, but a considerable part of this phosphorus sediments soon, thus getting out of circulation in epilimnion for the whole period of summer stagnation, i.e., the most important period considering the water purity. In polymictic lakes high phosphorus concentrations in surface water layers are maintained or increased by constant supply of phosphorus from bottom sediments which is especially intensive in summer. The bottom fauna is also significant in the phosphorus transfer from bottom sediments to water (Graneli 1979, R. J. Wiśniewski - unpublished data). In polymictic lakes it is usually more abundant per surface area unit (Wiśniewski and Dusoge 1983), but first of all it is more active (due to higher temperature and better oxygen conditions), on the entire bottom surface area, otherwise than in dimictic lakes.

3. THE PERCENTAGE OF VARIOUS FORMS OF PHOSPHORUS AND THE OXIDABILITY IN SURFACE WATER

The concentration and percentage of phosphate phosphorus in P_{tot} depend distinctly on the trophic state; the percentage increases with the trophic state (measured by P_{tot}) in both mictic types of lakes. Thus the percentage of the complementary component, namely organic phosphorus (sestonic and dissolved), and also the percentage of dissolved organic phosphorus in the total phosphorus concentration, decrease with the increasing trophic state. But the percentage of sestonic organic phosphorus concentration in the total phosphorus concentration increases together with the trophic state (undoubtedly due to increasing phytoplankton abun-

Table III. Percentage of various forms of phosphorus and oxidability in the epilimnion of lakes of different trophic state in summer (data acc. to Zdanowski 1982)

Mictic type of lakes	Trophic groups of lakes[1] acc. to P_{tot} $\mu g \cdot l^{-1}$	% P tot				% P org		Oxidability mg $O_2 \cdot l^{-1}$
		PO_4-P	P_{tot} org	P_{diss} org	P_{part} org	P_{diss} org	P_{part} org	
Dimictic	36 20-44	31	69	42	27	60	40	9.4 6.4-12.8
	91 59-147	29	71	20	51	29	71	11.2 9.9-16.0
	326 175-506	45	55	11	44	20	80	13.4 9.9-19.9
Polymictic	79 54-92	34	66	30	36	44	56	12.5 8.0-20.5
	169 134-285	37	63	17	46	26	74	17.5 9.9-27.8
	526 321-940	67	33	14	20	39	61	18.9 16.2-22.7

[1] The division used by Zdanowski (1982).

dance) up to relatively high concentration of P_{tot}, and decreases only at maximum P_{tot} concentrations for each mictic type. The same regularity stands for the percentage of sestonic organic phosphorus in the total organic phosphorus concentration (Table III).

The oxidability increases consequently with the increasing trophic state, but much slower (maximum value is only 3.5 times higher than the minimum) than the phosphorus concentration and many other indices (Table III).

4. DEPENDENCES OF VARIOUS ENVIRONMENTAL AND BIOCENOTIC PARAMETERS ON THE TROPHIC STATE AND MIXIS

4.1. Environmental indices and phytoplankton

The Secchi disc visibility [expressed also for the purpose of better comparison by Carlson's (1977) index of trophic state], phytoplankton biomass and chlorophyll concentration (r = = 0.867 and 0.770) show high positive correlation to the concentration of total phosphorus in the epilimnion in summer (Figs. 2, 3, Table IV). This relationship, for the above mentioned trophic state indices (especially for phytoplankton biomass and chlorophyll), is much more distinct for lower phosphorus concentrations - up to about 90, and then about 170 µg $P_{tot} \cdot l^{-1}$ (Figs. 2-4, Table IV); as the phosphorus concentration increases its effect becomes less limiting for the three above-mentioned parameters.

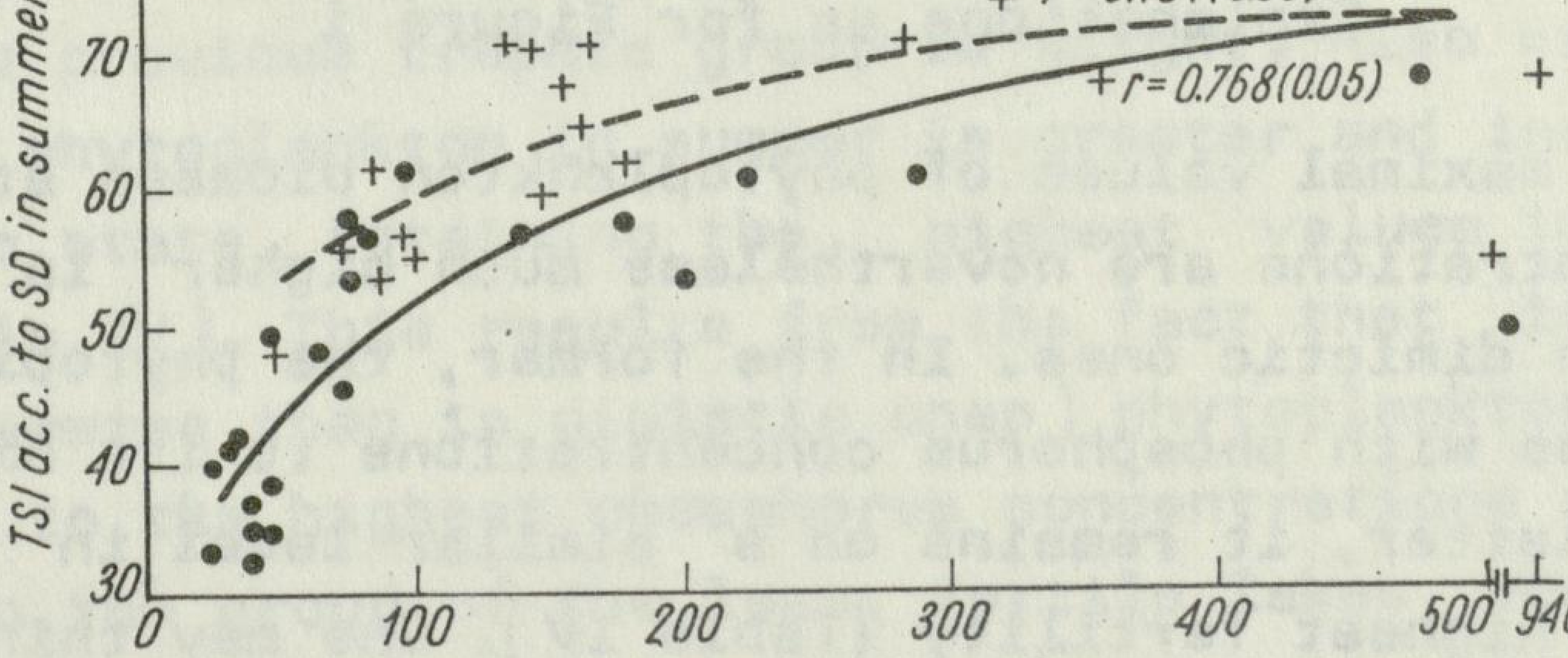

Fig. 2. Relationship between Carlson's (1977) trophic state index (TSI) based on Secchi disc visibility (SD) and total phosphorus concentration in the epilimnion in summer
Explanations as for Figure 1

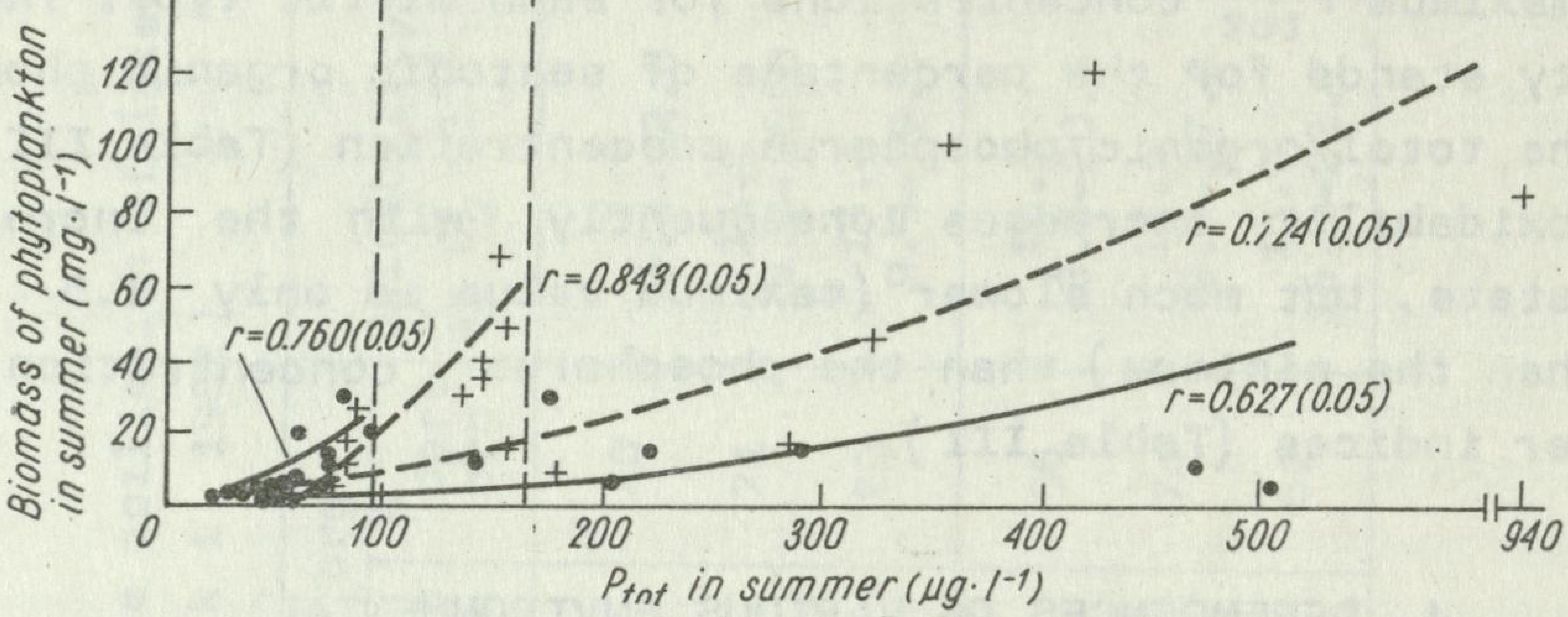

Fig. 3. Relationship between phytoplankton biomass and total phosphorus concentration in the epilimnion in summer
Apart from relationships for the entire material relationships for lower ranges of trophic state (indicated by a vertical broken lines) are also shown. Other explanations as for Figure 1

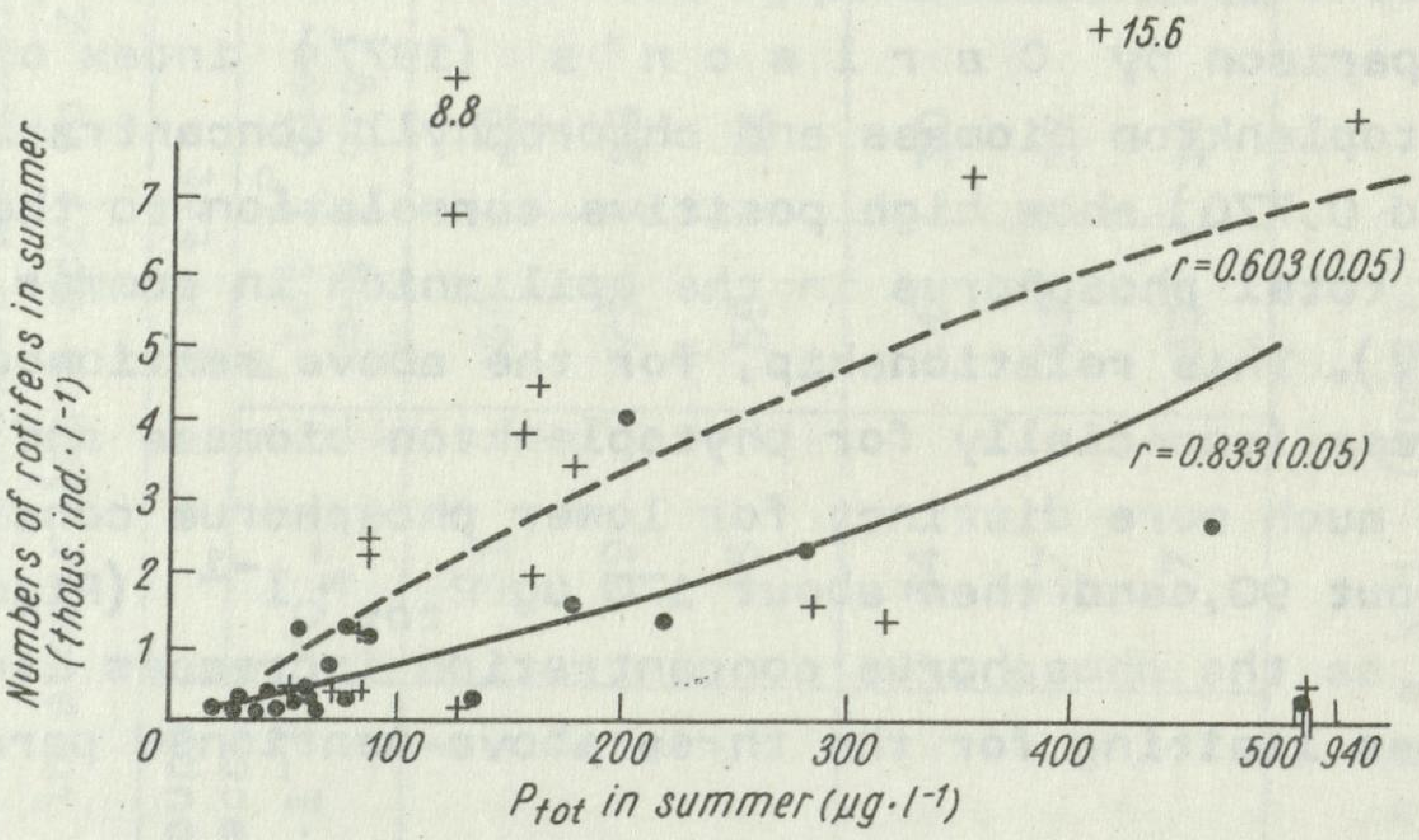

Fig. 4. Relationship between the number of rotifers and total phosphorus concentration in the epilimnion in summer
Explanations as for Figure 1

Mean and maximal values of phytoplankton biomass at high phosphorus concentrations are nevertheless much higher in polymictic lakes than in dimictic ones. In the former, the phytoplankton biomass increases with phosphorus concentrations to its highest values, in the latter, it remains on a similar level in groups of mean and the highest fertility (Table IV). One may think that besides the main nutrients, which at a high trophic state do not affect the phytoplankton biomass, there are perhaps other significant substances (microelements, vitamins, etc.) provided by bottom sediments and occurring more abundantly in polymictic lakes than in dimictic ones.

Despite a general regularity concerning the parameters discussed and their strong positive correlation, there is a considerable scatter of definite data for particular lakes at approximate values of total phosphorus. This scatter is especially great for data on phytoplankton - very low values besides very high ones at high concentrations of total phosphorus in hypertrophic lakes (Table IV).

The ratio of concentration of total nitrogen to total phosphorus in the epilimnion of both mictic types of lakes in summer and in spring decreases as the trophic state increases (r = = -0.959 and -0.819 in summer; -0.808 and -0.816 in spring). In groups having the highest trophic state its values are below 10.0 (Table I). This shows that in these lakes nitrogen, not phosphorus, may at certain periods decide (limit) the phytoplankton production, providing the light is not the limiting factor because of the rich phytoplankton.

In summer, the chlorophyll content in phytoplankton biomass shows a considerable scatter without a distinct dependence on phosphorus concentration in both mictic types of lakes (r = 0.168 and -0.005). The greatest differentiation and the highest values are in the group of lakes of the lowest trophic state (Table IV).

The ratio of phytoplankton biomass to total phosphorus concentration is treated as the ability to use (efficiency) phosphorus by algae for the production of their biomass. In summer, this ratio increases distinctly with the trophic state and decreases again at a very high trophic state, especially in dimictic lakes. In polymictic lakes, at a much higher trophic state, this index is much higher than in dimictic lakes, and its decrease in relation to the previous trophic group is slight. Also nitrogen utilization by phytoplankton in summer is greater and increases with the trophic state, attaining the highest values in polymictic lakes (Table IV). This results from the fact that in polymictic lakes (otherwise than in dimictic ones) phytoplankton biomass increases up to the highest phosphorus concentrations recorded.

Only in the group of the least fertile lakes the phosphorus utilization for phytoplankton biomass production is similar in spring and in summer. In remaining lakes this utilization is greater in summer, but the differences between the spring and the summer are smaller in polymictic lakes than in dimictic ones.

Table IV. Phytoplankton and its dependence on P_{tot} and N_{tot} concentration in trophic groups of lakes within two mictic types (trophic groups as in Table I, number of lakes in brackets)

Parameters	Trophic groups within mictic types of lakes					
	dimictic lakes			polymictic lakes		
	D_I (10)	D_{II} (6)	D_{III} (7)	P_I (6)	P_{II} (8)	P_{III} (5)
Phytoplankton biomass in summer,	2.7	17.2	13.6	14.3	33.5	71.5
$mg \cdot l^{-1}$	0.4-7.8	6.6-29.4	4.6-29.8	1.3-27.5	9.8-68.7	1.6-121.9
Secchi disc visibility in summer,	4.6	1.7	1.3	1.5	0.7	0.7
(m)	2.0-6.9	0.9-2.8	0.6-2.2	0.9-2.4	0.5-1.1	0.3-1.5
Phytoplankton biomass in spring,	2.1	1.9	5.2	4.6	20.8	13.8
$mg \cdot l^{-1}$	0.2-4.5	0.4-3.3	0.3-14.6	1.1-10.8	3.3-59.7	3.0-33.5
$\frac{\text{Phytoplankton biomass}}{P_{tot}}$ in summer	56.2	244.6	66.3	168.5	216.1	162.3
	11.2-178.2	99.9-402.3	9.1-170.2	24.5-305.5	55.7-437.6	3.2-290.2
$\frac{\text{Phytoplankton biomass}}{P_{tot}}$ in spring	69.4	33.2	13.2	103.7	166.6	55.3
	4.2-227.2	4.7-72.2	0.7-34.4	19.3-225.0	39.1-338.3	16.9-109.8
$\frac{\text{Phytoplankton biomass}}{N_{tot}}$ in summer	2.0	14.7	6.9	9.7	19.2	26.6
	0.2-8.3	10.2-29.4	1.9-14.9	2.1-16.6	6.7-40.1	0.4-39.2
Chlorophyll in summer,	6.0	18.0	51.4	17.9	65.5	115.7
$\mu g \cdot l^{-1}$	1.5-11.7	5.4-36.6	22.3-109.7	3.6-31.1	22.7-110.7	14.0-236.7
$\frac{\text{Chlorophyll}}{\text{Phytoplankton biomass}}$ ‰ in summer	5.6	1.3	4.6	1.5	2.1	3.0
	1-20	0.5-2	1-9	1-3	1-4	1-9

$\frac{\text{Chlorophyll}}{P_{tot}}$ in summer	0.16 0.1-0.3	0.25 0.1-0.4	0.20 0.04-0.3	0.22 0.1-0.3	0.33 0.1-0.5	0.28 0.03-0.7
$\frac{\text{Chlorophyll}}{N_{tot}}$ in summer	5.1 1.2-11.7	15.1 4.8-20.9	24.0 9.4-41.2	12.2 5.8-18.9	37.1 15.5-62.9	43.6 3.7-92.5
Chlorophyll in spring, $\mu g \cdot l^{-1}$	6.4 2.9-12.6	19.0 4.6-38.0	23.9 2.1-77.6	10.9 2.9-24.0	9.8 2.5-15.8	38.5 5.9-108.4
Biomass of blue-green algae in summer, $mg \cdot l^{-1}$	0.3 0.01-1.4	2.2 0.3-5.7	4.9 0.3-17.8	3.3 0.0-9.4	13.1 0.1-27.0	45.6 0.0-110.2
$\frac{\text{Biomass of blue-green algae}}{\text{Phytoplankton biomass}}$ % in summer	18.0 0.01-62	17.2 0.9-44	29.0 2.0-66	18.5 0.0-42	36.7 0.2-67	43.9 0.0-93
$\frac{\text{Biomass of blue-green algae}}{P_{tot}}$ in summer	9.2 0.1-32.6	29.2 3.8-65.3	22.8 1.2-101.5	39.6 0.0-104.4	84.6 0.7-201.5	90.3 0.0-262.4
Nannoplankton biomass in summer, $mg \cdot l^{-1}$	1.1 0.1-3.3	5.5 1.4-15.6	5.7 1.8-13.8	4.6 0.5-11.1	7.1 1.4-17.0	4.1 0.2-10.2
$\frac{\text{Nannoplankton biomass}}{\text{Phytoplankton biomass}}$ % in summer	52.3 13-90	34.3 11-78	45.1 14-93	39.8 9-86	23.9 3-48	23.8 0.2-88

In dimictic lakes the utilization of phosphorus by phytoplankton in spring definitely decreases as the trophic state increases, in polymictic lakes it increases and then decreases (in the group of most fertile lakes) (Table IV). Perhaps, this difference is due to varying light conditions; in deep dimictic lakes, already at medium fertility, the light conditions are a limiting factor because of a considerable depth of mixing during circulation, whereas in polymictic lakes the phytoplankton growth (and the utilization of phosphorus by phytoplankton) is limited by light only at the highest fertility and resulting from it poor light conditions.

The ratio of chlorophyll concentration to total phosphorus concentration in summer shows the same regularity as the ratio of phytoplankton biomass to total phosphorus in summer (Table IV), although the differences of the first index among particular trophic groups are much smaller. The ratio of chlorophyll to total nitrogen (utilization of nitrogen for chlorophyll production) increases systematically with the increase of trophic state in both mictic types of lakes (Table IV).

The biomass of blue-green algae - extremely unfavourable and undesirable phytoplankton component - distinctly increases with the trophic state (r = 0.565 and 0.478), attaining much higher values in polymictic lakes. This may be caused by some of the above-mentioned substances or by generally more favourable conditions for blue-green algae in shallow lakes (Sirenko and Gavrilenko 1978). As the trophic state increases the mean contribution of blue-green algae to phytoplankton biomass increases. The utilization of phosphorus for the production of blue-green algae in summer (ratio of blue-green algae biomass to P_{tot} concentration in epilimnion) increases with the trophic state, but it is much higher in polymictic lakes than in dimictic ones (Table IV).

Nannoplankton biomass is the lowest in the group of dimictic lakes having the lowest trophic state; it increases with the trophic state and decreases again in lakes having a very high trophic state (P_{III} - Table IV). The contribution of nannoplankton to phytoplankton biomass does not show a distinct dependence on the trophic state, it is greatly differentiated in its entire range (the highest in the group of the most fertile polymictic lakes), but high values frequently occur at a low trophic state (Table IV).

4.2. Zooplankton and benthos

The biomass of zooplankton, a potential factor for phytoplankton control, is relatively little differentiated (Table V). It is the lowest in the group of lakes of the lowest trophic state (D_I and P_I) within a given mictic type (but the trophic state of group P_I is much higher than of D_I!). This is due to the fact that in some of these lakes zooplankton biomass is very low, although in other - it approximates maximal biomass in other trophic groups. The same regularity applies for the biomass of non-predatory zooplankton.

The numbers of crustaceans (Table V) are the lowest in the group of lakes having the lowest trophic state, whereas the greatest variations in numbers are in groups, where the trophic values are extreme (D_I and P_{III}). The average numbers for particular trophic groups are similar, the maximal being only twice higher than the minimal one.

The numbers and biomass of rotifers increase distinctly as the trophic state increases. At an approximate trophic state the numbers and biomass of rotifers are much higher in polymictic lakes (Fig. 4, Table V). This is probably due to greater phytoplankton abundance (this and resuspending of bottom sediments result in greater amounts of rotifer food - detritus) in polymictic lakes than in dimictic ones.

The ratio of zooplankton biomass (also of non-predatory zooplankton) to phytoplankton biomass is the highest at the lowest trophic state (group D_I). This shows that zooplankton ability to control phytoplankton decreases as the trophic state increases. (This is probably connected with the increasing contribution of blue-green algae to phytoplankton biomass as the trophic state increases). The great scatter of values of this index, both at low and high trophic state, shows that the trophic state is not the only factor deciding about the possibilities of controlling the phytoplankton abundance by zooplankton. The highest values of the index for particular lakes are recorded in the group having the lowest trophic state, although in groups of the highest trophic state, of both mictic types, the values are sometimes also high (Table V).

Table V. Zooplankton and its quantitative relations with phytoplankton in trophic groups of lakes within two mictic types (trophic groups as in Table I, number of lakes in brackets)

Parameters	Trophic groups within the mictic types of lakes					
	dimictic lakes			polymictic lakes		
	D_I (10)	D_{II} (6)	D_{III} (7)	P_I (6)	P_{II} (8)	P_{III} (5)
Zooplankton biomass in summer, $mg \cdot l^{-1}$	3.6 0.6-6.2	4.7 3.5-6.4	4.6 2.7-9.3	3.3 1.2-5.3	5.5 2.7-8.6	5.3 2.4-8.5
Non-predatory zooplankton biomass in summer, $mg \cdot l^{-1}$	3.2 0.6-5.8	3.8 2.6-6.0	3.7 1.7-8.7	2,5 0.7-4.4	3,8 1.7-5.5	4.1 1.0-6.8
Predatory zooplankton biomass in summer, $mg \cdot l^{-1}$	0.4 0.05-0.7	0.9 0.7-1.5	0.8 0.4-1.3	0.7 0.4-1.4	1.7 1.0-4.6	1.3 0.01-1.8
Biomass of macrofiltrators in summer, $mg \cdot l^{-1}$	0.8 0.2-2.2	1.6 0.8-2.4	1.0 0.4-1.6	0.8 0.2-1.9	1.6 0.1-3.0	0.9 0.005-2.9
Biomass of big Cladocera in summer, $mg \cdot l^{-1}$	1.9 0.1-2.8	1.6 0.3-3.3	2.1 1.7-8.4	0.7 0.1-1.6	1.2 0.03-2.3	1.9 0.05-4.0
Biomass of rotifers in summer, $mg \cdot l^{-1}$	0.06 0.03-0.26	0.11 0.05-0.15	0.21 0.04-0.40	0.26 0.09-0.63	0.32 0.02-0.84	0.61 0.18-1.10
Numbers of rotifers in summer, thous. $ind. \cdot l^{-1}$	0.3 0.06-1.74	0.7 0.11-1.15	1.8 0.22-4.08	1.1 0.36-2.31	3.9 0.19-8.80	6.5 0.36-15.62
Numbers of crustaceans, $ind. \cdot l^{-1}$	175 35-409	290 204-423	245 161-328	317 182-634	347 205-486	309 49-661

Zooplankton biomass in summer	2.7	0.4	0.6	0.4	0.2	0.6
Phytoplankton biomass	0.2-7.5	0.1-1.0	0.2-2.0	0.1-0.9	0.1-0.4	0.04-2.6
Zooplankton biomass in summer	5.5	1.4	1.4	1.3	1.5	9.7
Nannoplankton biomass	0.5-13.5	0.3-3.2	0.2-3.9	0.4-2.8	0.4-3.5	0.2-42.5
Non-predatory zooplankton biomass in summer	2.4	0.3	0.5	0.2	0.2	0.6
Phytoplankton biomass	0.2-6.3	0.1-0.9	0.1-1.9	0.1-0.6	0.1-0.3	0.02-2.6
Predatory zooplankton biomass in summer	11.6	21.5	21.7	25.2	30.5	27.2
Zooplankton biomass	5.5-25.5	5.8-32.1	4.8-37.2	11.8-38.3	18.2-52.9	0.3-59.7
Predatory zooplankton biomass in summer	0.14	0.29	0.30	0.36	0.48	0.50
Non-predatory zooplankton biomass	0.06-0.34	0.06-0.47	0.05-0.59	0.13-0.62	0.22-1.12	0.01-1.48
Non-predatory zooplankton biomass in summer	5.0	1.1	1.2	1.0	1.1	7.8
Nannoplankton biomass	0.4-12.8	0.3-2.4	0.1-37	0.3-2.3	0.2-2.8	0.1-34.0
Biomass of macrofiltrators in summer	23.9	34.6	26.7	22.5	27.8	14.1
Zooplankton biomass	12.4-38.1	16.7-52.5	4.0-46.9	9.0-35.8	4.8-57.3	0.1-44.7
Biomass of Cyclopoida	0.2	0.7	1.0	0.9	1.7	0.4
Biomass of Cladocera	0.07-0.41	0.12-1.13	0.07-2.58	0.35-1.84	0.27-5.80	0.005-0.99
Biomass of big Cladocera in summer	26.1	2.1	2.3	0.7	0.2	0.04
Biomass of blue-green algae	2.0-143.4	0.1-7.0	0.02-12.0	0.1-2.7	0.002-0.50	0.001-0.1
Index of zooplankton diversity	2.2	2.4	2.0	2.4	2.0	1.4
(Shannon-Weaver) in summer	1.55-2.86	1.92-2.60	0.51-2.61	2.09-2.50	0.95-2.43	0.07-2.38

The ratio of biomass of non-predatory zooplankton to nannoplankton biomass is also high in the group of lakes of the lowest trophic state (D_I), and is low at the high trophic state, but in the group of most fertile lakes (P_{III}), in some cases this index is very high and (at a great scatter in this group) produces a very high arithmetical mean (Table V).

The contribution of macrofiltrators to the biomass of crustaceans is relatively little differentiated, but on the average distinctly smaller (at a broad range of values for particular lakes) in the group of the most fertile lakes (P_{III}) (Table V).

The biomass of predatory zooplankton is distinctly smaller at a lower trophic state (especially in dimictic lakes) and increases with the trophic state; it has the greatest scatter of values in the group of the most fertile lakes (P_{III}) (Table V). Also the contribution of predatory zooplankton to total biomass of zooplankton and the ratio of predatory to non-predatory zooplankton are much smaller in dimictic lakes of the lowest trophic state (D_I), and on the average slightly higher in polymictic lakes (this may be due to greater numbers and biomass of rotifers). Therefore, at a higher trophic state, the non-predatory zooplankton is controlled (reduced) to a greater extent than at a lower trophic state; this, apart from the effect of phosphorus and nitrogen concentration, may additionally favour the development of phytoplankton.

The index of zooplankton diversity is relatively similar in various groups of lakes; it is lower only in the group of polymictic lakes of the highest trophic state; the highest value of the index range in this group is similar to that for other lakes, whereas the lowest value is exceptionally low (Table V). This may be due to either excessive fertility or to the fact that some lakes receive the toxic wastes.

Comparison of the biomass of benthos in the sublittoral of dimictic lakes and in the middle of polymictic lakes (as environments of a similar depth), shows that at a moderate trophic state the biomass is much higher (but greatly differentiated) in polymictic lakes than in dimictic ones. In groups having the highest trophic state (in both mictic types), the biomass is smaller than at a moderate trophic state (Wiśniewski and Dusoge 1983), possibly as a result of periodical oxygen deficits.

Table VI. The rate of phosphorus and nitrogen regeneration in trophic groups of lakes (as in Table I) in the epilimnion in summer

Groups of lakes[1]		P_{tot} concentration in the epilimnion in summer $\mu g \cdot l^{-1}$	N_{tot} concentration in the epilimnion in summer $mg \cdot l^{-1}$	Rate of regeneration $\mu g \cdot l^{-1}$ d^{-1}		Zooplankton biomass in summer $mg \cdot l^{-1}$	$\frac{\text{Regeneration rate of P}}{\text{Zooplankton biomass}}$	$\frac{\text{Regeneration rate of N}}{\text{Zooplankton biomass}}$	$\frac{P_{tot}\text{ concentration}}{\text{Regeneration rate}}$	$\frac{N_{tot}\text{ concentration}}{\text{Regeneration rate}}$	N : P in products of excretion
				P	N						
Dimictic	D_I (9)	36.3 20-44	1.3 0.9-1.7	7.6 2.1-12.0	25.6 6.3-40.9	3.6 0.6-6.2	2.2 1.6-3.5	7.2 5.9-10.4	5.9 2.6-13.7	74.9 24.5-269.8	3.3 3.0-3.6
	D_{II} (6)	70.2 59-87	1.4 1.0-1.9	14.6 9.5-18.1	38.5 29.8-46.8	4.7 3.5-6.4	3.3 1.5-4.6	8.4 5.6-10.4	5.1 3.3-7.0	36.4 28.2-48.6	2.8 2.5-3.8
	D_{III} (7)	284.0 137-506	2.0 1.3-27	23.3 10.0-44.5	49.3 33.4-71.4	4.6 2.7-9.3	6.1 1.7-10.9	11.8 6.2-17.5	13.5 4.5-25.0	41.3 26.1-57.0	2.3 1.6-3.6
Polymictic	P_I (6)	78.8 53-92	1.4 0.6-1.7	16.2 6.7-31.6	36.2 16.4-60.5	3.3 1.2-5.3	4.8 2.2-6.9	22.8 8.8-76.4	6.6 2.9-11.1	46.8 21.8-89.4	2.4 1.9-2.9
	P_{II} (8)	169.5 134-285	2.0 1.1-3.3	43.6 9.5-92.2	75.3 35.4-133.5	5.5 2.7-8.6	9.0 1.1-14.9	15.4 4.1-25.3	6.1 1.5-15.0	32.5 9.7-92.1	2.1 1.5-3.7
	P_{III} (5)	508.4 321-940	2.9 1.8-3.8	76.5 8.2-88.6	111.0 27.0-231.3	5.3 2.4-8.5	13.7 2.0-38.0	19.9 6.4-46.5	21.0 2.2-61.5	52.8 15.4-139.3	1.9 1.2-3.3

[1] Number of lakes in brackets.

The concentrations of phosphorus and nitrogen - the main conditions for phytoplankton development, depend largely on the excretion of these elements by zooplankton. The rate of phosphorus and nitrogen release by zooplankton per unit of time and water volume increases considerably with the trophic state in both mictic types of lakes (Table VI). The comparison of extreme trophic groups D_I and P_{III} shows that this increase is 10-fold for phosphorus and over 4-fold for nitrogen. The rate of excretion per unit of zooplankton biomass also increases (about 6 times for phosphorus and almost 3 times for nitrogen), mainly because of the numbers and biomass of rotifers. The N : P ratio in excretion products decreases (almost twice) together with the trophic state (Table VI).

The ratio of phosphorus and nitrogen concentration in water to the rate of excretion of these elements by zooplankton, i.e., the number of days necessary for the excretion of phosphorus and nitrogen in amounts equal to their concentration in water, is much higher for phosphorus in lakes having the highest trophic state within a given mictic type (D_{III} and P_{III}) but the differentiation in group P_{III} is almost 30-fold, much higher than in other groups. For nitrogen this ratio is the highest in the group of the lowest trophic state (D_I) (Table VI).

5. BIOLOGICAL INDICES OF THE TROPHIC STATE

There are many publications, where species or communities of species characteristic of a specific trophic state are given. The idea of indices has been born together with the concept of trophic types of lakes. However, these indices usually deal with lakes between ultra-oligotrophy and eutrophy. This is not so simple for the range between the advanced mesotrophy and hypertrophy, to which the lakes discussed belong. For this range of trophic state, practically no indices can be found in the literature. On the basis of lakes examined in the present paper the following regularities can be indicated:

1. Ceratium hirundinella (O. F. M.) Bergh. frequently dominates in phytoplankton biomass in mesotrophic and in moderately eutrophic lakes; the phytoplankton biomass, and also the biomass of blue-green algae and its contribution to total phytoplankton

increases together with the trophic state (Spodniewska 1983; Table IV).

2. Three groups of species have been distinguished among rotifers and planktonic crustaceans (Karabin 1983): (a) with decreasing dominance in a given taxonomic group as the trophic state increases, (b) with the dominance increasing together with the trophic state, (c) having no connection with the trophic state. Communities characteristic of lakes of a low trophic state (group I) are formed within the rotifer community by: *Chromatogaster ovalis* (Berg.), *Conochilus hippocrepis* (Schr.), *Ascomorpha ecaudis* Perty, *Gastropus stylifer* Imhof, *Polyarthra major* Burck; within crustacean zooplankton by: *Heterocope appendiculata* Sars, *Bythotrephes longimanus* Leydig, *Bosmina beriolensis* Imhof, *Daphnia cucullata* Sars., *D. cristata* Sars, and *D. longispina galeata* Leydig. Communities characteristic of lakes of the strong trophic state (II group) are formed by *Keratella cochlearis* f. *tecta* Gosse, *K. quadrata* Müller, *Pompholyx sulcata* Huds., *Filinia longiseta* (Ehrb.), *Trichocerca pusilla* (Jenn.), *Anuraeopsis fissa* (Gosse), species of the genus *Brachionus*, and also Microdidae and Bdelloidae (rotifer community) and *Mesocyclops leuckarti* Claus, *M. oithonoides* Sars, *Diaphanosoma brachyurum* Lievin, *Chydorus sphaericus* (Müll.), *Bosmina longirostris* (Müll.), *B. coregoni thersites* Baird. (crustacean community).

Morphological changes of *K. cochlearis* are closely connected with the trophic state of the lakes (Karabin 1983). In mesotrophic lakes the "*tecta*" form occurs sporadically, whereas in polytrophic lakes it makes 90-100% of biomass of *K. cochlearis* population. As this species commonly occurs the morphological changes of *K. cochlearis* can be considered as a good index of the trophic state of lakes.

Two groups of organisms - Cyclopoida and Cladocera - decide about the character of changes in the community of Crustacea. These changes are expressed by an increase in dominance (and biomass) of Cyclopoida and a decrease in dominance of Cladocera in the biomass of this community. In dimictic lakes the biomass ratio of Cyclopoida to Cladocera is a good index of changes in the structure of crustacean zooplankton during the eutrophication.

The numbers and biomass of rotifers are positively correlated with the increasing trophic state, whereas this kind of relationship is not displayed by crustaceans. With the increasing trophic state the individual size of rotifers and crustaceans decreases as well as the number of species (Karabin 1983).

3. A good index of high trophic state, especially in polymictic lakes, is Dreissena polymorpha (Pall.), which does not occur in environments of this type ($>100\ \mu g\ P_{tot} \cdot l^{-1}$) (Stańczykowska, Jurkiewicz-Karnkowska and Lewandowski 1983).

4. Among the littoral and sublittoral fauna the Mollusca can be used as an index of the trophic state; the number of their species increases to a certain trophic level, but decreases at a further increase; this is also true for the numbers and biomass of molluscs (Stańczykowska, Jurkiewicz-Karnkowska and Lewandowski 1983).

5. Benthos (apart from molluscs) is not a good index of the trophic state; only the number of Chironomidae and Oligochaeta species decreases with the increase of the trophic state in all environments examined, but at the same trophic state is higher in polymictic lakes. In the profundal, the increase of the trophic state is simultaneous with the increasing dominance of Chaoborus, but the contribution of Chironomidae and Oligochaeta to benthic biomass decreases accordingly (Wiśniewski and Dusoge 1983).

6. All above regularities of the occurrence of organisms may be used as indices of trophic state. They cannot, of course, be applied mechanically. They should be confronted with other indices, and especially with total phosphorus, phosphate phosphorus, total nitrogen and its forms, the Secchi disc visibility, etc. One should also remember that under special circumstances, e.g., strong hypertrophy or the presence of toxic substances, untypical species may occur (quite frequently single species occur) and they cannot be treated as indicators of trophic state. This applies both for phyto- and zooplankton. These circumstances require an especially thorough analysis.

6. GENERALIZATION OF RESULTS

The polymictic lakes examined have in summer on the average a higher trophic state (measured by the concentration of total phosphorus in epilimnion, or by other indices such as Secchi disc visibility, chlorophyll concentration, etc.) than dimictic lakes (Tables I, IV, V).

This is first of all due to the fact that surface waters of polymictic lakes are enriched with nutrients, especially phosphorus, from the bottom sediments. Besides, because these lakes have less water than deep lakes, the loads from the drainage basin are less diluted.

In polymictic lakes the concentration of total phosphorus in summer is usually higher than in spring (and the ratio of the first to the second increases with the trophic state), opposite to that in dimictic lakes in which it is lower in summer than in spring (and the ratio decreases slightly with the increasing trophic state) (Table I). In both mictic types of lakes the phosphorus is transferred from bottom sediments into the water, however, in deep, dimictic lakes the majority of this phosphorus remains in deep water layers, being inaccessible for phytoplankton. In polymictic lakes the phosphorus transferred from bottom sediments is directly available for planktonic algae.

Assuming the phytoplankton biomass 10 mg $\cdot$ l^{-1} as the lower limit of water blooms, the spring blooms occurred in 10% of dimictic lakes and in 50% of polymictic lakes, and the summer blooms in 40% of dimictic lakes and in 80% of polymictic lakes. In summer in 5 polymictic lakes the phytoplankton biomass exceeded 50 mg $\cdot$ l^{-1} (in 2 lakes - 100 mg $\cdot$ l^{-1}); these lakes had summer phosphorus concentrations over 100 µg $\cdot$ l^{-1} (Spodniewska 1983).

Several of the indices applied are distinctly correlated with low and moderate trophic states, whereas quite indistinctly with the high trophic state (Tables I, III, IV). In polymictic lakes as compared to dimictic ones of a similar trophic state the phytoplankton biomass (including blue-green algae), numbers and biomass of rotifers and the number of zoobenthic species are greater. In summer, the phytoplankton biomass in dimictic lakes becomes stable already at average concentrations of phosphorus in the epilimnion, whereas in polymictic lakes it increases to the highest phosphorus concentrations.

The increase in the trophic state is accompanied by a number of distinct regularities:

Dinoflagellates (mainly Ceratium hirundinella) begin to dominate in phytoplankton, and blue-green algae at a further increase of the trophic state (Spodniewska 1983).

Apart from an increase in total phosphorus concentrations, assumed as a measure of the trophic state, the total nitrogen concentration also increases (but the ratio of nitrogen to phosphorus decreases) as well as phytoplankton biomass, chlorophyll concentration, biomass of blue-green algae and their contribution to phytoplankton biomass, utilization of phosphorus for the production of biomass of blue-green algae (the ratio of biomass of blue-green algae to total phosphorus concentration in summer), the ratio of chlorophyll to total nitrogen concentration, the ratio of phytoplankton biomass to total nitrogen concentration, numbers and biomass of rotifers, transparency expressed by Carlson's index of trophic state, excretion of nitrogen, and especially of phosphorus, per unit of zooplankton biomass and unit of water volume and time. Some indices have high values only in lakes of the lowest trophic state (group D_I); these are, e.g., contribution of nannoplankton biomass to phytoplankton biomass, the ratio of zooplankton biomass to phytoplankton biomass (i.e., utilization of phytoplankton for production of zooplankton biomass).

Some indices decrease as the trophic state increases, e.g., number of mollusc species, numbers and biomass of molluscs (Stańczykowska, Jurkiewicz-Karnkowska and Lewandowski 1983), the number of species from main groups of profundal benthos - Chironomidae and Oligochaeta (Wiśniewski and Dusoge 1983), the ratio of phosphorus to nitrogen in the epilimnion and also in the products of zooplankton excretion.

The values of some indices increase with the trophic state to a certain degree, and then, at the highest trophic state, decrease again; e.g., the ratio of phytoplankton biomass and also chlorophyll concentration to total phosphorus concentration (i.e., utilization of phosphorus for the biomass production of phytoplankton and chlorophyll). However, the maximal values of these indices occur at much higher concentrations of total phosphorus in polymictic lakes as compared with dimictic lakes.

Although these tendencies of changes of indices according to changes in the trophic state are distinct, it should be pointed out that for particular lakes the scatter of values of these indices is great. (This scatter may be to some extent due to accidental fluctuations of parameters analysed - in summer the material was sampled only once.) Therefore, there is a definite probability of structural and functional characters of particular lakes of a given degree of trophic state, but considerable deviations have to be taken into consideration.

Several publications present lists of species characteristic of various levels of trophic state. These data are, of course, reliable, but of little use for the region examined, where the majority of lakes have a high or very high trophic state, whereas only few have a moderate or low trophic state. And the above-mentioned indices concern as a rule lakes of a very low, low and at the utmost moderate trophic state. For the lakes examined one can point out only few species characteristic of a definite trophic level. For example, Dreissena polymorpha is not found in summer in lakes of a total phosphorus concentration in the epilimnion over 100 $\mu g \cdot l^{-1}$ (Stańczykowska, Jurkiewicz-Karnkowska and Lewandowski 1983); the crustacean Heterocope appendiculata does not go beyond the moderate eutrophy, i.e., up to several tens of $\mu g\ P_{tot} \cdot l^{-1}$ (and this species does not occur abundantly). As for rotifers, in more fertile lakes occurs Keratella cochlearis f. tecta, and in less fertile lakes - K. cochlearis f. typica (Karabin 1983).

Among rotifers there is a group, which distinctly dominates in lakes of a low trophic state, and another, which distinctly dominates in lakes of a high trophic state, both dimictic and polymictic. This regularity has been also observed for crustaceans, but only in dimictic lakes. Perhaps this is not connected with the mixis, but with the averagely lower trophic state of these lakes. As regards higher taxonomic units the Cladocera are an indicator of relatively lower trophic state, and Cyclopoida are an indicator of relatively high trophic state; Calanoida do not show any connection with the trophic state of lakes (Karabin 1983).

The food conditions are significant here. In lakes of a lower trophic state dominate species feeding to a considerable extent on nannoplankton - big filtrating species, in very fertile lakes - species feeding mainly on the detritus-bacteria suspension. To a certain trophic state the intensity of phosphorus excretion by zooplankton per unit of its biomass increases (mainly due to decreasing mean biomass of a zooplankton individual), the time of phosphorus circulation in epilimnion is being shortened - up to a relatively high trophic state. At a very high trophic state (trophic groups D_{III} and P_{III}) the phosphorus turnover time is several times longer than at a lower trophic state (Ejsmont-Karabin 1983; Table VI).

The intensity of phosphorus and nitrogen excretion by zooplankton which increases with the increasing trophic state, excretion of ammonia nitrogen (whereas in the epilimnion usually nitrate nitrogen dominates among inorganic forms), and the high P : N ratio in products of zooplankton excretion, may affect significantly the development and dominance relations of phytoplankton, including stimulation of the growth of blue-green algae (Ejsmont-Karabin 1983).

With consideration to all these regularities, it can be said that zooplankton is a factor intensifying the eutrophication (in polymictic lakes this is cumulated with greater excretion of phosphorus from the bottom sediments as the trophic state increases). Only in hypertrophic lakes this is no longer significant. In these lakes phosphorus concentrations are, however, so high that its possible regeneration by zooplankton would not be so significant.

Dimictic lakes have the mechanism which neutralises or rather slows down the rate of eutrophication - sedimentation of matter, including phosphorus, which increases with the trophic state of a lake.

As the trophic state increases the trophic relations also undergo significant changes. In lakes of the lowest trophic state (group D_I) nannoplankton dominates in phytoplankton, and it can be efficiently controlled by numerously occurring big filtrating species, feeding directly on algae. Phytoplankton biomass is used there by zooplankton to the greatest extent (Table II). In lakes of a high trophic state, among planktonic phytophages, dominate species of small filtrators, which feed on detritus and bacteria and thus cannot control the phytoplankton directly. Big filtrating crustaceans (Cladocera) are perhaps limited in their numbers in lakes of a high trophic state due to competition with small filtrators, for which the abundance of suitable food (bacteria and detritus) makes the competition easier for them. Also the phytophagous zooplankton in these lakes is probably reduced to a greater extent by predatory zooplankton, which is proved by an increasing quantitative ratio of the latter to the former as the trophic state increases (Table V).

Excessively hypetrophic lakes have specific and sometimes surprising characters. The water blooms there are usually heavy and long lasting, but sometimes the phytoplankton biomass is very low and single species, mainly blue-green algae, distinctly dominate. Sometimes nannoplankton, including green algae, occurs abundantly and dominates (Spodniewska 1983). As for rotifers, species rare in other lakes occur, e.g., Brachionus rubens Ehrb. and Polyarthra dolichoptera Idelson (considered as a cold-water species), out of crustaceans - Cyclops colensis Lillj. and Daphnia pulex Leydig (considered as a mesosaprobic species) (Karabin 1983). Perhaps, extremely high trophic state and toxic substances from the wastes disturb the biocenotic bonds, weaken or destroy the competition, and thus allow for the occurrence of species not typical of these environments.

Thus, up to the moment when the lake reaches the stage of moderate eutrophy, it has effective mechanisms for controlling the rate of eutrophication. Past this stage these mechanisms no longer work, and other mechanisms come to head, which stimulate the process of eutrophication. So in order to have clean lakes this critical point should be avoided as afterwards not only allochthonous but also intensive auto-eutrophication takes place. This can be avoided by stopping the inflow of wastes and by rational management in the drainage basin (including the construction or maintenance of soil-plant barriers which counteract excessive surface flows of nutrients from the drainage basin to surface waters).

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7. SUMMARY

The obtained in team research physical, chemical and biological data for 42 (23 dimictic and 19 polymictic) lakes, ranging between moderate eutrophy to strong hypertrophy - 20-940 µg $P_{tot} \cdot l^{-1}$, during spring circulation and summer stagnation, allow

to characterize the structural and functional characters of their ecosystems according to their trophic status and mixis. Total phosphorus concentration in summer in the epilimnion is on the average higher in polymictic lakes (Table I), because of their smaller volume and the greater phosphorus loads transferred from bottom deposits into water as compared with dimictic lakes. The latter have lower phosphorus concentrations in the epilimnion in summer than in spring, whereas in polymictic lakes it is the opposite - the trophic state in summer increases in relation to the spring (Fig. 1, Table I), mainly as a result of phosphorus load from bottom sediments.

As the trophic state (measured by total phosphorus concentration) increases the percentage of phosphate phosphorus in P_{tot} increases as well as total nitrogen concentration (whilst the N:P ratio decreases), chlorophyll concentration, biomass of phytoplankton and blue-green algae, the contribution of blue-green algae to phytoplankton biomass, efficiency of phosphorus utilization by blue-green algae and of nitrogen by phytoplankton, numbers and biomass of rotifers. But the numbers and biomass of crustaceans undergo very little changes. Of course, Secchi disc visibility, number of species, numbers and biomass of molluscs, number of species of Chironomidae and Oligochaeta in environments beyond the littoral - decrease (Tables I, IV, V).

Polymictic lakes of a similar trophic state as the dimictic ones have a higher phytoplankton biomass, including blue-green algae. This increase is observed up to the highest phosphorus concentrations recorded, whereas in dimictic lakes the biomass becomes rather stable already at mean concentrations. Thus the efficiency of phosphorus utilization by phytoplankton is better in polymictic lakes (Fig. 1, Table IV). As the trophic state increases the possibility of controlling phytoplankton by zooplankton decreases because of changes in the qualitative composition of the latter and the connected with it changes of food consumed, and also because of probably higher reduction of non-predatory zooplankton by the predatory one.

Despite all these regularities connected with changes of total phosphorus concentration in epilimnion the scatter of values (around the mean) is very high for particular lakes.

Not many species can be treated as definite indicators of the trophic state. And so, e.g., the crustacean Heterocope appendiculata occurs in summer in lakes of P_{tot} concentrations in the epilimnion not higher than several tens of $\mu g \cdot l^{-1}$, the mollusc Dreissena polymorpha - up to about 100 $\mu g \cdot l^{-1}$. But the dominance of particular groups of rotifer and crustacean species depends distinctly on the trophic state. Among other things, with the increasing trophic state the contribution of Cyclopoida to the biomass of crustaceans increases and of Cladocera decreases, also the size of rotifer and crustacean specimens decreases.

The greatest differentiation and some surprising characteristics are observed in the most hypertrophic lakes. The phytoplankton biomass is sometimes low and the dominance of single species very strong. Sometimes nannoplankton including green algae occurs abundantly and dominates, or not typical of high trophic state zooplankton species occur.

In both mictic types of lakes the ratio of phosphorus concentration in the epilimnion in summer to its concentration in bottom sediments greatly increases with the trophic state (Table II). This, of course, does not change the fact, that phosphorus resources in bottom sediments exceed many times the amount of phosphorus in water. In polymictic lakes the phosphorus concentration in bottom sediments increases parallelly to its increase in water. However, in the most fertile dimictic lakes, the phosphorus concentration in bottom sediments is not higher than in the group of lakes of a lower trophic state. In the most hypertrophic lakes of both mictic types the phosphorus concentration in bottom sediments in summer is slightly higher than in spring.

Together with the increase of the trophic state phosphorus is more intensively excreted by zooplankton per unit of its biomass and unit of water volume, the ratio of phosphorus concentration in water to its amount excreted by zooplankton decreases (Table VI). But these regularities do not concern the excessively hypertrophic lakes, because some of them have unexpectedly low zooplankton biomass and as a result of this - small amounts of phosphorus excreted by zooplankton. Phosphorus is excreted by zooplankton relatively more intensely than nitrogen and this causes the lowering of the N : P ratio as the trophic state increases. This is undoubtedly significant for the qualitative composition of phytoplankton and favourable for the growth of blue-green algae.

Intensive phosphorus and nitrogen excretion by zooplankton as the trophic state increases is cumulated with intensive phosphorus release from bottom sediments, especially in polymictic lakes.

8. POLISH SUMMARY

Na podstawie - uzyskanego w badaniach zespołowych - zbioru podstawowych danych fizycznych, chemicznych i biologicznych z 42 jezior (23 dymiktycznych i 19 polimiktycznych), od umiarkowanej eutrofii do silnej hypertrofii (20-940 μg całkowitego $P \cdot l^{-1}$), w okresie cyrkulacji wiosennej i stagnacji letniej scharakteryzowano cechy strukturalne i funkcjonalne ich ekosystemów na tle trofii i miksji. W jeziorach polimiktycznych stężenie fosforu całkowitego latem w epilimnionie było przeciętnie wyższe (tab. I) ze względu na ich mniejszą objętość, a także większe ładunki fosforu przechodzące z osadów dennych do toni wodnej niż w jeziorach dymiktycznych. Te ostatnie wykazują niższe stężenia fosforu w epilimnionie latem niż wiosną, podczas gdy jeziora polimiktyczne odwrotnie - wzrost trofii latem w stosunku do wiosny (rys. 1, tab. I), głównie na skutek ładunku fosforu z osadów dennych.

Wraz ze wzrostem trofii (mierzonej stężeniem fosforu całkowitego) rośnie udział fosforu fosforanowego w całkowitym, rośnie także stężenie azotu całkowitego (ale maleje stosunek azotu do fosforu), stężenie chlorofilu, biomasa fitoplanktonu oraz sinic, a także udział sinic w biomasie fitoplanktonu, efektywność wykorzystania fosforu przez sinice i azotu przez fitoplankton, liczebność i biomasa wrotków. Bardzo małym zmianom ulega natomiast liczebność i biomasa skorupiaków. Maleje oczywiście widzialność krążka Secchi'ego, liczba gatunków oraz liczebność i biomasa mięczaków, liczba gatunków <u>Chironomidae</u> i <u>Oligochaeta</u> w środowiskach pozalitoralnych (tab. I, IV, V).

Przy podobnej trofii jeziora polimityczne cechuje wyższa niż dymiktyczne biomasa fitoplanktonu, w tym sinic. Wykazują one wzrost do najwyższych stwierdzonych stężeń fosforu, podczas gdy w jeziorach dymiktycznych ulegają w zasadzie stabilizacji już przy średnich stężeniach. Tak więc w jeziorach polimiktycznych lepsza jest efektywność wykorzystania fosforu przez fitoplankton (rys. 1, tab. IV). Wraz ze wzrostem trofii maleje możliwość kontroli fitoplanktonu przez zooplankton ze względu na zmiany składu jakościowego tego ostatniego i związane z tym zmiany pobieranego pokarmu, a także ze względu na silniejszą prawdopodobnie redukcję zooplanktonu niedrapieżnego przez drapieżny.

Mimo istnienia wyżej omówionych prawidłowości związanych ze zmianami stężenia fosforu całkowitego w epilimnionie, rozrzut wartości z poszczególnych jezior wokół przeciętnej jest bardzo duży.

Tylko niewiele gatunków można traktować jako zdecydowane wskaźniki trofii. Tak np. skorupiak Heterocope appendiculata występuje w jeziorach o stężeniach całkowitego P latem w epilimnionie nie większych niż kilkadziesiąt $\mu g \cdot l^{-1}$, małż Dreissena polymorpha - do ok. 100 $\mu g \cdot l^{-1}$. Natomiast wyraźnie zależy od trofii dominacja określonych grup gatunków wrotków i skorupiaków. Między innymi wraz ze wzrostem trofii rośnie udział Cyclopoida, a maleje Cladocera w biomasie skorupiaków, maleje także wielkość osobników wrotków i skorupiaków.

Największe zróżnicowanie i cechy nieraz zaskakujące obserwuje się w jeziorach najbardziej hypertroficznych.Niekiedy biomasa fitoplanktonu jest tu niska, z bardzo silną dominacją pojedynczych gatunków. Niekiedy występuje obficie i dominuje nannoplankton, w tym zielenice, bądź też nietypowe dla wysokiej trofii gatunki zooplanktonu.

W obu typach miktycznych jezior stosunek stężenia fosforu w epilimnionie latem do jego stężenia w osadach dennych poważnie rośnie wraz z trofią (tab. II). Nie zmienia to oczywiście faktu, że zasoby fosforu w osadach dennych wielokrotnie przewyższają jego ilość w wodzie. Ze wzrostem stężenia fosforu w wodzie jezior polimiktycznych systematycznie rośnie jego stężenie w osadach dennych. Natomiast w najżyźniejszych jeziorach dymiktycznych stężenie fosforu w osadach dennych nie jest wyższe niż w grupie jezior o niższej trofii. W najbardziej przeżyźnionych jeziorach obu typów miktycznych latem stężenie fosforu w osadach dennych jest nieco wyższe niż wiosną.

Wraz ze wzrostem trofii rośnie intensywność wydzielania fosforu przez zooplankton na jednostkę jego biomasy oraz jednostkę objętości wody, ulega obniżeniu stosunek stężenia fosforu w wodzie do jego ilości wydzielanej przez zooplankton (tab. VI). Prawidłowości te nie dotycza jednak jezior najbardziej przeżyźnionych, niektóre z nich wykazują bowiem niespodziewanie niskie biomasy zooplanktonu, a w konsekwencji - małe ilości fosforu wydzielanego przez zooplankton. Ponieważ zooplankton wydziela stosunkowo znacznie intensywniej fosfor niż azot, wpływa to na obniżenie stosunku

N : P wraz ze wzrostem trofii. Jest to niewątpliwie istotne dla składu jakościowego fitoplanktonu, korzystne dla rozwoju sinic.

Wzmożone wydzielanie fosforu i azotu przez zooplankton wraz ze wzrostem trofii kumuluje się ze wzmożonym wydzielaniem fosforu z osadów dennych, zwłaszcza w jeziorach polimiktycznych.

9. REFERENCES

1. Bajkiewicz-Grabowska E. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. II. Lake catchment areas - physico-geographical environment. Description of the region and 43 lakes - Ekol. pol. 31:257-286.
2. Carlson R. E. 1977 - A trophic state index for lakes - Limnol. Oceanogr. 22: 361-369.
3. Ejsmont-Karabin J. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. VIII. Role of nutrient regeneration by planktonic rotifers and crustaceans in 42 lakes - Ekol. pol. 31:411-427.
4. Fee E. J. 1979 - A relation between lake morphometry and primary productivity and its use in interpreting while lake eutrophication experiments - Limnol. Oceanogr. 24: 401-416.
5. Gliwicz Z. M. 1979 - Thermal stratification, organic matter loss to the hypolimnion and residence time of a nutrient unit in the epilimnia of small temperate lakes - Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 27: 621-626.
6. Graneli W. 1979 - The influence of Chironomus plumosus larvae on the exchange of dissolved substances between sediment and water - Hydrobiologia, 66: 149-159.
7. Kajak Z. 1978 - The characteristics of the temperate eutrophic dimictic lake (Lake Mikołajskie, Northern Poland) - Int. Rev. ges. Hydrobiol. 63: 451-480.
8. Kajak Z. 1979 - Eutrofizacja jezior [Eutrophication of lakes] - Państwowe Wydawnictwo Naukowe, Warszawa, 233 pp.
9. Kajak Z. 1981 - Skuteczność różnych metod rekultywacji jezior w celu poprawy czystości ich wód [Efficiency of various methods of recultivation of lakes for purity of their waters] - Wiad. ekol. 27: 331-357.
10. Kajak Z., Zdanowski B. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their

trophic gradient. I. General characteristics of 42 lakes and their phosphorus load. Study objectives and scope - Ekol. pol. 31:239-256.

11. Karabin A. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. VII. Variations in the quantitative and qualitative structure of the pelagic zooplankton (Rotatoria and Crustacea) in 42 lakes - Ekol. pol. 31: 383-409.

12. Patalas K. 1960 - Mieszanie wody jako czynnik określający intensywność krążenia materii w różnych morfologicznie jeziorach okolic Węgorzewa [Water mixing as a factor determining the intensity of matter cycling in morphologically different lakes of the Węgorzewo surroundings] - Roczn. Nauk roln. B, 77: 223-242.

13. Prejs K., Papińska K. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. XI. Meiobenthos and near-bottom meiofauna in 20 lakes - Ekol. pol. 31: 477-493.

14. Ryding S. A., Forsberg C. 1976 - Six polluted lakes: a preliminary evaluation of the treatment and recovery processes - Ambio, 5: 151-156.

15. Sirenko L. A., Gavrilenko M. L. 1978 - Cvetenie vody i évtrofirovanie - Naukova Dumka, Kiev, 231 pp.

16. Spodniewska I. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. VI. The phytoplankton of 43 lakes - Ekol. pol. 31: 353-381.

17. Stańczykowska A., Jurkiewicz-Karnkowska E., Lewandowski K. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. X. Occurrence of molluscs in 42 lakes - Ekol. pol. 31: 459-475.

18. Wiśniewski R. J., Dusoge K. 1983 - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. IX. The macrobenthos of 44 lakes - Ekol. pol. 31: 429-457.

19. Zdanowski B. 1982 - Variability of nitrogen and phosphorus contents and lake eutrophication - Pol. Arch. Hydrobiol. 29.

20. Zdanowski B. 1983a - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. III. Chemistry of the water in 41 lakes - Ekol. pol. 31: 287-308.

21. Zdanowski B. 1983b - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. IV. Chemistry of bottom sediments in 37 lakes - Ekol. pol. 31:309-331.

22. Zdanowski B. 1983c - Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. V. Chlorophyll content and visibility of Secchi's disc in 46 lakes - Ekol. pol. 31:333-351.