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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*

ABSTRACT: Analyses have been carried out of the rate of phosphorus and nitrogen regeneration by the zooplankton of 42 lakes representing a trophic and morphometric gradient. For unpolluted lakes a high growth of the rate of P and N regeneration has been found, as well as a reduction of the turnover time of phosphorus and of the value of the N : P ratio in the products of regeneration following an increase in the pool of total phosphorus. The importance is discussed of changes in the internal cycles of P and N, connected with changes in the trophical conditions of the lakes, to the consequences of the process of eutrophication.

KEY WORDS: Lakes, phosphorus, nitrogen, regeneration, zooplankton, eutrophication.

C o n t e n t s

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1. INTRODUCTION

Lake eutrophication is a process leading to an increased lake fertility, that is to say, an increased pool of nutrients contained in a lake, as a result of an increase in their inflow from outside a lake ecosystem. If not expelled from an ecosystem permanently, these nutrients are recycled within it, the recycling consisting of rapid continual changes of their chemical forms. Some of the changes, those limited to the euphotic zone and including a rapid flow of nutrients between the phyto- and the zooplankton, is called the internal recycling (G a n f and B l a ž k a 1974, T a f t, T a y l o r and M c C a r t h y 1975, S c a v i a 1979). According to S c a v i a (1979), phosphorus would be completely exhausted in less than 24 hours from the epilimnion of Lake Ontario, a eutrophic water body, if processes of mineralization did not take place in this layer. In this lake as much as 86% of the phosphorus assimilated by the phytoplankton remains in the epilimnion, entering the internal recycling. This indicates an important role of the processes of nutrient mineralization to the primary production.

On account of their negative effects on the quality of lake waters, eutrophication processes have been intensely studied, and there have been, also in Poland, some more complete studies devoted to them (K a j a k 1979). However, these studies and analyses most often concern the causes and results of eutrophication, and while they also cover the problem of the effect of an increase in the supply of nutrients in lakes on the fate of these nutrients in lakes, they ignore the role of this increase in the processes making up the internal recycling. One of the basic mechanisms of nutrient regeneration is their supravital excretion by the zooplankton (B a r l o w and B i s h o p 1965, D u g d a l e and G o e r i n g 1967, H a r g r a v e and G e e n 1968, B l a ž k a 1976,

Table I. Rate of regeneration of phosphorus (b) and nitrogen (c) by zooplankton against total-P concentration (a) in 42 lakes differing in nutrient content and morphometry ($a - \mu g \cdot l^{-1}$; b and c $- \mu g \cdot l^{-1} \cdot 24\ hours^{-1}$)

Lake type		Lake name	a	b	c
Unpolluted	stratified	Piłakno	20	4.60	14.49
		Ołów	29	2.11	6.30
		Sarż	31	11.97	40.90
		Kierzlińskie	38	8.44	28.34
		Probarskie	38	8.57	28.41
		Kuc	40	4.06	13.94
		Gim	43	8.49	30.65
		Skanda	44	11.79	40.78
		Maróz	44	8.33	26.70
		Jaśkowskie	59	17.67	46.81
		Grom	66	9.45	35.66
		Czos	68	15.91	41.78
		Szeląg Mały	68	18.11	40.78
		Lampackie	73	12.15	29.79
		Rzeckie	87	14.31	36.02
		Małszewskie	137	10.02	35.80
	nonstratified	Kołowin	53	6.47	16.37
		Burgale	74	6.69	18.01
		Mój	80	8.16	23.33
		Siercze	84	21.97	53.19
		Sędańskie	90	22.41	45.86
		Rańskie	92	31.60	60.48
		Warpuńskie	134	78.68	114.11
		Bądze	141	92.24	133.46
		Brajnickie	157	44.28	77.28
		Stryjewskie	160	23.94	48.39
		Sambród	161	34.66	67.18
		Tuchel	357	86.19	145.38
Polluted	stratified	Kokowo	147	31.51	62.12
		Juno Północne	175	22.72	50.13
		Ełckie	202	44.51	71.37
		Lidzbarskie	222	17.45	33.41
		Juno Południowe	282	23.24	37.59
		Wobel	464	24.81	46.63
		Sztumskie	506	20.25	69.96
	nonstratified	Sasek Mały	142	9.46	35.82
		Hartowiec	176	40.33	64.19
		Długie	285	25.28	62.81
		Liwieniec	321	12.26	24.86
		Iławskie	420	188.63	231.32
		Kraksy Duże	504	8.20	27.00
		Barlewickie	940	87.01	126.22

LaRow and McNaught 1978, Devol 1979, Nikulina and Gutelmacher 1979, Scavia 1979 and many others). The rate of excretion depends on the size of the organisms (Johannes 1964, Peters and Rigler 1973 and others), as well as on their taxonomic position, concentration and kind of their food (Ejsmont-Karabin 1982), that is, on factors that are to a large extent subject to changes connected with variations in the trophic conditions of the water bodies (Hillbricht-Ilkowska 1977). For eutrophication leads to a gradual change in the structure of the zooplankton connected, among other things, with changes in the concentration and structure of its food (Karabin 1982). Significant directional changes should therefore be expected to occur in nutrient regeneration processes associated with changes in the trophical state of lakes.

The objective of the present research was to study the role of nutrient regeneration by the zooplankton in lakes of varying trophic conditions, and reversely, the effect of an increase in the phosphorus content in the pelagic zone on the part of the internal recycling comprising the processes of nutrient regeneration by the zooplankton.

The objective has been achieved by assessing the rate of regeneration of phosphorus and nitrogen by the zooplankton (rotifers and crustaceans) in the pelagic zone of 42 lakes forming a gradient of water bodies differing in their trophic conditions and morphometry (Table I), the morphometric and physico-chemical properties of which have been described in the papers by Bajkiewicz-Grabowska (1983), and Kajak and Zdanowski (1983).

2. MATERIAL AND METHODS

The rate of regeneration has been assessed by using regression equations describing the effect of the individual weight of animals on the rate of excretion of P and N (Ejsmont-Karabin 1982). Different environmental temperatures used in the calculations could have blurred the effect of the trophic conditions themselves on the rate of nutrient regeneration, for this reason the temperature used in all the calculations was the mean, for the period, temperature of the epilimnion of the lakes under study, amounting to about 20°C. The following equations were used:

for the rate of excretion of $P\text{-}PO_4$

Rotatoria	$E_P = 0.105\ W^{-1.27}$
Cladocera	$E_P = 0.870\ W^{-0.230}$
Copepoda	$E_P = 0.652\ W^{-0.645}$

for the rate of excretion of $N\text{-}NH_4$

Rotatoria	$E_N = 0.511\ W^{-1.01}$
Cladocera	$E_N = 3.50\ W^{-0.191}$
Copepoda	$E_N = 2.90\ W^{-0.593}$

where: E_P and E_N – the rate of excretion of phosphorus and nitrogen, respectively, in $\mu g \cdot mg$ dry weight$^{-1} \cdot hour^{-1}$, W – individual weight in μg dry weight.

The data used in the calculations were values of the abundance and biomass of all rotifer and crustacean species obtained from quantitative samples collected in August 1977 and 1978 (the method of material collecting and examination has been described by K a r a b i n 1983). On the basis of these data the mean dry weight of an individual of each species has been calculated, and in the case of crustaceans also of a developmental stage. Then by using the above-given regression equations the excretion rate was calculated for the particular species and the values were totalled each lake separately.

The study covered the epilimnion layer, the average values for which were used.

Since the objective of the present study was to assess the effect of an increase in the supply of nutrients in lakes on their fate in the pelagic zone, it was decided that the best indicator, for the purpose of the study, of the trophic conditions of the lakes, would be the size of the pool of total phosphorus contained in the water of the pelagic zone. The results were used of total P analyses carried out by Z d a n o w s k i (1983) in samples of natural water (with seston) by the colorimetric method with ammonium molybdate after previous burning of the water samples in sulphuric acid with an addition of ammonium perphosphate.

3. RESULTS

An increase in total-P concentration in the water of the lake pelagic zone is accompanied by an increased rate of regeneration of phosphorus and nitrogen by the zooplankton (rotifers and crustaceans) in lakes not polluted with industrial effluents and municipal sewage, both those thermally stratified and the shallow ones with no stratification in summer (Fig. 1 A, B). Differences in the course of this relationship for these two lake types, in respect of the regeneration of both phosphorus and nitrogen, are not great (Fig. 2). Thus it may be assumed that the same type and

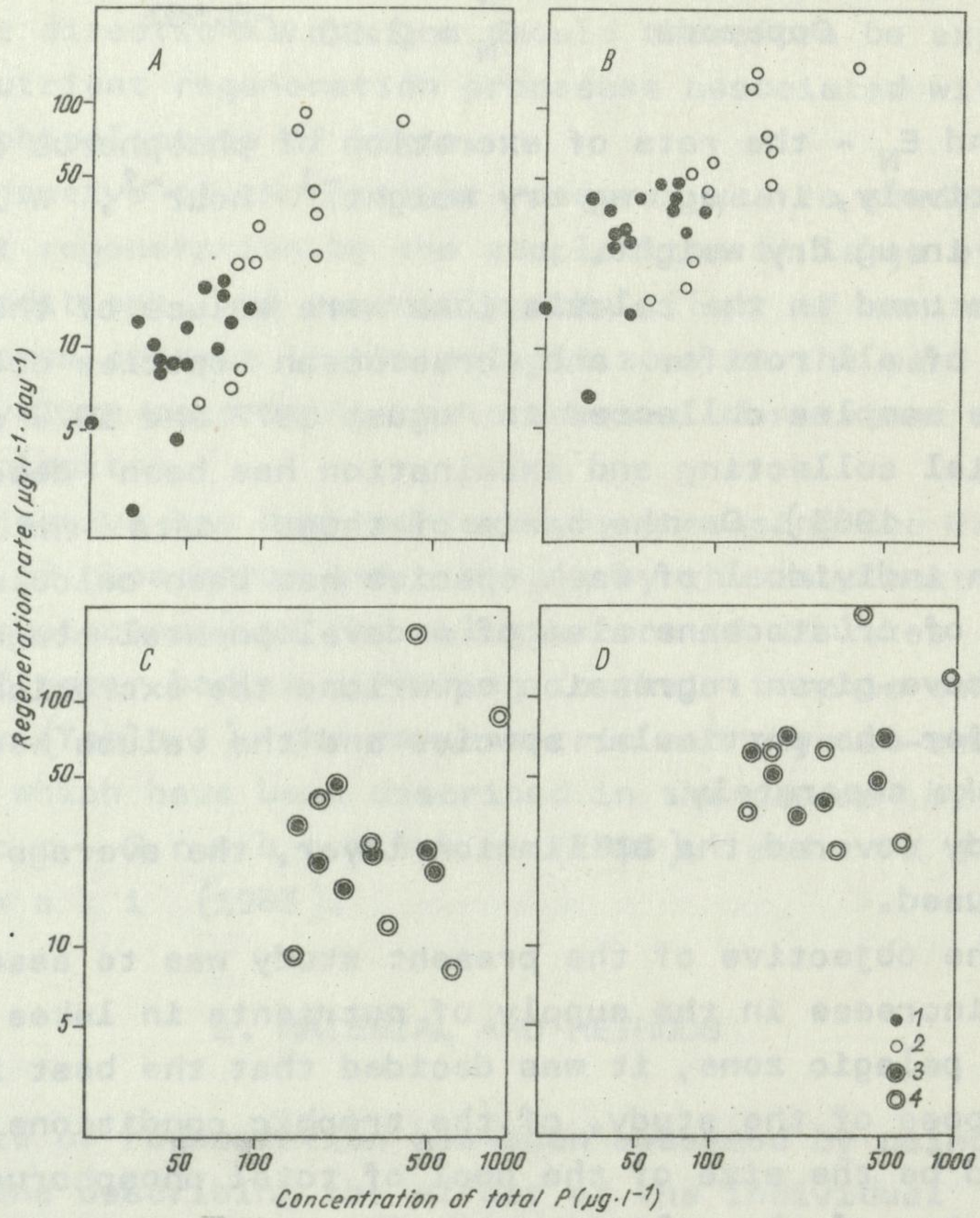

Fig. 1. Rate of regeneration of $P-PO_4$ (A and C) and $N-NH_4$ (B and D) by zooplankton in relationship to total-P concentration in lakes differing in nutrient content
1 - in unpolluted (UP) stratified (S) lakes, 2 - in unpolluted nonstratified (NS) lakes, 3 - in polluted (P) stratified (S) lakes, 4 - in polluted (P) nonstratified (NS) lakes

degree of relationship are characteristic of these two kinds of water body, and that this relationship can be described with a regression equation comprising both stratified and unstratified water bodies, provided there is no major discharge of effluents into them.

The relationship between the rate of phosphorus and nitrogen regeneration and the trophical conditions of lakes indicated by the pool of total phosphorus can be described with values raised to a power: a 25-fold increase in the content of phosphorus in the pelagic zone waters of a lake is followed by a 48-fold growth of the rate of phosphorus regeneration, and only a 15-fold increase in the rate of nitrogen regeneration (Fig. 2). The correlations

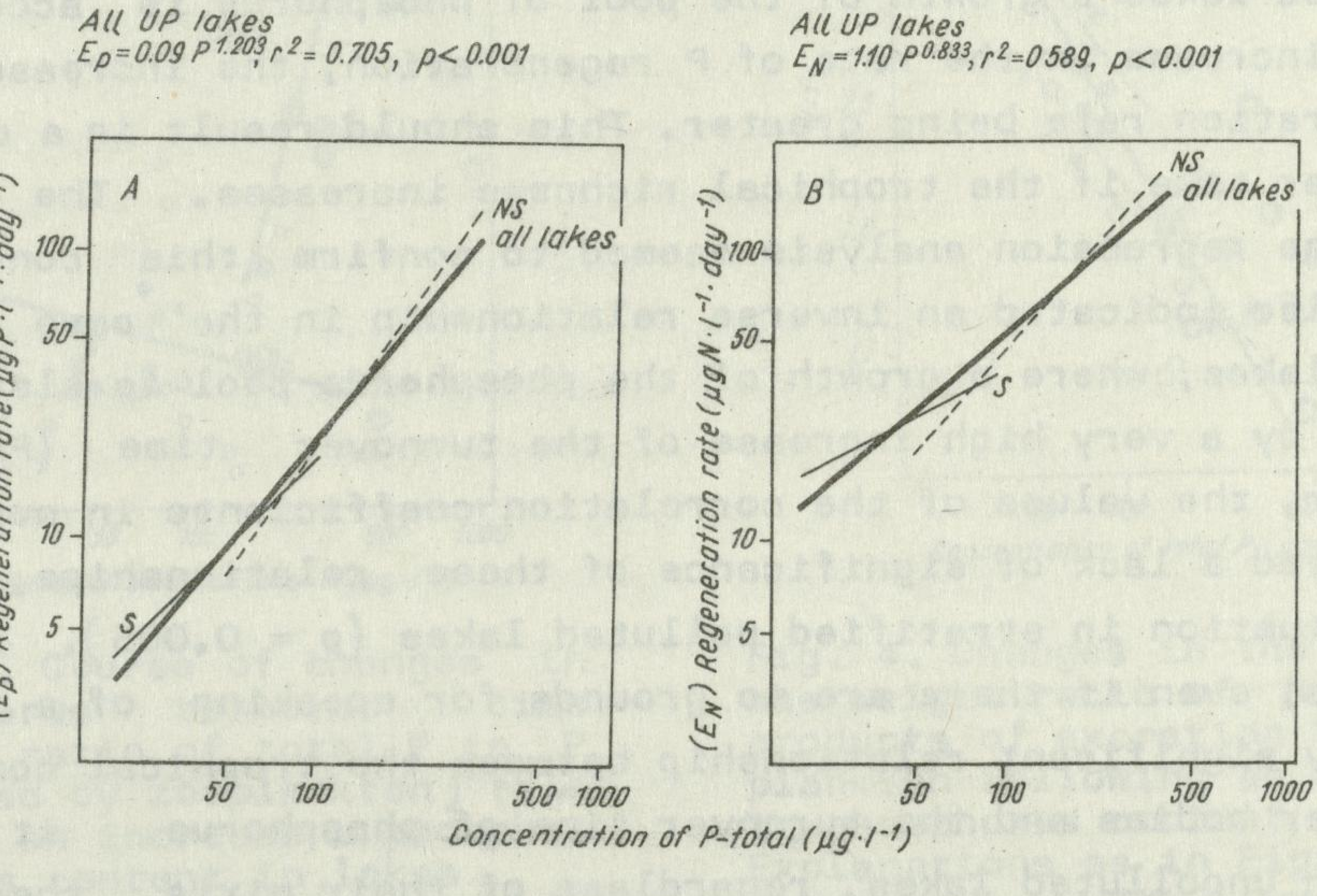

Fig. 2. Course of the relationship between the rate of regeneration of $P-PO_4$ (A) and $N-NH_4$ (B) by zooplankton and total-P concentration in thermally stratified (S) and nonstratified (NS), unpolluted (UP) lakes of different nutrient content

(after a logarithmic transformation of the data) for the relationship between the rate of P and N regeneration, and the pool of total phosphorus in unpolluted shallow lakes are highly significant ($p < 0.001$ in all cases). In the case of stratified lakes the correlation for nitrogen regeneration rate is insignificant, but even there a tendency can be seen towards a growth of the regeneration rate with an increase in the trophical richness (Fig. 1 B).

A different situation has been recorded for polluted lakes (Fig. 1 C, D, Fig. 2). With a total-P level similar to that found in unpolluted lakes, the rate of regeneration of both phosphorus and nitrogen is clearly lower. Due to a considerable dispersion of the values of the regeneration rate, with similar phosphorus content levels, the correlations are in all cases insignificant ($R = 0.01$ up to 0.38, $n = 7$ up to 14).

The turnover time for phosphorus, that is, in the case of the present study the time needed for all the phosphorus present in the environment to be regenerated by the zooplankton (i.e., total-P · regenerated-P^{-1}) under the conditions of an increasing total-phosphorus pool and a lack of changes in the regeneration rate, should grow. However, as has been mentioned above, in unpolluted lakes a growth of the pool of phosphorus is accompanied by an increase in the rate of P regeneration, the increase in the regeneration rate being greater. This should result in a decreased turnover time if the trophical richness increases. The results from the regression analysis seemed to confirm this conclusion. They also indicated an inverse relationship in the case of polluted lakes, where a growth of the phosphorus pool is also accompanied by a very high increase of the turnover time (Fig. 3). However, the values of the correlation coefficients in most cases indicated a lack of significance of these relationships, except the situation in stratified polluted lakes ($p = 0.005$). In spite of this, even if there are no grounds for speaking of a statistically significant relationship between the trophical conditions of water bodies and the turnover time of phosphorus, it seems that in unpolluted lakes, regardless of their mixis, there is no growth of the turnover time of phosphorus following an increase in the trophical richness, but conversely - a certain tendency to decrease can be seen (Fig. 3). The picture of changes in the turnover time in polluted lakes is also clearly different, its values generally remaining at a considerably higher level than in clean lakes. While the turnover time values in unpolluted lakes vary between 1 and 14 24-hour periods (on an average 5.3 24-hour periods), in polluted lakes they vary between 3 and 72 24-hour periods (on an average 16.3 24-hour periods).

The above-mentioned higher growth of the rate of regeneration of phosphorus than of nitrogen, following an increase in the content of phosphorus in lakes, leads to a considerable decrease of the value of the weight ratio of N : P in the products of excretion by the zooplankton following an increase in the trophical richness of unpolluted water bodies. This is confirmed by the results from the regression analysis (Fig. 4). With a similar nature of the relationships in shallow and deep unpolluted lakes, in the former this ratio is always lower by about 0.4.

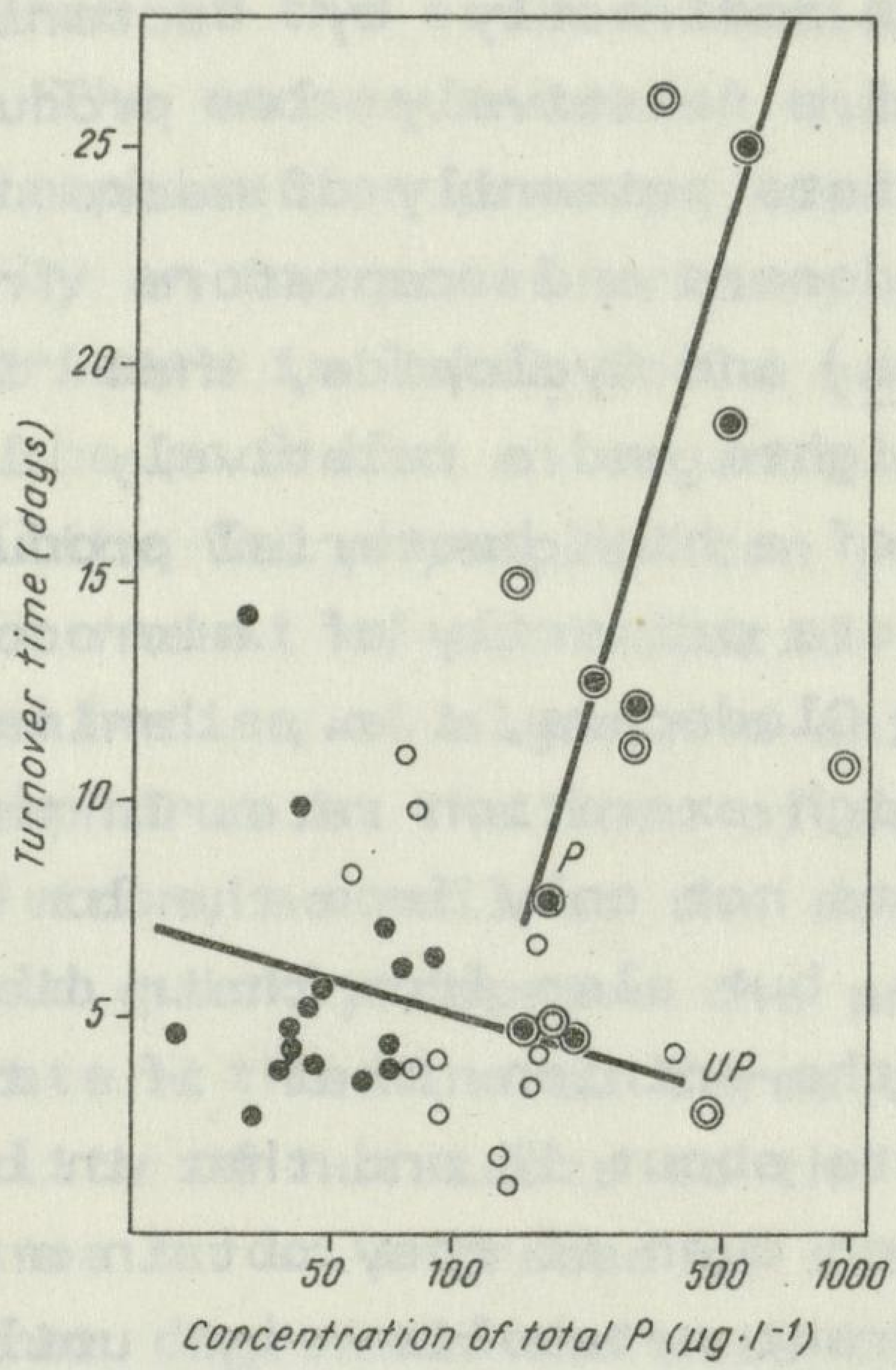

Fig. 3. Course of changes in phosphorus turnover time (e.g., ratio of total P to P excreted by zooplankton) following an increase in phosphorus content in lakes
Explanations as in Figure 1

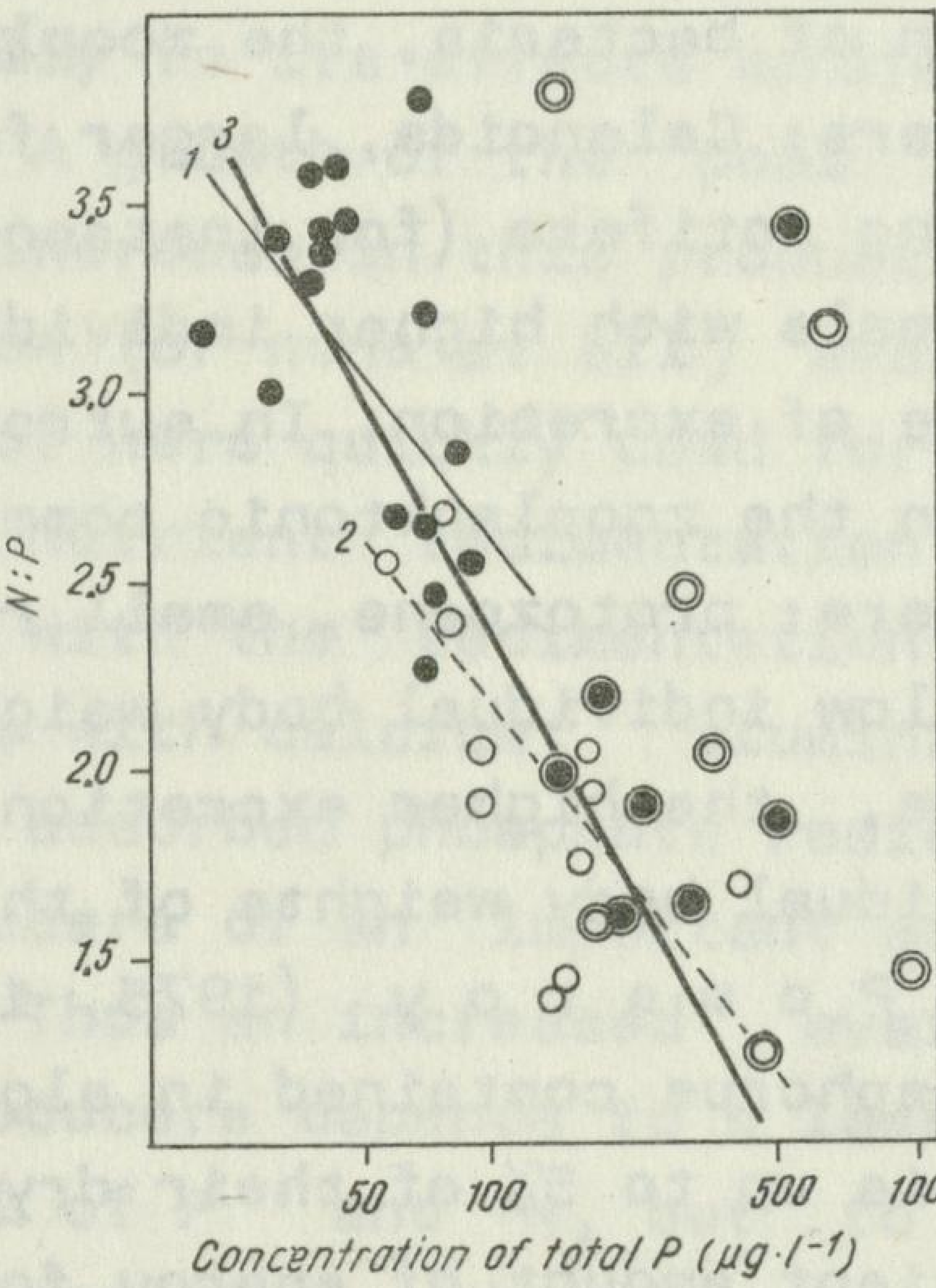

Fig. 4. Changes in the value of the weight ratio of N : P in products of excretion by zooplankton following an increase in phosphorus content in lakes
Explanations as in Figure 1. Regressions for unpolluted lakes: 1 - stratified: $N : P = 5.55 - 0.64 \ln P$ ($r^2 = 0.28$, $p = 0.05$), 2 - nonstratified: $N : P = 5.11 - 0.64 \ln P$ ($r^2 = 0.48$, $p = 0.02$), 3 - all: $N : P = 6.47 - 0.90 \ln P$ ($r^2 = 0.68$, $p < 0.001$)

For polluted lakes these relationships were found to be insignificant in all cases, and the range of the N : P values extremely wide, for instance with the same total-P level (about 500 µg · litre^{-1}) they ranged from 1.2 to about 3.5, while in the case of unpolluted lakes similar variations were recorded for the whole range of total-P concentrations taken into account.

4. DISCUSSION

An increase in the content of nutrients in lakes entails far-reaching changes in abundance and structure of the plankton. According to Hillbricht-Ilkowska (1977), the more eutrophic a lake, the smaller the proportion of phytoplankton production that can be directly utilized by the phytophagous zooplankton, and the greater that utilized indirectly by bacteriophages. In oligotrophic water bodies of a relatively low production of bacteria, the zooplankton consists primarily of macroconsumers: Calanoida, larger forms of Cladocera and raptators from among rotifers (for instance Asplanchna) and Cyclopida, that is, animals with higher individual body weights and a relatively low rate of excretion. In eutrophic lakes of a high bacterial production the zooplanktonic community consists primarily of microconsumers: protozoans, small rotifers and Cladocera, i.e., animals of low individual body weights and a high excretion rate. In this case, the higher excretion rate results not only from the low individual body weights of these animals, but also from their diet.

Pomeroy (1975, 1980) holds the opinion that if the phosphorus contained in algae represents about 1% and that in bacteria up to 5% of their dry weight, then even if they obtain a sufficient amount of energy for their current metabolism by utilizing dead algae, bacteria still need additional P and N for their growth. Therefore they act in a way similar to that of algae, and under the conditions of a strong competition with algae for the mineral forms of P and N. However, on account of a high P and N content, the bacterioplankton plays an important role in the processes of nutrient regeneration, for if bacteria are eaten by the zooplankton with a 1-2% P content in its dry weight, then after meeting its energy requirements the zooplankton must excrete, in mineral form, the P surplus resulting from the quantitative ratios of these elements between the bacteria and zooplankton. Accordingly, the lowest excretion rates may be expected in phytophages and predators whose prey have bodies poorer in P and N, or of a chemical composition similar to that of the consumers.

Thus also under the conditions of an unchanged value of the biomass of the zooplankton a structural change of the plankton, in the course of a eutrophication, towards an increased abundance of the bacterioplankton and its consumers, should lead to an increased rate of P and N regeneration. This tendency is further strengthened in connection with the decrease of the individual weights of the animals following an increase in the content of nutrients, as has been observed by K a r a b i n (1982). This decrease causes an increase in the rate of excretion per unit of animal biomass. An increased rate of nutrient regeneration by the zooplankton has been observed during the present research in the course of the eutrophication of unpolluted lakes (Figs. 1, 2).

The consequences of this process can be very important to the eutrophication process itself, especially to its effects manifested by an increased primary production. A growth of the pool of nutrients in lakes would not cause an increase in this production if the pool had an organic form of a low (or none at all) availability for phytoplankton production, or were quickly used for it as a result of assimilation processes. Nutrient sedimentation in dead bodies of algae and animals along with the sedimentation of phosphorus in the form of its compounds with calcium, aluminium and iron, as well as the detritus with adsorbed phosphate residua would quickly deprive the primary producers of an important substrate - the mineral forms of P and N. Thus an increased availability of nutrients to the primary producers depends to a lesser degree on an increase of the total pool of P and N, but to a higher degree on the rate of their regeneration, therein also on the rate of their excretion by the zooplankton.

From this point of view, an increased rate of nutrient excretion by the zooplankton, following an increase in their pool, is very important. This process determines the possible level of primary production growth following an increase in the nutrient content of water bodies. As a result of such an acceleration, the rate of flow of nutrients in their cycles does not drop in spite of the growth of their pool, but conversely, as has been observed for phosphorus, it slightly rises, as indicated by a certain decrease of the turnover time of phosphorus in unpolluted lakes (Fig. 3).

Of the three taxonomic groups of the zooplankton (Rotatoria, Cladocera and Copepoda) rotifers show the lowest, relatively, value of the N : P ratio in excretion products (E j s m o n t - K a r a b i n 1982). A growth of the percentage of rotifers in a zooplanktonic community, following an increase in the trophic richness (K a r a b i n 1983), causes a decrease in the value of regenerated N : P following a growth of the pool of total P (Fig. 4). Even in trophically poor lakes this ratio (amounting to about 3) is much lower than that required by algae (about 7), which indicates an important role of nitrogen mineralization mechanisms other than the excretion by the zooplankton. In the eutrophication process its value drops yet further to about 1.5. This situation would lead to a limitation of the primary production by nitrogen, not by phosphorus. This happens relatively rarely, although such situations have been recorded for highly eutrophic lakes (K a j a k 1979). In this situation the role should become more important of other mechanisms (most likely bacterial) supplying mineral nitrogen, or alternatively or in parallel, the role of those groups of phytoplankton which prefer mineral nitrogen compounds (e.g., nitrates) other than those excreted by the zooplankton (ammonium N), or can utilize atmospheric nitrogen (e.g., many blue-green algal species). A fact has indeed been known of a growth of the role of blue-green algae with a decreasing value of the N : P ratio in the water following an increased nutrient content (V a n d e r h o e f, H u a n g and M u s i l 1974, S c h i n d l e r 1977). The above indicates that the structure of the zooplankton may be the factor controlling the species-composition of the phytoplankton.

The process of eutrophication is thus connected with directional changes in the rate of flow of nutrients in their internal cycles, and with changes in the relationship between the rate of mineralization of organic compounds with P and N. This may lead to great changes in the functioning of whole lake ecosystems. At varying nutrient levels and different patterns of P cycles they maintain a relative balance of the processes of assimilation of mineral forms of P and N, as well as mineralization and inflow of mineral forms of these elements. Such an equilibrium can be maintained by way of directional changes in the structure of all planktonic communities.

An excess inflow of effluents throws an ecosystem off this state. The relationships defined for unpolluted lakes cease to be valid. Limited by adverse environmental conditions resulting from pollution (therein both a direct inflow of toxic substances and their formation due to bacterial activity), the zooplankton is unable to efficiently mineralize excess phosphorus flowing in from outside, and as the pool of phosphorus grows, the rate of its regeneration does not increase (Figs. 1, 2). This leads to a rapid growth of the turnover time of phosphorus (Fig. 3), because at a high level of pollution the natural sequence ceases to be valid of changes in the structure of the zooplankton towards increased proportions of small detritus-eating forms and dominance is gained by those species which are better fitted for the current conditions and can win the competition against species with which they always lose under normal conditions. So the specific composition and thereby also the size composition of the zooplankton in such lakes is often fortuitous, because it is determined by specific factors other than trophical conditions. This may account for the wide dispersion of the values of the rate of regeneration in lakes of this type and a lack of significance of the correlation between the rate of regeneration and the pool of total P (Fig. 1).

The above observations lead to the generalization that changes in the internal cycles of nutrients due to an increase in their pool are of great importance to the eutrophication process itself and to its effects as well. However, for an exact description of this problem it is necessary to study the role of P and N mineralization mechanisms other than the excretion by zooplankton. Only by analysing all the pathways that nutrients follow in their cycles, and relating the changes they are subject to with the process of eutrophication will it be possible to clarify the relative role of one of them, leading through the zooplankton, in the eutrophication itself, its course and effects. However, it may be stated already now that on account of its scale nutrient regeneration by the zooplankton must play an important role in the process of eutrophication.

5. SUMMARY

The role was studied of phosphate and ammonia regeneration by zooplankton in the course of lake eutrophication. The analysis was carried out by assessing the rate of P and N regeneration by the zooplankton of 42 lakes representing a gradient of trophically and morphometrically different water bodies. In unpolluted lakes, regardless of the type of mixis, an increase in total-P concentration was accompanied by a rise of the rate of P and N regene-

ration by the zooplankton (Figs. 1, 2), a reduction of the turnover time of phosphorus (Fig. 3) and a decrease in the value of the N : P ratio in excretion products (Fig. 4). In polluted lakes no significant relationship has been found between the pool of phosphorus in the water and the rate of regeneration (Fig. 1), but a considerable increase was found in the turnover time of phosphorus (Fig. 3).

Directional changes in the rate of P and N regeneration by the zooplankton, as well as a reduction of the N : P ratio, following an increase in the nutrient content of water bodies may play a significant role in changes in the value of primary production in the course of eutrophication, and cause changes in the specific structure of the phytoplankton. An analysis of the cause of differences in the reaction of polluted water bodies to changes in the total-P concentration suggests that being limited by factors other than the trophical conditions, the zooplankton of such water bodies is unable to efficiently mineralize excess phosphorus flowing in from outside.

6. POLISH SUMMARY

Zbadano rolę regeneracji fosforanów i amoniaku przez zooplankton w procesie eutrofizacji jezior. Analizy tej dokonano na podstawie oceny tempa regeneracji P i N przez zooplankton 42 jezior tworzących gradient zróżnicowanych troficznie i morfometrycznie zbiorników. W jeziorach nie zanieczyszczonych, niezależnie od typu miksji, wzrostowi koncentracji P ogólnego towarzyszył wzrost tempa regeneracji P i N przez zooplankton (rys. 1, 2), spadek czasu rotacji fosforu (rys. 3) i spadek wartości stosunku N : P w produktach ekskrecji (rys. 4). W jeziorach zanieczyszczonych nie stwierdzono istotnej zależności między pulą fosforu w wodzie a tempem regeneracji (rys. 1), zanotowano natomiast silny wzrost czasu rotacji fosforu (rys. 3).

Kierunkowe zmiany w tempie regeneracji P i N przez zooplankton, jak też spadek wartości stosunku N : P w trakcie wzrostu trofii zbiorników mogą mieć istotne znaczenie dla zmian wartości produkcji pierwotnej w procesie eutrofizacji, jak też wpływać na zmianę struktury gatunkowej fitoplanktonu. Analiza przyczyn odmienności reakcji zbiorników zanieczyszczonych na zmiany koncentracji P ogólnego sugeruje, że zooplankton tych zbiorników limitowany czynnikami pozatroficznymi nie jest w stanie efektywnie regenerować nadmiaru dopływającego z zewnątrz fosforu.

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