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Regular research paper

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## ROLE OF ZOOPLANKTON (CILIATA, ROTIFERA AND CRUSTACEA) IN PHOSPHORUS REMOVAL FROM CYCLING: LAKES OF THE RIVER JORKA WATERSHED (MASURIA LAKELAND, POLAND)

**ABSTRACT:** According to a theory of lake restoration through food web manipulation, the removal of planktivorous fish results in the development of large cladocerans (mostly daphnids) and, consequently, in reduction of algal biomass. However, as a rule, publications devoted to different aspects of the theory completely neglected other groups of plankton invertebrates, thought they may reach very high densities. Investigations carried out in five Masurian lakes differing in trophic state and mixis showed that in most lakes the role of small cladocerans, copepods, rotifers and protozoans in the consumption of algal food and nutrient regeneration was more important than the role of large daphnids. *Daphnia cucullata* played more significant role (excreting 28% of the regenerated P) during “clear water phase” only in one lake – Lake Głębokie. In the remaining lakes more important was an impact of *Bosmina longirostris* (11–59% of the regenerated P), younger stages of cyclopoids (23%), ciliate *Strobilidium humile* (20%) or detritophagous rotifer *Keratella cochlearis* (21%). Evidenced in many papers special role of large cladocerans in clearing lake water is explained by their combined direct (by “efficient” filtering) and indirect (suppression of ciliates and rotifers through predation, interference and resource competition) impact on nutrient sedimentation or exclusion from internal cycling.

**KEY WORDS:** Ciliata, Rotifera, Crustacea, lakes, phosphorus regeneration

### 1. INTRODUCTION

A theory of lake restoration through food web manipulation is widely accepted as one of tools for “biomanipulation” (Shapiro and Wright 1984). The theory is based on well-documented ability of fish predation to influence phytoplankton biomass through predation on zooplankton (Henrikson *et al.* 1980, Lynch and Shapiro 1981, Benndorf *et al.* 2002 and many others). According to Ramcharan *et al.* (1996), by reducing large-bodied daphnids (and thus herbivory), planktivorous fish cause decrease in both zooplankton grazing and nutrient recycling. However, the role of the fish in controlling nutrient cycling is probably different. Though it is often assumed that the greater phytoplankton abundance in the presence of fish is the result of reduced grazing pressure by zooplankton, the same may result from increased nutrient regeneration by smaller zooplankton (Vanni 1987) which

is usually strongly suppressed by large *Daphnia* (Gilbert 1988).

Hudson *et al.* (1999) have confirmed that planktonic nutrient regeneration is a fundamental process that maintains most of the primary productivity in freshwater environments, and the phosphorus supply for lake plankton comes primarily from within the plankton community, rather than from external loading or from larger organisms such as fish. Calculated by Horppila (1998), P excretion by the pelagic roach stock corresponding to 18% of the annual external P loading is negligible comparing to the regeneration rates by small zooplankton. The process of P regeneration is rather dominated by small-bodied zooplankton like protists (Dolan 1997) or rotifers (Ejsmont-Karabin 1983) because metabolic rates per unit weight are inversely related to size (Peters 1975, Ejsmont-Karabin 1984). Also a kind of food consumed is very important in determining

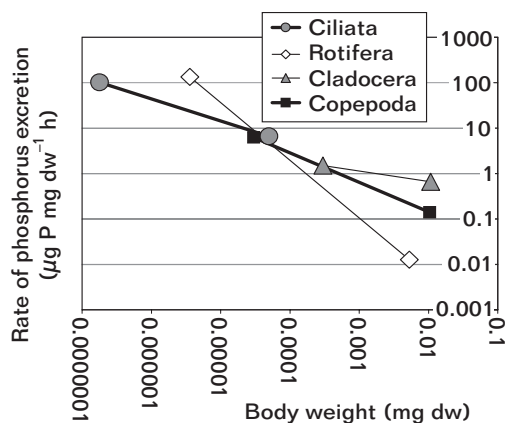


Fig. 1. Relationship between the rate of phosphorus excretion and individual body weights for four taxonomic groups of zooplankton (after Ejsmont-Karabin 1984 and Bownik-Dylińska 1981).

Table 1. Comparison of the role of *Daphnia* and other zooplankton species in phosphorus regeneration (calculated from formulas by Ejsmont-Karabin 1984 and Bownik-Dylińska 1981).

Zooplankton	Dry weight in $\mu\text{g ind.}^{-1}$	Phosphorus excretion rate in $\mu\text{g P ind.}^{-1}\text{h}^{-1}$	Number of individuals excreting the same unit of phosphorus
<i>Daphnia cucullata</i>	16.0	0.2	1
<i>Bosmina longirostris</i>	1.18	0.036	6
Calanoida	10.0	0.033	6
Cyclopoida	3.0	0.025	8
<i>Polyarthra dolichoptera</i>	0.042	0.0059	34
<i>Cyclopoid nauplii</i>	0.03	0.0045	45
<i>Synchaeta pectinata</i>	0.3	0.0035	57
<i>Coleps spetai</i>	0.006	0.0026	77
<i>Strobilidium humile</i>	0.0004	0.00064	313

the rate of phosphorus sedimentation to the bottom deposits. Small planktonic detritophages foraging on detritus with bacteria counteract P sedimentation with dead organisms or faeces. Thus P sedimentation is possible only in places and periods with low zooplankton densities and the dominance of larger phytophages (Ejsmont-Karabin *et al.* 1989).

Why then *Daphnia* are thought to clear lake water? Being a large animal *Daphnia* should not be very efficient in nutrient regeneration. However, comparison of P excretion rates by this cladoceran with other groups of animals (Fig. 1) shows that large daphnids excrete (what means also eat) more per unit of their weight than other groups of zooplankton. Though small rotifers are most efficient in the process of P remineralisation, this group consists of sedimentators feeding mainly on bacteria and detritus. Rotifers and copepods of adequate body size have their specific rates of P excretion one or two orders of magnitude lower.

Assuming that *Daphnia cucullata* Sars excrete 1 unit of phosphorus, one can calculate the number of individuals of other species that can be able to regenerate the same quantity of the nutrient (Table 1). It is clear that other groups of plankton animals should be more numerous to regenerate phosphorus in the same rate like *Daphnia*. However, it becomes also clear that the situation when smaller animals may be sufficiently numerous to take large cladocerans' place in clearing lake water is possible as well.

The aim of this paper is to test the hypothesis that small-bodied zooplankton can play the same role as large cladocerans in clearing lake water and/or that the cladocerans influence phytoplankton biomass rather indirectly through decreasing phosphorus regeneration.

## 2. METHODS

The study was carried out on five lakes in the Masurian Lakeland, north-east Poland (Table 2), differing in their depth and trophic state.

Zooplankton and phytoplankton samples were collected at the deepest sites of the lakes, from April to November 1997. Rotifer and crustacean samples were collected with a 5-litre sampler at 1m intervals and then pooled separately for epi-, meta- and hypolimnion. The samples were concentrated using a plankton net of a mesh size 30  $\mu\text{m}$  and preserved with Lugol's solution and then 4% formalin.

The species composition, numbers and biomass of ciliates and phytoplankton were determined from a sample representative of the water column or layer, composed of subsamples of 100 ml taken from each consecutive 1m. Samples were preserved with Lugol's solution and 2% formalin and analysed under the microscope after sedimentation.

About 10 individuals of each species were measured to determine the body length. The length:wet weight relationship was used to derive the mean body weight of individuals of particular crustacean (Bottrell *et al.* 1976) and rotifer (Ruttner-Kolisko 1977) species. Methods descri-

bed by Foissner and Berger (1996) were used to calculate the body weight in ciliates.

The rate of phosphorus excretion by ciliates was assessed using the regression equations:

$$E = 0.000226 e^{0.096T} W^{0.515},$$

where:  $E$  = excretion rate in  $\mu\text{g P ind.}^{-1} \text{h}^{-1}$ ,  $T$  = temperature in  $^{\circ}\text{C}$ ;  $W$  = dry weight in  $\mu\text{g}$  (Bownik-Dylińska 1981).

The remaining formulas used to calculate the excretion rate were:

$$E = 0.0154 e^{0.096T} W^{-1.27} \text{ for rotifers}$$

$E = 0.519 e^{0.039T} W^{-0.230}$  for cladocerans and

$$E = 0.299 e^{0.039T} W^{-0.645} \text{ for copepods,}$$

where:  $E$  = excretion rate in  $\mu\text{g P mg dw}^{-1} \text{h}^{-1}$ ,  $T$  = temperature in  $^{\circ}\text{C}$ ;  $W$  = dry weight in  $\mu\text{g}$  (Ejsmont-Karabin 1984).

Phytoplankton biomass was calculated on the basis of numbers and volumes of the plankton components. The phytoplankton community was divided into two size fractions: nanoplankton ( $< 30 \mu\text{m}$ ) and microplankton ( $> 30 \mu\text{m}$ ), which correspond to edible and non-edible algae.

Table 2. General characteristics of the study lakes.

Lake	Depth (m)		Area (ha)	Description
	mean	maximum		
Majcz Wielki	6.0	16.4	164	Dimictic, mesotrophic
Inulec	4.6	10.2	178	More or less stratified, eutrophic
Jorzec	5.5	11.6	42	More or less stratified, highly eutrophic
Głębokie	11.8	34.3	47	Dimictic, meso-eutrophic
Zelwążek	3.7	7.4	12	Polimictic, hypertrophic

## 3. RESULTS

The rate of phosphorus regeneration by ciliates, rotifers and crustaceans was strongly fluctuating (Fig. 2). In each of the studied lakes several sharp increases and then decreases of the regeneration rate were observed. The highest range of the fluctuations was observed in two lakes of the highest trophic, i. e. Zelwążek Lake (from 4 to 111 in ciliates, from 2 to 194 in rotifers and 3 to 63  $\text{mg P m}^{-2} \text{day}^{-1}$  in crustaceans) and Jorzec Lake (1–84, 0–109 and 4–126  $\text{mg P m}^{-2} \text{day}^{-1}$ , re-

spectively). The smallest range was noted in the lake of the lowest trophic, Majcz Wielki (5–61, 0–63 and 4–62  $\text{mg P m}^{-2} \text{day}^{-1}$ , respectively). The highest peaks were created by all three zooplankton groups: ciliates (108  $\text{mg P m}^{-2} \text{day}^{-1}$  in Głębokie Lake), rotifers (111  $\text{mg P m}^{-2} \text{day}^{-1}$  in Zelwążek Lake) and crustaceans (109  $\text{mg P m}^{-2} \text{day}^{-1}$  in Jorzec Lake). The complicated character of the seasonal dynamics is markedly different than that noted in 1976, when only one – summer peak of the regeneration rate was observed in each of the studied lakes (Ejsmont-Karabin *et al.* 1983).

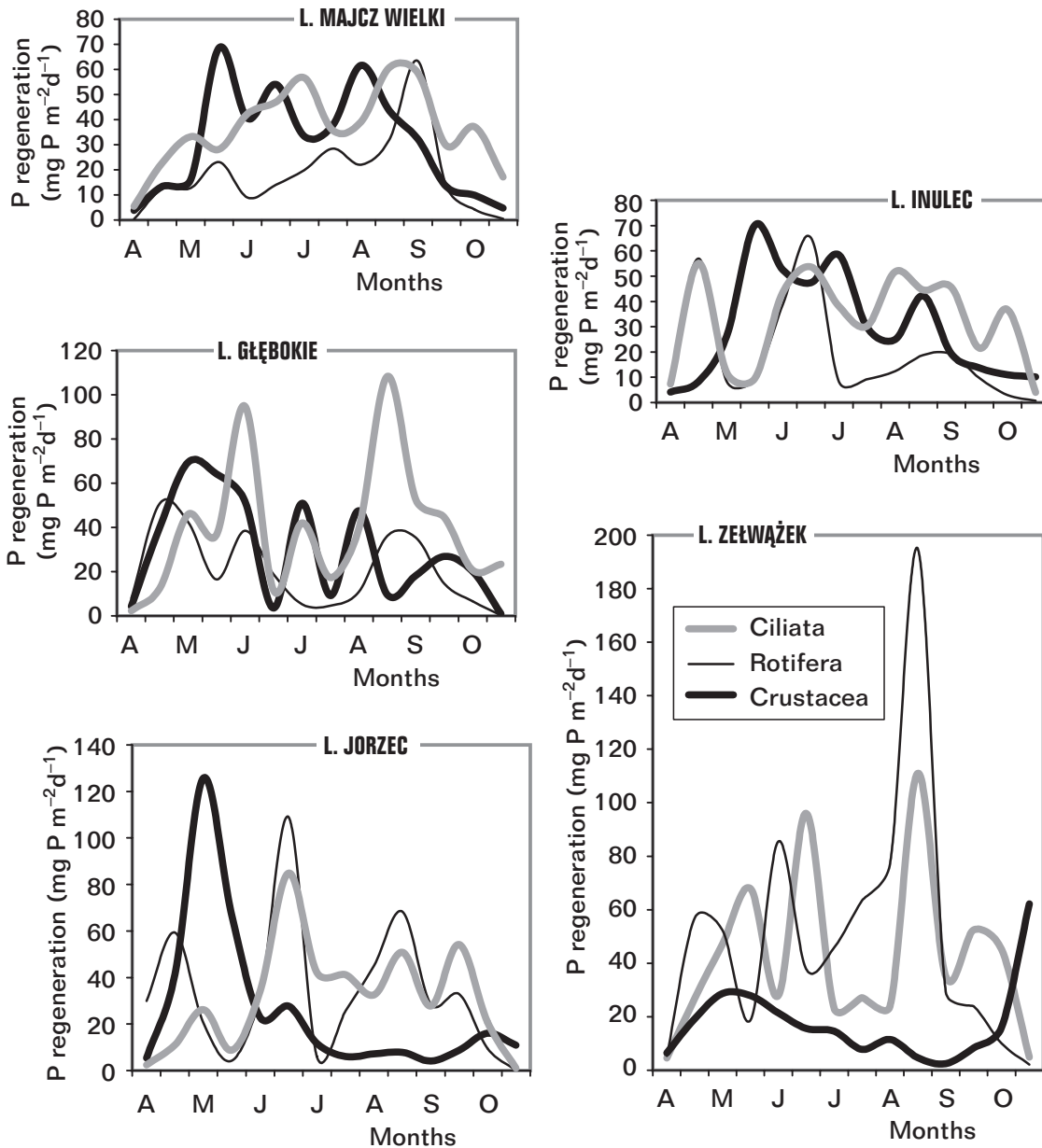


Fig. 2. Dynamics of seasonal changes in phosphorus regeneration by three taxonomic groups of zooplankton in trophogenic zone of five lakes in River Jorka (Masurian Lakeland) watershed in 1997.

In all lakes under study non-edible algae prevailed in summer. Their share in total biomass of phytoplankton ranged from 76% in Majcz Wielki Lake to 94% in Głębokie Lake). Nevertheless any increase of consumption (and thus – excretion) by herbivorous zooplankton was followed by a decrease in the net phytoplankton biomass (Fig. 3). Those summer drops in net algae biomass were particularly noticeable in lakes Jorzec, where 1.9-fold increase in regeneration coincided with 1.6-fold decrease

in biomass of net-algae, Zełwążek (2-fold increase of regeneration and 1.7-fold decrease in algae biomass) and Głębokie (2.5-fold increase of P regeneration and 4-fold decrease in net algae biomass). Similar tendency (however in this case much easier to explain) may be seen in a relation between the dynamics of P regeneration rate and nanophytoplankton biomass. Summer drops of edible fraction of phytoplankton occurred concurrently to decreases in net phytoplankton biomass and were 3.1-, 2.8- and 4.5-fold,

respectively (Fig. 3). Lake Majcz Wielki is the only lake where the increase in regeneration rate of phosphorus coincides with

the increase of biomass both edible and non-edible algae.

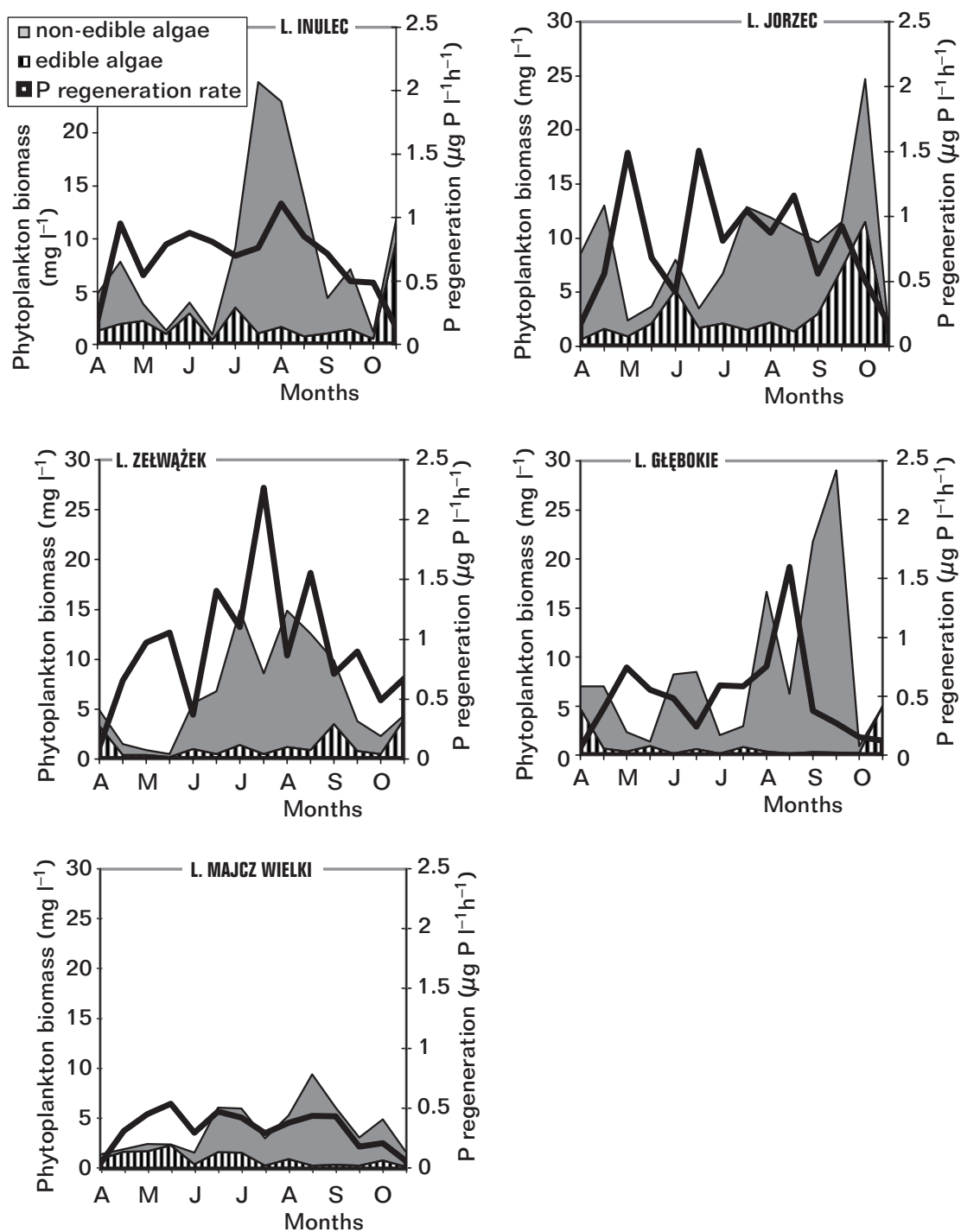


Fig. 3. Relation between P regeneration by herbivorous zooplankton and biomass of edible and non-edible phytoplankton in trophogenic zone of five lakes in River Jorka watershed in 1997.

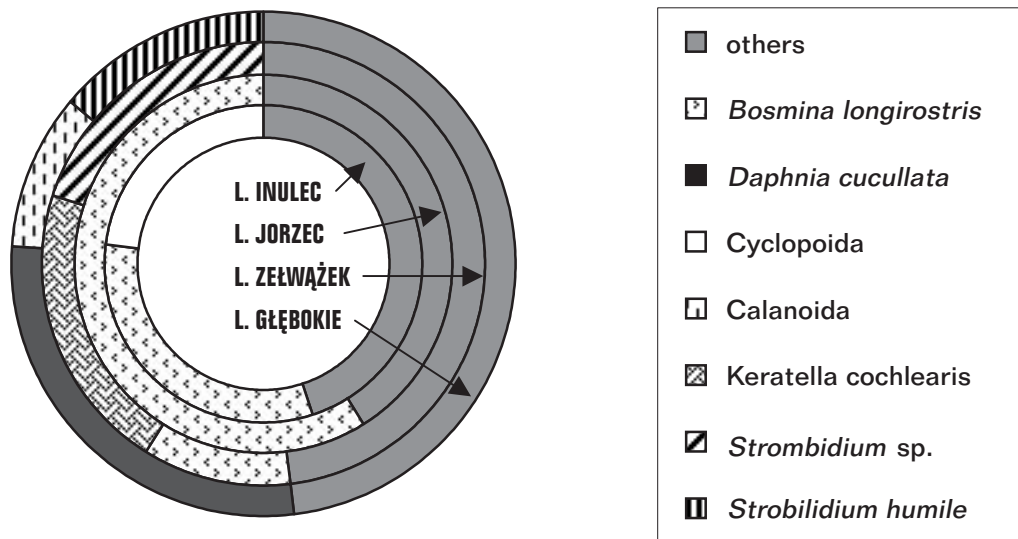


Fig. 4. The role of dominant zooplankton species in P regeneration at the time of the lowest values of chlorophyll *a* concentrations in four lakes of the River Jorka watershed.

However, very different zooplankton taxa play a role in causing the rapid drop in algal biomass in late spring (leading to so called "clear water phase") (Fig. 4). Lake Majcz Wielki seems to be permanently "a clear water lake" and phytoplankton biomass is there rather low in all winter and spring months, i.e. below 3 mg ww l<sup>-1</sup> (Fig. 3). *Daphnia cucullata* played more significant role (excreting 28% of the regenerated P) during "clear water phase" only in one lake – deep and less eutrophicated Lake Głębokie (Fig. 4). But even there the species was competing for food with calanoids (10% of the regenerated P) and ciliate species *Strobilidium humile* Penard (14%). In more eutrophicated lakes Inulec, Jorzec and Żelwążek a small cladoceran *Bosmina longirostris* (O. F. Müller) has weaker or stronger impact on algae excreting from 11 to 59% of the regenerated P. In Lake Inulec younger stages of cyclopoids played important role as well (23%). In Lake Żelwążek phosphorus was regenerated in high rate by detritivorous *Keratella cochlearis* (Gosse) (21%), and the process should counteract sedimentation of P build up into phytoplankton biomass (Ejsmont-Karabin *et al.* 1989).

*Daphnia cucullata* played significant role in P regeneration (and thus edible algae consumption) in no one of the studied lakes during the whole study period (Fig. 5). However, each increase in P regeneration by *Daphnia* clearly coincided with rapid decreases in biomass of edible algae. The ro-

le of the cladoceran in P regeneration was markedly lower in more eutrophicated lakes Jorzec and Żelwążek (Fig. 5).

#### 4. DISCUSSION

The general hypothesis based on the cascading model by Carpenter *et al.* (1985) and the biomanipulation model by Shapiro *et al.* (1982) says that changes in fish communities cascade down through the food web to influence primary producers. The hypothesis has been supported by very many field and enclosure studies (Christoffersen *et al.* 1993, De Melo *et al.* 1992). However McQueen *et al.* (1992) studying long-term and short-term trends in relationships between several trophic levels found that though in long-term studies the relationship between densities of planktivores and zooplankton were always negative, the relationships between the abundance of zooplankton and phytoplankton were unpredictable and insignificant. In short-time studies, strong top-down relationships between zooplankton and chlorophyll occurred but they were unpredictable and usually not fish influenced.

Taking into account that in five lakes described above decreases in phytoplankton density coincided with the increasing role of large and small cladocerans, rotifers and ciliates (Fig. 4), some of them never being influenced indirectly by fish, unpre-

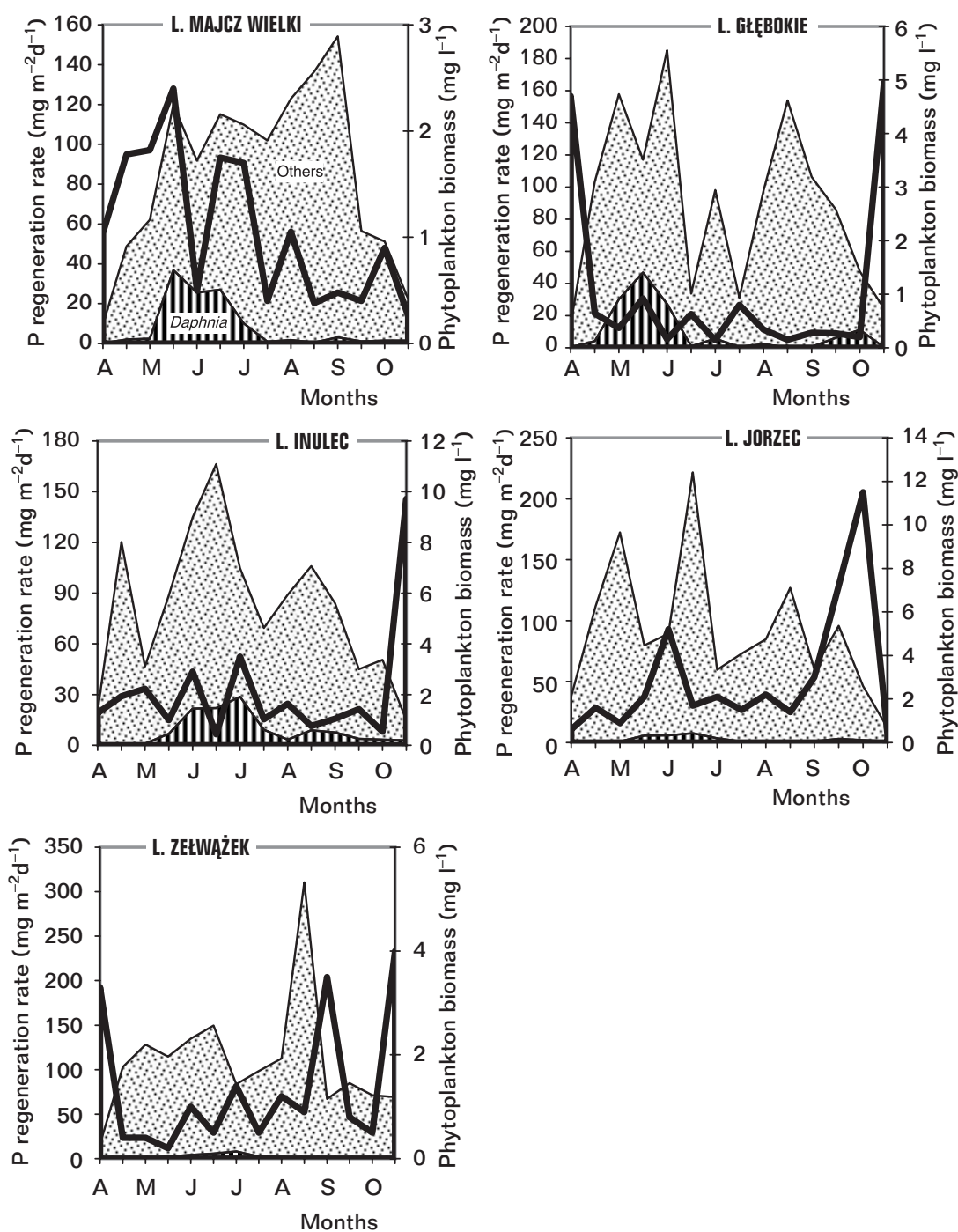


Fig. 5. Seasonal changes of phosphorus regeneration rate by *Daphnia* spp and the remaining groups of zooplankton versus biomass of edible algae in trophogenic zone of five lakes.

dictability of short-term relations between trophic levels is easy to understand. The role of rotifers and ciliates in lakes heavily influenced by planktivorous fish has been beyond the interest of “biomanipulation researchers” but some observations support-

ing the possibility of small cladocerans playing an important role in fish stocked lakes were published by Sarvala *et al.* (1998). If small herbivorous zooplankton can do the same what large cladocerans do and the only condition is to achieve an appropriate

density, then one should be able to find at least one case of phytoplankton controlled by small zooplankton. A phenomenon of this kind was observed in the shallow, covered with macrophytes Lake Łuknajno – one of the Great Masurian Lakes (Northern Poland) (Karabin *et al.* 1997).

In complex studies on phyto- and zooplankton of Lake Łuknajno a rapid decrease in chlorophyll a concentrations was observed in May 1993. At that time P regeneration rate (and so consumption rate) by herbivores increased. Animals responsible for the chlorophyll decrease were rotifers of the genera *Polyarthra* and *Synchaeta* at the beginning of May and *Bosmina longirostris* in the second half of May (Ejsmont-Karabin *et al.* 1996, Karabin *et al.* 1997).

Another fact that makes trophic relations even more complicated is that at each trophic level consumption of organic matter leads to nutrient regeneration. Thus high zooplankton biomass may stimulate both primary and bacterial production because algae and bacteria can balance grazing losses by compensatory growth (Reche *et al.* 1997).

It seems however clear that although different larger and smaller crustaceans, rotifers, ciliates (Ejsmont-Karabin *et al.* 1983) and planktonic flagellates (Dolan 1997) can be equally active in phosphorus excretion, large *Daphnia* are most efficient in lake water clearing (Christoffersen *et al.* 1993).

This special role of *Daphnia* in producing clear water state is evidenced in many papers showing that replacement of small cladocerans with *Daphnia* increased filtration rates to > 200% (Hanson and Butler 1994), 100–140% (Shapiro and Wright 1984) and 100–200% (Gulati 1989). Large cladocerans like *Daphnia* seem also to be the most important factor regulating ciliate communities and their responses to nutrients and resources. Marchessault and Mazumder (1997) have observed that shifts of zooplankton from copepods to *Daphnia* dominance may result in large reductions in ciliate abundance.

Thus the special role of large cladocerans in clearing lake water can be explained by their combined direct and indirect impact on nutrient sedimentation or exclusion from cycling – as only nutrients excluded from internal cycling are deposited into bottom sediments (Ejsmont-Karabin *et*

*al.* 1989). “Efficient” large-sized cladocerans (Gliwicz 1977) clear lake water from algae at a rate higher than primary production (direct impact). They also suppress small detritophagous zooplankton (rotifers and protists) (Christoffersen *et al.* 1993) both directly (predation, interference) and indirectly (resource competition) (Jack and Gilbert 1994). In the absence of zooplankton and thus lack of nutrient regeneration by zooplankton, deficiency of available nutrients increases the mortality of algae and their sedimentation (indirect effect) (Ejsmont-Karabin *et al.* 1989). These two mechanisms accelerate sedimentation of nutrients into bottom deposits.

Results of Lampert and Rothhaupt (1991) studies in a shallow hypertrophic lake support the above statement. The authors observed a clear coincidence of *Daphnia* biomass peaks with clear water phases and reduced concentrations of sestonic carbon. At the same time rotifer densities were negatively correlated with *Daphnia* and positively – with particulate organic carbon.

In conclusion, the results from five lakes of different trophic clearly show that small-bodied zooplankton can play important role in clearing lake water, however large cladocerans (if present) are more efficient in controlling phytoplankton biomass. This special role of large cladocerans in clearing lake water can be explained by their combined direct (clearing lake water from algae at a rate higher than primary production) and indirect (suppression of rotifers and protists by predation, interference and resource competition) impact on internal cycle of nutrients.

## 5. SUMMARY

The aim of this paper is to test the hypothesis that small-bodied zooplankton can play the same role as large cladocerans in clearing lake water and/or that the cladocerans influence phytoplankton biomass rather indirectly through decreasing phosphorus regeneration. The hypothesis is derived from the well known relationship between the rate of phosphorus excretion by different groups of zooplankton and their body weights (Fig. 1) and the calculation of the number of different zooplankton species able to regenerate nutrient quantity equal to the quantity regenerated by one *Daphnia* (Table 1). It is assumed that small plankton animals should be more numerous to regenerate phosphorus in the same rate like *Daphnia* but the situation when

smaller animals may be sufficiently numerous to take large cladocerans' place in clearing lake water is possible as well.

The study was carried out on five lakes in the Masurian Lakeland, Poland (Table 2), differing in their depth and trophic state. The rate of phosphorus excretion was assessed using the regression equations describing its dependence on body weights of ciliates, rotifers and crustaceans and ambient temperature.

The rate of phosphorus regeneration by ciliates, rotifers and crustaceans was strongly fluctuating (Fig. 2) and more or less similar. Any increase of P excretion by herbivorous zooplankton was followed by a decrease in the net phytoplankton biomass (Fig. 3). Similar tendency was observed in a relation between the dynamics of P regeneration rate and nano-phytoplankton biomass.

Different zooplankton taxa played a role in causing the rapid drop in algal biomass in late spring (leading to so called "clear water phase") (Fig. 4). *Daphnia cuculata* played significant role in P regeneration (and thus edible algae consumption) in no one of the studied lakes during the whole study period (Fig. 5), but each increase in P regeneration by *Daphnia* coincided with rapid decreases in biomass of edible algae.

The results from five lakes of different trophicity showed that small-bodied zooplankton can play important role in clearing lake water, however large cladocerans (if present) are more efficient in controlling phytoplankton biomass. This special role of large cladocerans in clearing lake water can be explained by their combined direct (clearing lake water from algae at a rate higher than primary production) and indirect (suppression of rotifers and protists by predation, interference and resource competition) impact on internal cycle of nutrients.

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