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ABUNDANCE AND STRUCTURE OF PLANKTONIC CRUSTACEAN COMMUNITY OF A HUMIC LAKE SMOLAK TWENTY YEARS AFTER THE EXPERIMENTAL MINERAL FERTILISATION

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ABSTRACT. Planktonic crustacean community of a humic Smolak Lake responded to liming and mineral fertilisation (N, P, K) carried out in 1971-1974 with a strong increase of numbers and biomass, as well as a change of species composition and trophic structure, indicating eutrophication of the lake. Discontinuation of fertilisation did not considerably affect the community. Twenty years after the nutrient supply, high density and biomass of crustaceans are still observed. The community is dominated by small, detritivorous cladocerans (*Chydorus sphaericus* and *Bosmina longirostris*), and predatory Cyclopoida typically found in productive, alkaline waters.

Key words: CRUSTACEA, HUMIC LAKE, LIMING, FERTILISATION, N, P, K

INTRODUCTION

Dystrophic, humic lakes are usually very sensitive to any anthropogenic impacts involving acidification and nutrient supply. Their sensitivity results from small size of these lakes, poor buffering capacity, and closed hydrologic cycle. Eutrophication is favoured by „oligotrophic“ status of humic lakes, naturally poor in nutrients (nitrogen and phosphorus), which prevents algal blooms and promotes high water transparency. Such sensitivity used to be observed in Smolak Lake, which in 1971-1974 was subjected to experimental liming and fertilisation (N, P, K), simulating eutrophication. The treatment resulted in many considerable changes of water chemistry and bottom sediments, 2-3 fold increase of gross primary production, and changes of abundance and composition of phytoplankton and macrophytes (Zdanowski 1976, 1982, Zdanowski et al. 1975, 1978, Hillbricht-Ilkowska, Zdanowski 1983). Zooplankton community responded to mineral fertilisation with strong, immediate increase of the density and considerable change of species and trophic structure, indicating water eutrophication (Węgleńska et al. 1975, Ejsmont-Karabin et al. 1980). Discontinuation of the nutrient supply, did not cause serious changes of

abundance and community structure of Lake Smolak crustaceans in the first years after the experiment (Ejsmont-Karabin, Węgleńska 1985). It is still not clear, however, whether the effect of liming and fertilisation is stable, lasting for only several, or for many years.

The aim of the present study was a qualitative and quantitative assessment of planktonic crustacean community in Smolak Lake twenty years after the fertilisation.

STUDY AREA, MATERIAL, METHODS

The study was performed in a small (5.3 ha, maximum depth 5.1 m, average depth 2.4 m, total volume $125.9 \times 10^3 \text{ m}^3$), forest, humic Lake Smolak, originally acidic (pH 4.6), and at present neutral (pH 7-8), situated in Masurian Lakeland. For detailed description of the lake see Zdanowski and Hutorowicz (1998).

Zooplankton was sampled in 1990-1995, from three to nine times per season, using 5 dm³ Bernatowicz sampler, every 1 m at the deepest point of the lake. Samples were pooled and filtered through a plankton net of mesh size 30 µm, and preserved with Lugol solution and 5% formaldehyde. They were analysed using standard methods (Hillbricht-Ilkowska, Patalas 1967). Biomass of particular crustacean species was estimated using the equation describing the length-weight relationship (Bottrell et al. 1976). Shannon-Weaver index (Margalef 1957) was used to calculate species diversity of the community:

$$D = -\sum n_i / N \log n_i / N$$

where:

N – total number of individuals of all species,

n_i – number of individuals of the i species.

Percentage Similarity index of the community (PSc) was calculated according to the formula:

$$PSc = 100 - 0.5 \sum (a-b) = \sum_{min.} (a,b)$$

where:

a and b – percentage of individuals of each species in total numbers of the communities observed in years A and B, compared in pairs (Whittaker, Fairbanks 1958).

The results of the earlier studies (Ejsmont-Karabin et al. 1980 and Ejsmont-Karabin, Węgleńska 1985) were also used in the present paper.

RESULTS

Before the beginning of fertilisation and liming (1970), numbers and biomass of planktonic crustacean community of Smolak Lake were low, on the average 56 ind. and 1.2 mg per dm^3 , and maximum 85 ind. and 2 mg per dm^3 respectively. These values are typical of moderately acidic and little productive lakes. Fertilisation resulted in an immediate and considerable increase of the numbers and biomass of crustaceans. During four years of the treatment, average and maximum numbers increased 4 and 10 fold respectively, and the biomass – 2 and 6 fold (Tab. I-IV).

When fertilisation was discontinued, crustacean number and biomass remained very high. Maximum numbers (about 1500 ind. dm^{-3}) and biomass (about 17 mg dm^{-3}) were observed in 1995 (Tab. I).

Comparison of seasonal changes of crustacean numbers and biomass in the control year (1970), the last year of fertilisation (1974), and the last year of this study (1995) revealed that seasonal dynamics differed in particular years (Fig. 1). In 1970 the numbers and biomass of crustaceans remained very low over the entire season (about 10-80 ind. and 2 mg per dm^3). In 1974, after fertilisation, considerable increase of crustacean density took place in early summer and autumn. Maximum number (over 1000 ind. dm^{-3}) was observed in mid-June, and maximum biomass (over 14 mg

TABLE I

Average and maximum (in parentheses) number (N, ind. dm^{-3}), biomass (B, mg dm^{-3} of fresh mass) and average individual body weight (C, mg) of planktonic crustaceans in Smolak Lake in 1970-1995 (March-October).

	Year	N	B	C
Control	1970	56(85)	1.2(2.0)	0.027
Fertilisation NPK + Ca	1971	68(250)	2.0(7.8)	0.029
	1972	137(1020)	2.4(13.1)	0.017
	1973	170(515)	2.5(8.0)	0.015
	1974	200(1000)	3.2(14.7)	0.016
After fertilisation 1 year	1975	158 (390)	3.0 (4.2)	0.013
After fertilisation 19-21 year	1993	283 (535)	2.1 (5.0)	0.007
	1994	262 (560)	2.4 (4.8)	0.009
	1995	338 (1580)	2.9 (17.2)	0.008

TABLE II

Number of particular taxa (ind. dm⁻³) and planktonic crustacean community structure in Smolak Lake during spring turnover (March-May) in 1970-1972, 1990-1995

Taxon	Control	Fertilisation					After fertilisation		
	1970	1971	1972	1990	1991	1992	1993	1994	1995
<i>Cyclopoida</i>	5.0	5.0	2.0	86.0	49.0	67.0	196.0	42.3	57.0
<i>Calanoida</i>	5.0	15.0	3.0	2.0	2.6	1.2	6.2	6.4	
<i>Ceriodaphnia quadrangula</i>	0.5	45.0					8.0	1.3	0.1
<i>Bosmina longirostris</i>	0.5						62.7	25.2	0.1
<i>Bosmina coregoni thersites</i>				1.0					
<i>Chydorus sphaericus</i>								0.9	11.0
Total number	10.5	65.5	16.0	88.0	51.6	68.2	274.8	86.2	57.2
Number of species	3	5	5	3	3	5	8	8	5
Species diversity index (D)	0.3	0.5	0.5	0.4	0.3	0.4	0.9	0.9	0.7

TABLE III

Number of particular taxa (ind. dm⁻³) and planktonic crustacean community structure in Smolak Lake during summer stagnation (June-August) in 1970-1972, 1990-1995

Taxon	Control	Fertilisation					After fertilisation		
	1970	1971	1972	1990	1991	1992	1993	1994	1995
<i>Cyclopoida</i>	5.0	2.1	20.6	87.4	25.4	61.0	91.6	166.4	247.0
<i>Calanoida</i>	10.0	18.3	5.2	34.3	14.4	0.2	15.4	2.9	
<i>Ceriodaphnia quadrangula</i>	70.0	230.0	10.0	92.9	25.2	50.0	191.4	197.6	1.7
<i>Bosmina longirostris</i>	0.2	3.2	120.2	5.0	17.6	326.6	23.3	130.7	136.6
<i>Bosmina coregoni thersites</i>		10.0	0.2						
<i>Diaphanosoma brachyurum</i>			2.0	0.9	1.2	4.0	0.3		0.8
<i>Daphnia sp.</i>				0.9	2.4	0.2	1.0	1.5	
<i>Chydorus sphaericus</i>		0.2	0.4	0.4	1.2	4.0	3.7	8.8	62.4
Total number	85.2	263.8	168.6	221.8	87.4	446.0	326.7	507.9	448.2
Number of species	4	6	20	9	10	12	10	8	7
Species diversity index (D)	0.4	0.5	1.2	2.1	2.2	2.5	2.4	1.8	1.9

dm⁻³) in late August. In 1995, the highest numbers (over 1500 ind. dm⁻³) and biomass (about 17 mg dm⁻³) were observed in autumn.

In 1970 planktonic crustacean community structure was typical of moderately acidic lakes (Patalas, Patalas 1968, Roff, Kwiatkowski 1977, Stenson 1985). This was reflected in poor species composition (4 species) and homogenous taxonomic structure, with one dominant only (*Ceriodaphnia quadrangula* O. F. Müller). Simple dominance structure of planktonic crustacean community and low number of species

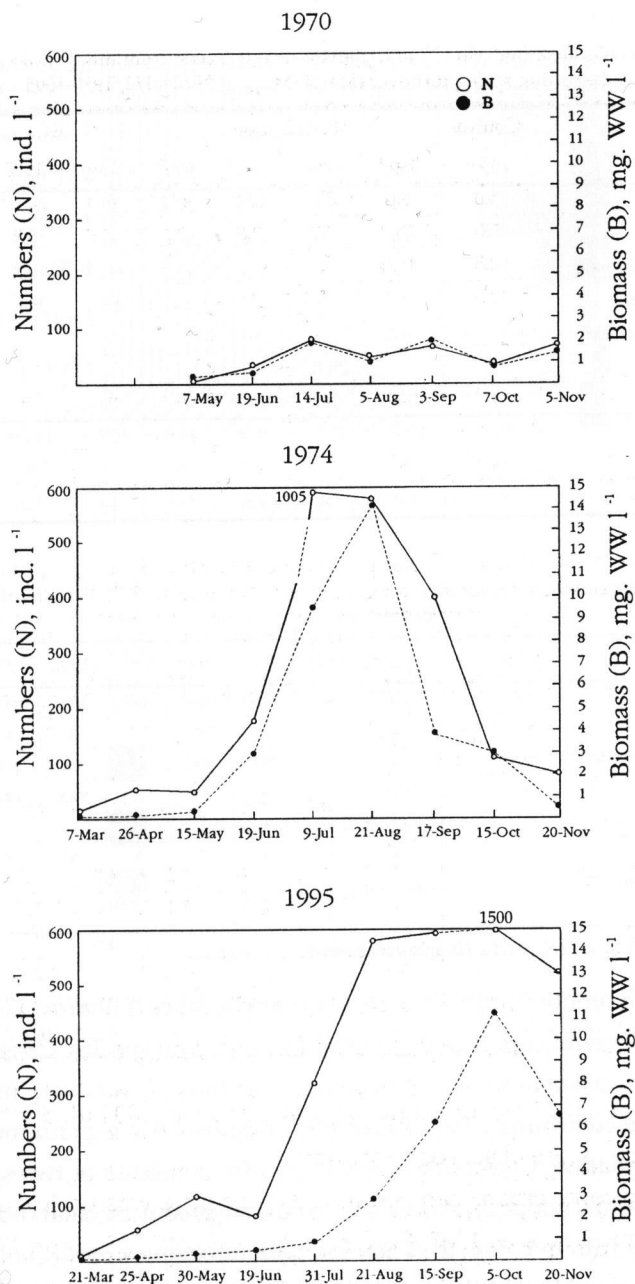


Fig. 1. Seasonal dynamics of Smolak Lake crustacean number and biomass, in the control year before fertilisation (1970), last year of fertilisation (1974), and 20 years after the treatment (1995)

TABLE IV

Number of particular taxa (ind. dm⁻³) and planktonic crustacean community structure in Smolak Lake during autumn turnover (September-November) in 1970-1972, 1990-1995

Taxon	Control	Fertilisation					After fertilisation			
	1970	1971	1972	1990	1991	1992	1993	1994	1995	
<i>Cyclopoida</i>	25.0	0.6	6.0	69.0	27.4	35.7	36.6	236.0	137.0	
<i>Calanoida</i>	2.0	6.0	5.0	6.0	3.6	6.3	12.5	2.4		
<i>Ceriodaphnia quadrangula</i>	55.0	0.2		0.3	10.0	69.7	99.3	40.0	5.3	
<i>Bosmina longirostris</i>			1.5	1.1	3.6	15.6	0.4	0.8	634.0	
<i>Bosmina coregoni thersites</i>		15.0								
<i>Daphnia</i> sp.			25.0				1.1		1.4	
<i>Chydorus sphaericus</i>	0.2	0.4	0.2			0.6				
Total number	82.2	22.2	37.3	76.4	44.6	127.3	149.9	279.2	778.0	
Number of species	4	5	6	6	6	7	8	6	6	
Species diversity index (D)	0.5	1.0	1.1	0.9	0.8	1.6	1.2	1.6	1.1	

TABLE V

Species structure of planktonic crustacean community in 1970 (control), 1971-1974 (fertilisation), and 1990-1995 (after fertilisation)

Taxon	1970	1971	1972	1973	1974	1990	1991	1992	1993	1994	1995
<i>Cyclopoida</i>	xx	x	xx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx
<i>Calanoida</i>	xx	xx	x	xx	x	x	x	x	x	*	
<i>Ceriodaphnia quadrangula</i>	xxx	xxx	x	x	x	xx	xx	xx	xx	xxx	*
<i>Bosmina longirostris</i>	x	x	xxx	x	xx	xx	xxx	xxx	xxx	xxx	xxx
<i>Bosmina coregoni thersites</i>		x	x	x	x						
<i>Daphnia</i> sp.		*	x	x	x	*	x	x	x	x	x
<i>Diaphanosoma brachyurum</i>		*	x		*	x	x	x	x	x	x
<i>Chydorus sphaericus</i>		x	*	x	*	*	*	*	*	x	xx

xxx - 20%, xx - 11-20%, x - 1-10%, * - 1% of total numbers

resulted in low diversity (under 1), typical for acidic lakes (Giliarov, Gorelova 1974) (Tab. II-IV). Cladoceran community consisted of only two species: *Ceriodaphnia quadrangula* and *Bosmina longirostris* O. F. Müller. *C. quadrangula* was very numerous and dominated in the community (60-90% of total number) during summer stagnation and autumn circulation. Copepoda community also consisted of two species only – predatory cyclopoid *Cyclops strenuus* Fisch., and non-predatory calanoid *Eudiaptomus graciloides* (Lillj.) (Tab. II-V, Fig. 2). They are both eurytopic species, tolerating wide range of environmental conditions, especially as regards food resources. Very typical for Smolak Lake crustacean community in 1970 was, similarly as in the case of rotifers, a complete lack of acidophilic species (Berzins, Bertilsson 1990).

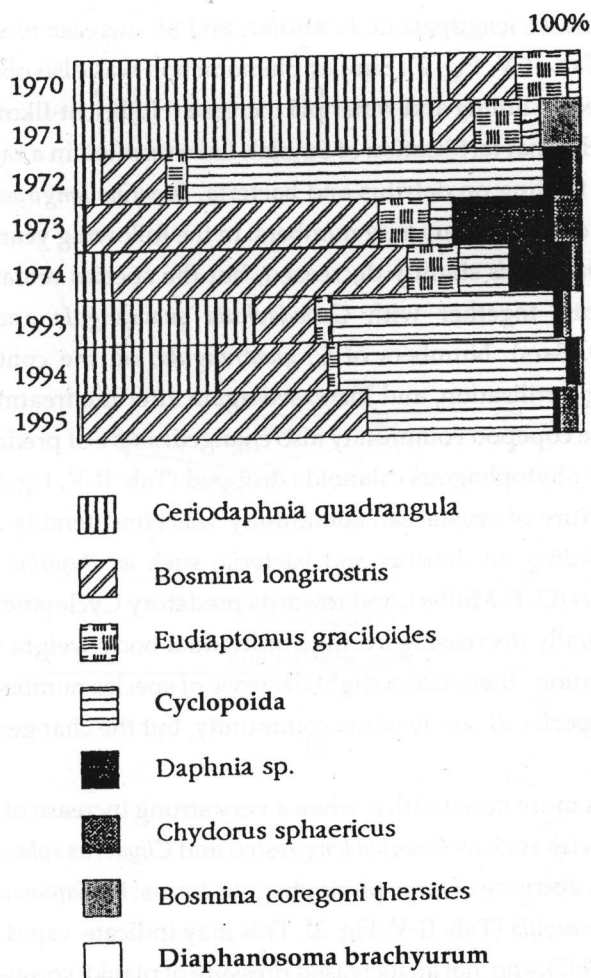


Fig. 2. Dominance structure (%) of particular crustacean taxa in Smolak Lake in the control year (1970), during fertilisation (1971-1974), and in selected years after the treatment (1993-1995)

In trophic structure of crustacean community in the control year, phytophagous forms dominated, mainly macro filtrators (*Eudiaptomus graciloides*), and efficient micro filtrators (*Ceriodaphnia quadrangula*), as well as facultative predators (*Cyclops strenuus*). For all these species, phytoplankton is the unique or the main source of food (Geller, Müller 1981).

Direct effect of water pH increase in Smolak Lake during the treatment was an increase of species numbers, especially appearance of two *Daphnia* species: *D. cucul-*

lata G. O. Sars, and *D. longispina* O. F. Müller, and an increase of species diversity index (over 2) (Tab. II-V, Fig. 2). Similar phenomenon was also observed in humic Lake Flosek subject to liming and water pH increase (Hillbricht-Ilkowska et al. 1977).

It is noteworthy that fertilisation of Smolak Lake resulted in a rapid increase of a common species feeding on detritus and bacteria, *Bosmina longirostris*, which comprised up to 90% of total community numbers. In the following years of fertilisation, numbers of *B. longirostris* slightly decreased, but the species remained among the three codominants, together with *Ceriodaphnia quadrangula* and *Thermocyclops oithonoides* (G. O. Sars). Numbers of *C. quadrangula*, on the contrary, gradually decreased during fertilisation, and increased again after the treatment. Taxonomic composition of the copepod community also changed: share of predatory cyclopoids increased, and of phytophagous calanoids dropped (Tab. II-V, Fig. 2).

Trophic structure of crustacean community was considerably altered towards small species feeding on detritus and bacteria, such as *Bosmina longirostris* and *Chydorus sphaericus* (O. F. Müller), and towards predatory Cyclopoida. This was confirmed by a gradually decreasing average individual body weight (Tab. I). Several years after fertilisation, there was a slight decrease of species numbers, accompanied by a decrease of species diversity of the community, but the changes were not significant (Tab. II-IV).

Year 1995 was more noteworthy, when a very strong increase of abundance and share of small species such as *Bosmina longirostris* and *Chydorus sphaericus* took place, accompanied by a decrease of large phytophagous forms: *Eudiaptomus graciloides* and *Ceriodaphnia quadrangula* (Tab. II-V, Fig. 2). This may indicate rapid increase of lake trophity (Karabin 1985), and not an increased pressure of planktivorous fish on the zooplankton, as their density in Smolak Lake was low (Zdanowski, Hutorowicz 1998).

The changes observed in Lake Smolak in the post-fertilisation period are also reflected in the index of Percentage Similarity of community (PSc), calculated for particular years in two series:

- for pairs: control year (1970) – next years (Fig. 3A),
- for pairs: last year of study (1995) – previous years (Fig. 3B).

Index values were calculated for summer and autumn crustacean communities.

Similarly as in the case of rotifers, summer and autumn crustacean communities of Smolak Lake in all years of fertilisation and afterwards considerably differed from the communities observed in the control year (Fig. 3A, B).

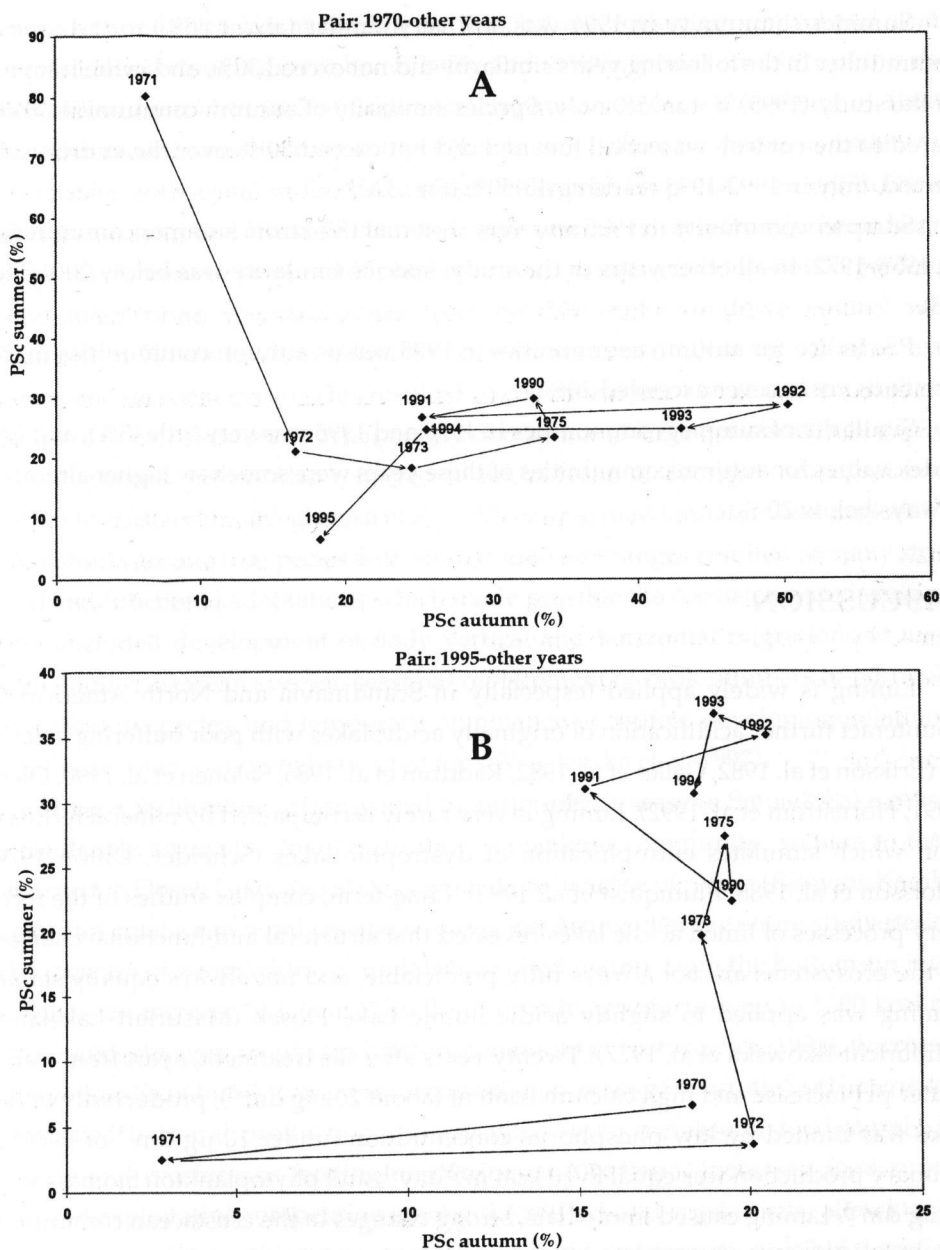


Fig. 3. Long-term changes of summer-to-autumn values of Percentage Similarity of community index (PSc) calculated for pairs: crustacean communities in 1970 versus communities in the following years (A), and: communities in 1995 versus communities in the previous years (B)

Summer community in 1991 was still very similar (about 80%) to the control community. In the following years similarity did not exceed 30%, and in the last year of the study (1995) it was 5% only. Species similarity of autumn communities compared to the control was small too, and did not exceed 30 % over the entire study period, only in 1992-1993 reaching 40-50% (Fig. 3A).

Summer community in 1995 was very different (5%) from summer communities in 1970-1972. In all other years of the study, species similarity was below 20% (Fig. 3B).

PSc index for autumn communities in 1995 versus autumn communities in the previous years never exceeded 20%.

Similarity of summer communities in 1970 and 1995 was very little (5%), and PSc index values for autumn communities of these years were somehow higher although always below 20 %.

DISCUSSION

Liming is widely applied (especially in Scandinavia and North America) to counteract further acidification of originally acidic lakes with poor buffering capacity (Erikson et al. 1982, Geller et al. 1982, Raddum et al. 1986, Salonen et al. 1990, Olem 1991, Hornstrom et al. 1992). Liming is very rarely accompanied by mineral fertilisation which simulates eutrophication of dystrophic lakes (Scheider, Dillon 1976, Olofsson et al. 1988, Blumquist et al. 1993). Long-term, complex studies of the recovery processes of limed acidic lakes revealed that structural and functional changes in the ecosystems are not always fully predictable, and not always equally stable. Liming was applied to slightly acidic humic Lake Flosek (Masurian Lakeland) (Hillbricht-Ilkowska et al. 1977). Twenty years after the treatment, apart from stable water pH increase and high calcium content (about 20 mg dm^{-3}), productivity of the lake was limited by low phosphorus concentration (under $10 \text{ } \mu\text{g dm}^{-3}$ of P-PO_4). Primary production was equal to $10 \text{ kcal m}^{-2} \text{ day}^{-1}$, and phytoplankton biomass to $1\text{--}5 \text{ mg dm}^{-3}$. Liming caused immediate, strong changes in the crustacean community structure: increase of species number from 4 to 12, and increase of species diversity above 2.5. These changes were not accompanied by any increase of crustacean numbers and biomass. Appearance of large *Daphnia* species was a direct effect of water pH increase. Most structural and functional changes observed in Lake Flosek after

liming resulted from biocenotic interactions. Strong bottom-up control and severe food limitation resulting from low density and simple species structure of the phytoplankton (dominance of dinoflagellates, and low share of „edible algae“ of diameter under 20 μm) caused strong competition among particular species of rotifers and crustaceans with a similar food size range (Hillbricht-Ilkowska et al. 1977). On the other hand, temporal increase of invertebrate predators' density (Cyclopoida and *Chaoborus flavicans* larvae), and of planktivorous fish intensified top-down (predator-prey) interactions. Rapid changes from bottom-up to top-down control were observed in Flosek Lake in a limited time-scale (in the following years, or even within one seasonal cycle). This resulted in codominance of large and small planktonic crustacean filtrators or in temporary dominance of large genera such as *Daphnia* or *Eudiaptomus*. It was also reflected in an increase of average individual body weight of crustaceans (Węgleńska et al. 1997). Strong food limitation and exploitative competition among the species with similar food size ranges resulted in many structural and functional adaptations which made possible the coexistence and survival. They included development of daily vertical and horizontal migrations of many rotifer and crustacean species, seasonal replacement of peak numbers of particular zooplankton species, and temporary dominance of rotifers developing gelatinous sheaths, resistant to invertebrate predators (Węgleńska et al. 1997).

Mineral fertilisation accompanied by water pH increase in Smolak Lake caused considerable structural changes in the zooplankton community, similar to those observed in Flosek Lake, and strong, immediate increase of rotifer (Ejsmont-Karabin 1998) and crustacean numbers and biomass, persisting over the entire study period. The increase of zooplankton abundance resulted mainly from the bottom-up interactions – an increase of lake trophic (high primary production up to 1500 kcal $\text{m}^{-2} \text{day}^{-1}$, and changes in phytoplankton community, Hutorowicz 1998). Increased mineralisation of humic compounds caused an increase of substrate for bacteria and intensified bacterial production. This resulted in an increase of food supply for rotifers and crustaceans feeding on detritus and bacteria. Increased food supply reduced exploitative competition among the rotifers and crustaceans, allowing for their increase. Competition among small and large cladocerans possibly decreased as well (contrary to Flosek Lake), since large *Daphnia* species which appeared after water pH increase did not compete with small cladocerans: *Bosmina longirostris* and *Chydorus sphaericus*. Large planktonic filtrators such as *Daphnia* and *Eudiaptomus* out-

compete (thanks to higher feeding efficiency at lower threshold food concentration) small crustaceans only under conditions of food depletion or unstable concentration. Such situation occurred in Lake Flosek. Abundant food resources in Smolak Lake favoured small species of faster development and reproduction rate (De Mott 1989, Gliwicz 1990). In the zooplankton community of Smolak Lake, mechanical interference (destruction of rotifer in cladoceran filter apparatuses) was unlikely (Gilbert 1988) as the density of *Daphnia* sp. never exceeded several individuals per dm³. Reduced number of predatory rotifers (Ejsmont-Karabin 1998) and large carnivorous copepods indicates weaker, comparing to Flosek Lake, top-down control – invertebrate predation upon zooplankton.

All these observations contribute to the explanation of the differences in structure and functioning between zooplankton communities of the two humic lakes: Flosek and Smolak, subjected to liming and mineral fertilisation. Changes in planktonic crustacean community of Flosek Lake after liming were partly reversible (species number and diversity decreased, so did the number of crustaceans and share of Cyclopoida in copepod community) (Węgleńska et al. 1997). In Smolak Lake, on the contrary, no recovery was observed after treatment.

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STRESZCZENIE

OBFITOŚĆ I STRUKTURA ZESPOŁU SKORUPIAKÓW PLANKTONOWYCH (*Crustacea*) W HUMUSOWYM JEZIORZE SMOLAK PO DWUDZIESTU LATACH OD ZAKOŃCZENIA EKSPERYMENTU NAWOŻENIA MINERALNEGO

Badania prowadzono w płytkim, humusowym, śródleśnym jeziorze Smolak. Jezioro to w latach 1971-1974 zostało poddane zabiegowi wapnowania i nawożenia (N, P, K) symulującym procesy eutrofizacji.

Nawożenie mineralne spowodowało natychmiastowy, silny (kilkakrotny) wzrost liczebności i biomasy skorupiaków planktonowych. Wysoka liczebność i biomasa tego zespołu utrzymywała się nieprzerwanie przez dwadzieścia lat od zakończenia zabiegu nawożenia (Tabela 1). Sezonowa dynamika liczebności i biomasy skorupiaków w roku kontrolnym (1970) istotnie różniła się od obserwowanej w latach następnych (Fig.1). Obserwowano również drastyczne zmiany w składzie gatunkowym, strukturze dominacji i różnorodności gatunkowej skorupiaków (Tabela 2-5, Fig. 2). W rezultacie zespoły letnie i jesiennie skorupiaków planktonowych we wszystkich latach nawożenia i po jego zaprzestaniu różniły się bardzo silnie od zespołów występujących w roku kontrolnym (Fig. 3 A i B).

Zasadniczej przebudowie uległa również struktura troficzna zespołu skorupiaków zdominowanego przez drobne detrituso-bakteriożerne gatunki *Cladocera* (*Bosmina longirostris* i *Chydorus sphaericus*) oraz drapieżne *Cyclopoida* typowe dla żyznych, alkalicznych wód (Tabela 3-5, Fig. 2).

Obserwacje powyższe świadczą, że ekosystem małego, śródleśnego jeziora zmieniony w swojej strukturze i funkcjonowaniu przez zabieg nawożenia mineralnego może nie powrócić do sytuacji wyjściowej nawet gdy czynnik wywołujący te zmiany przestaje działać.

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