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LONG-TERM CHANGES IN THE ABUNDANCE AND STRUCTURE OF THE COMMUNITY OF PLANKTONIC *ROTIFERA* IN A HUMIC LAKE, AS A RESULT OF LIMING

ABSTRACT: Work carried out at Lake Flosek – a small, humic mid-forest lake – involved an assessment of the scale and permanence of the changes wrought in the rotifer fauna by the liming of the lake carried out in 1970. In all the years of the study, the rotifer community remained typical for humic lakes, being dominated by species preferring low pH, having low abundance and low species diversity. However, the factor considered to determine such characteristics was not the reaction of the water (neutral or even weakly alkaline), but rather the low trophy of the lake. The changes that were observed in the rotifer community after 1966 would seem to have been a consequence of the paucity of algal food and of strong control of both the "top-down" and "bottom-up" types. The elevation of the pH associated with liming was directly implicated in the reconstruction of the species composition of rotifer communities by way of changes in the food base.
KEY WORDS: rotifers, humic lake, liming.

1. INTRODUCTION

It is generally considered that both individual species of rotifers and rotifers as a group display a broad range of pH tolerances, albeit with more species preferring acidic waters than alkaline ones (Berzins and Pejler 1987). In spite of this, there is a series of features of rotifer communities that are typical for acid lakes, and the lakes in question are in turn characterized by a specific species composition of rotifers (Berzins and Pejler 1987); as well as by relatively low numbers, low species diversity and low total abundance (Roff and Kwiatkowski 1977, Brezonik et al. 1984, Brett 1989, Siegfried and Sutherland 1992, Osborne and Jansen 1993).

Liming is a measure often used (especially in Scandinavian countries – Hornstrom et al. 1993) to raise the pH of acid lakes – and hence also their productivity. The general result of this are about visible changes in the qualitative and quantitative structure of communities of rotifers (Keller et al. 1992) making these communities more similar to those typical of pH neutral lakes. The changes are usually manifested through a clear increase in the number of taxa and total numbers of rotifers (Hillbricht-Ilkowska et al. 1977, Hornstrom et al. 1993).

Similarly, the acidification of waters following the cessation of liming may in as little as one year lead to changes in the species structure of rotifers, if the change in pH is sufficient (Keller et al. 1992).

The aim of the research described here was to assess the scale and permanence of the changes in the rotifer fauna of Lake Flosek – a small, mid-forest humic lake – which resulted from the application of lime in 1970.

2. STUDY AREA

The work focused on Lake Flosek – a forest lake covering 4 ha and attaining mean and maximum depths of 3 and 8 m respectively.

In 1970, the lake was limed. During the next three years this resulted in increased calcium concentration (from 3 to 18 mg l^{-1}), and increased pH (from 5.5–6.0 to about 7.0–8.0).

The inorganic phosphorus concentrations remained at a level typical for moderately eutrophic lakes (0.01–0.04 mg l^{-1}) (Hillbricht-Ilkowska et al. 1977).

The in-depth study carried out almost 20 years later (1992–1993) demonstrated that – in spite of the non-repetition of liming in the successive years – the concentration of calcium had remained at the elevated level of 10–16 mg l^{-1}, while the pH range continued to vary between 7 and 8, and the concentrations of phosphates and total phosphorus had remained low (at 0.001–0.026 and 0.012–0.100 mg l^{-1} respectively) (A. Hillbricht-Ilkowska and I. Kufel, unpublished material). The biomass of phytoplankton remained at a low level close to that noted a few years before the liming, although there had been an increase in the contribution of dinoflagellates and Chrysophyta, especially the taxa typical of dystrophic lakes (I. Jasser and I. Spodniewska, unpublished material).

3. METHODS

Samples were taken with a 5-litre Bernatowicz sampler from the deepest part of Lake Flosek, at 1 m intervals between the surface and the bottom. Samples were concentrated with the plankton net of 50 µm mesh size in 1966–1974, and a mesh size of 30 µm in 1992–1993. This difference may create significant difficulties where comparison of data from the two periods are concerned, because the mesh size is obviously important in determining the rotifer material lost or retained in the course of filtering (Ejsmont-Karabin 1978). The losses in question may be reduced by filtering a greater amount of lake water (Ejsmont-Karabin 1978), and were probably not in excess of a few per cent in the research described here, since the filtering of 10–30 litres of water ensured that more than 3000 rotifers were collected on most occasions.

Samples of zooplankton were fixed in Lugol's solution and then in formalin, and were studied by routine methods. The body weight of rotifers were determined in accordance with the relationship between body length and weight described by Ruttner-Kolisko (1977).

The Shannon-Weaver Index (Margaler 1957) was used to assess the species-related differences encountered.

4. RESULTS

The list of rotifers drawn up by Berzins and Pejler (1987) for waters of differing pH were used to list species preferring low-pH lakes and encountered in Lake Flosek. The list included (in order of preference for a low pH): *Keratella hiemalis* Carlin, *Filinia longiseta longiseta* (Ehrbg), *Trichocerca longiseta* (Schrank), *Polyarthra vulgaris longiremis* (Carlin), *Chromogaster ovalis* (Bergendal), *Gastropus hyptopus* (Ehrbg), *Trichocerca similis* (Wierzejski), *Conochilus hippocrepis* (Schrank), *Kellicottia longispina* (Kellicott), *Asplanchna priodonta priodonta* Gosse, *Conochiloides dossuarius coenobasis* (Skorikov), *Ascomorpha ecaudis* Perty, *Conochilus unicornis* (Rousselet), *Synchaeta pectinata* Ehrbg, *Keratella cochlearis robusta* (Lauterborn), *Polyarthra remata* (Skorikov), *Gastropus stylifer* Imhof, *Bipalpus hudsoni* (Imhof), *Polyarthra dolichoptera* (Idelson), *Collotheca mutabilis* (Hudson) and *Polyarthra major* (Buckhardt).

The occurrence of species from this list in Lake Flosek between the years 1966 and 1993 was analyzed and it was found that the community accounted for 93–100% of numbers of all rotifers in both the spring and summer periods (Table 1). At any one time 3–10 species from this list were encountered.

The rotifer community was of low species diversity in each year, in both the spring period and at the beginning and middle of the summer. In general, values for the Shannon-Weaver Index did not exceed 2.0. Indeed, in the years 1991–1993 they reached only 1.23 to 1.68 in May, and 0.77 to 1.69 in July (Table 2). Liming was not found to have been associated with directional changes in species diversity.

Though the species lists for all the years of the study are similar, the spring communities of rotifers underwent complete restructuring (Table 3). The community from the control year (1966) was almost entirely composed of two species: *Polyarthra vulgaris* and *Keratella hiemalis*. The former still appeared

Table 1. Percentage share of species indicative of pH < 7 in the total populations of rotifers noted in Lake Flosek through the years of the study in the spring period (May) and the summer period (June and July)

Year of the study		May	June	July
Control	1966	100	100	95
Liming	1970		100	100
First years after liming	1971	98	93	96
	1972	99	99	99
	1973	100	99	97
	1974	99	100	
20–23 years after liming	1990	100	100	
	1991	100	98	98
	1992	100	99	98
	1993	100	100	99

Table 2. Index for the species diversity of the rotifer populations noted in different years of the study for the spring period (May) and the summer period (June and July)

Year of the study		May	June	July
Control	1966	1.03	1.52	2.09
Liming	1970		1.97	1.80
First years after liming	1971	0.71	2.25	1.70
	1972	0.39	0.30	1.57
	1973	1.03	1.66	1.39
	1974	1.59	1.27	
20–23 years after liming	1990	1.91	1.19	
	1991	1.31	0.84	0.87
	1992	1.68	2.01	1.69
	1993	1.23	0.91	0.77

abundantly in spring of the 20 successive years after liming but was often accompanied by another species of the genus *Polyarthra*, namely *P. dolichoptera*. In contrast, the second of the aforementioned species had disappeared permanently from the community while the significance of *Keratella cochlearis* had increased.

Rather more limited restructuring was noted in the case of the community of rotifers present in early summer (Table 3). The greatest difference related to three species which either appeared in the 1990s (*Polyarthra remata*) or increased considerably in significance (*Conochiloides dossuarius coenobasis*, *Collotheca mutabilis*). However, the species present in the community before the liming (namely *Asplancha periodonta, Polyarthra vulgaris* and *Keratella cochlearis*) did not disappear and continued to play a quite important role in the rotifer community.

Table 3. List of the species of Rotifera occurring in Lake Flosek in different years of the study in the spring period (1) and the early (2) and mid-summer periods (3)
* – no data

Species	Year of study									
	1966	1970	1971	1972	1973	1974	1990	1991	1992	1993
Polyarthra vulgaris	123	*23	2	3	23	*	12*	3	123	123
P. dolichoptera			1	1	1	12	1	1	1	123
P. major				12						
P. remata							1	2	123	12
Keratella hiemalis	1				1			1	12	
K. cochlearis	123	23	123	123	1 3	12	12	123	123	123
K. quadrata			123	123	1	1				
Filinia longiseta	23	2	12					1		2
F. terminalis						1				
Asplanchna priodonta	2	2	1 3	2				12	23	123
Synchaeta pectinata			1	1	1	1		2	123	12
S. oblonga									1	
S. kitina					23	2	2	23		23
Gastropus stylifer	3	2	23	23	123	12	2	3	123	3
G. hyptopus							1		3	
Ascomorpha ecaudis					12	2	2			
A. saltans						1				
Collotheca sp.		23	3		3	1		1		
Collotheca mutabilis					2	2	2	23	23	123
Trichocerca (D) similis		2			3	12			3	
T. longiseta	23									
T. capucina	23			3	2	2		3		
Kellicottia longispina			3		23	12				
Conochilus unicornis						2	2	1	1	
C. hippocrepis								3		
Anuraeopsis fissa				23					123	
Conochiloides dossuarius coenobasis		23	2	2			2	2	12	123
Chromogaster ovalis				2			2		12	
Lecane luna		3	3	3						
Pompolyx sulcata			23		3					
Bipalpus hudsoni								23		3
Macrochaetus subquadratus										3
Notholca squamula		2								

In the years 1992 and 1993, the situation noted in the middle of the summer (July) (Table 3) was very similar to that described previously for the June zooplankton. *C. dossuarius coenobasis* – absent in 1966 – continued to dominate, while *Polyarthra vulgaris* and *Keratella cochlearis* played important roles. This attests to the limited variability of the species structure of rotifers in the course of the season.

The phenomena described above are reflected clearly in the mean species composition of Rotifera for the season in all the years of the study (Fig. 1). Very characteristic changes occurred – especially in the common detrivorous/bacterivorous species *Keratella cochlearis*, which was present in rather small numbers in the control year 1966, but which increased steadily in percentage terms until 1972 (2 years after liming). There was slight decline in the two subsequent years, and the species had disappeared almost completely by 1993. The reverse phenomenon was noted in the case of the *Polyarthra* species, which played a significant structural role in the community of 1966 before decreasing in importance in the four years after liming and then increasing again as the years passed. In general the 1992/1993 community of rotifers was not identical to that from the period prior to liming. The main difference lay in the marked dominance of *Conochiloides dossuarius coenobasis*, a species which was not present in 1966 and not very numerous either in the first few years after liming.

Important and seemingly permanent changes have occurred in the dynamics of the rotifer population (Fig. 2). Beginning in 1972 (i.e. 2 years after liming), the changes in the populations of rotifers proceeded similarly each year. The most

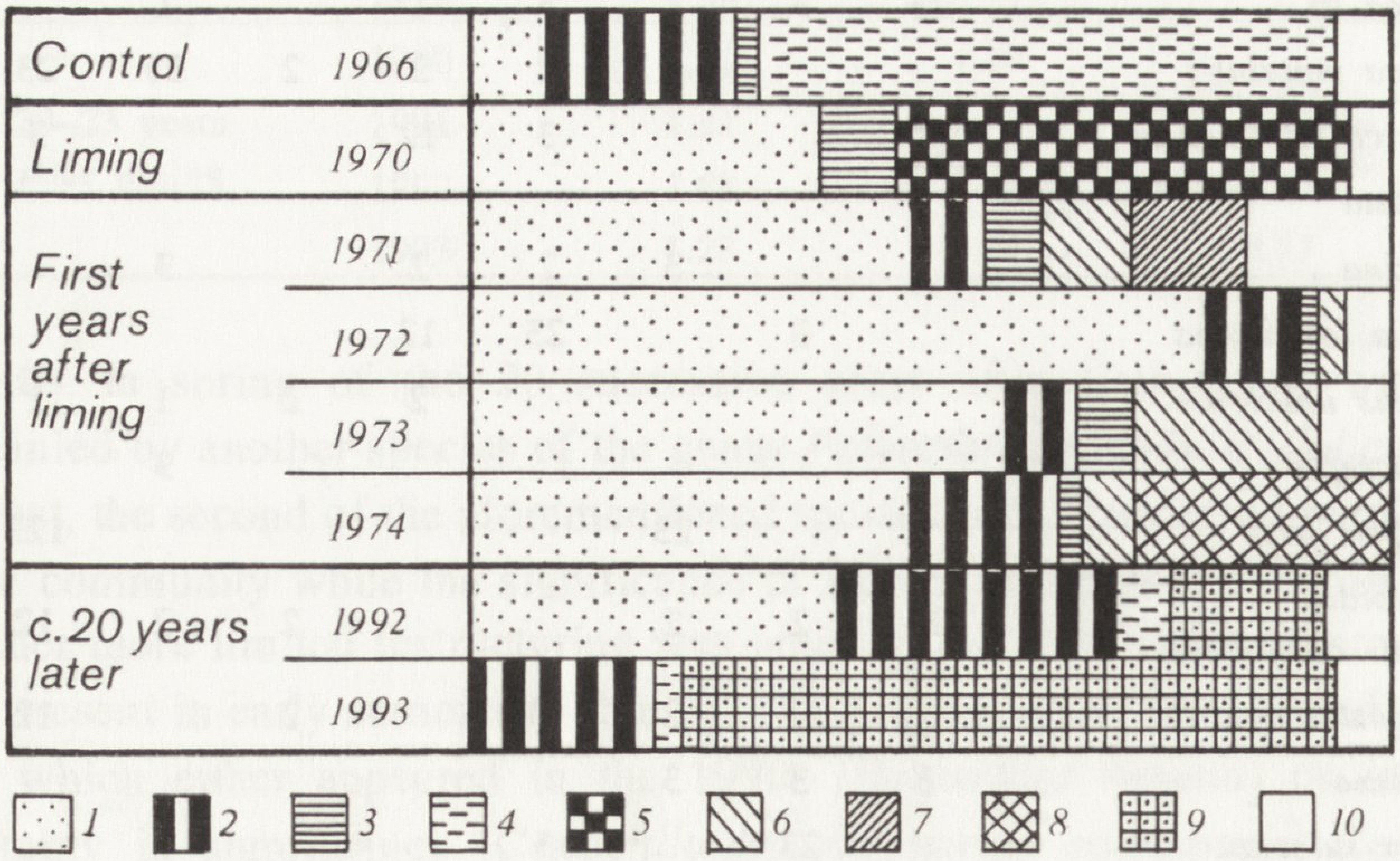

Fig. 1. Changes in the proportions of different taxa in the total numbers of planktonic rotifers occurring in Lake Flosek in the years before and after liming
1 – *Keratella cochlearis*; 2 – *Polyarthra* sp. div.; 3 – *Collotheca mutabilis*; 4 – *Asplanchna priodonta*; 5 – *Conochilus unicornis*; 6 – *Gastropus stylifer*, 7 – *Synchaeta* sp. div.; 8 – *Kellicottia longispina*; 9 – *Conochiloides dossuarius coenobasis*; 10 – others

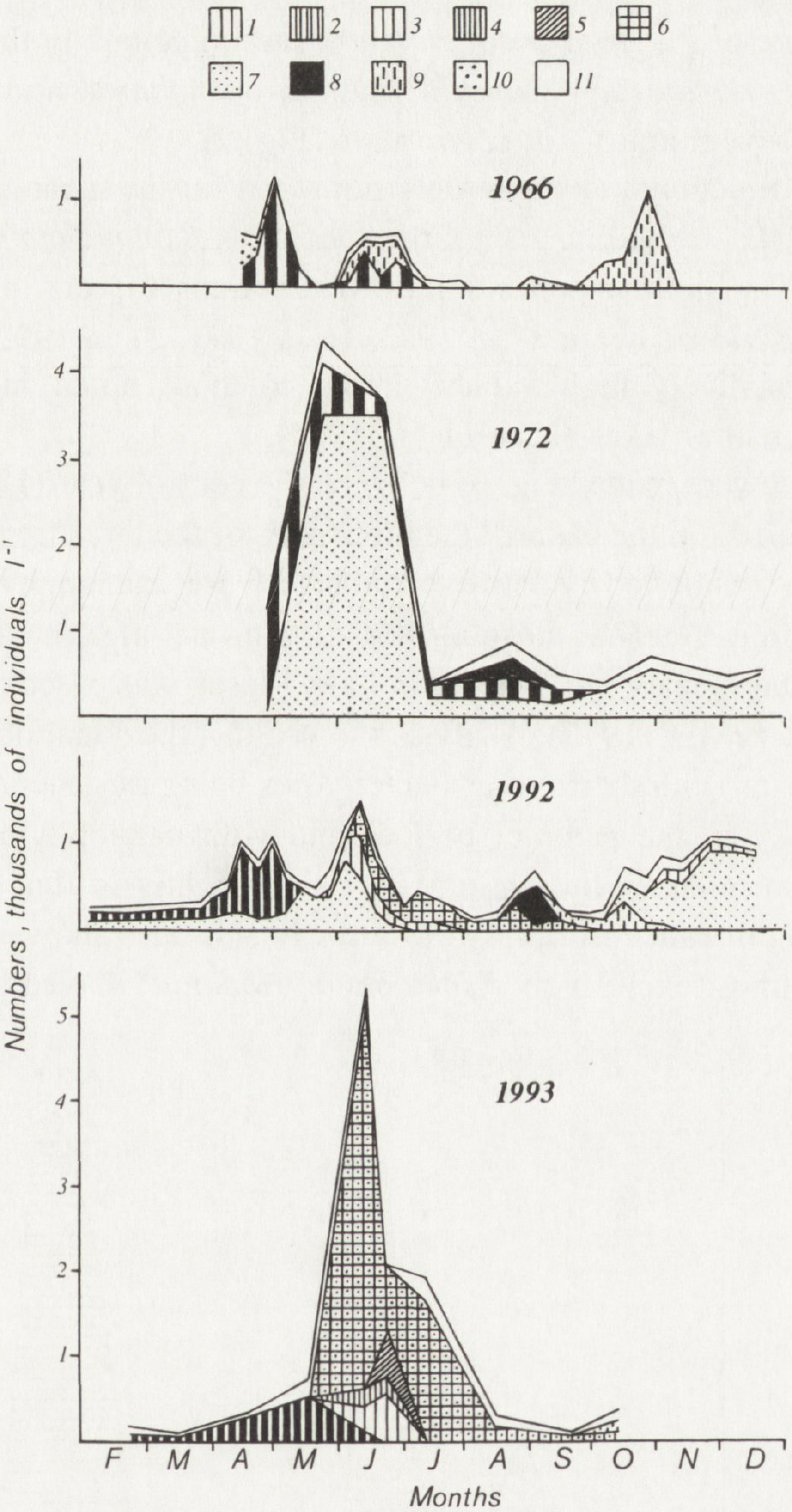

Fig. 2. The course of seasonal changes in rotifer numbers with an indication of the species dominant in Lake Flosek in the years: 1966 (prior to liming), 1972 (2 years after liming) and 1992 and 1993

1 – *Polyarthra* sp.; 2 – *Polyarthra dolichoptera*; 3 – *Polyarthra remata*; 4 – *Polyarthra vulgaris*; 5 – *Synchaeta kitina*; 6 – *Conochiloides d ossuarius oenobasis*; 7 – *Keratella cochlearis*; 8 – *Anuraeopsis fissa*; 9 – *Asplanchna priodonta*; 10 – *Keratella testudo*; 11 – others

characteristic feature of the progressive changes noted within a year was the clear peak of numbers in May and June and the sharp falls in July and August. The spring peaks in the years 1972–1974 mainly involved *Keratella cochlearis* accompanied by species of the genus *Polyarthra* (Hillbricht-Ilkowska et al. 1977); while the 1992 and 1993 spring peaks in numbers were caused by the abundant presence of *Polyarthra dolichoptera* (accompanied in the former year by *K. cochlearis, P. remata* and *Conochiloides d. coenobasis*, and in the latter by *P. remata, P. vulgaris* and *C. d. coenobasis* (Fig. 2).

In contrast, directional changes were not noted for the mean individual weight of small rotifers (i.e. excluding such large species as *Asplanchna priodonta*) which was calculated for summer communities. The values for this parameter (in mg 10^{-5} w.w. per individual) were 27 in 1973, 16 in 1991, 31 in 1992 and 42 in 1993. These are relatively high values similar to those noted in mesotrophic or meso-eutrophic neutral lakes (Karabin 1985).

Comparisons were made (Fig. 3) between the control year (1966) and the year 22 years after liming, on the basis of the biomasses of the three trophic groups of rotifer zooplankton constituted by detritivores/bacterivores, nannophytoplanktonivores and facultative predators (i.e. those also feeding on net algae). The assignment to these groups of the species encountered in Lake Flosek was based on information in the paper by Pourriot (1977). Analysis showed that the dynamics was quite similar in the two years, with detritivores/bacterivores being of generally limited significance (especially in the summer period) and with nannophytoplanktonovorous biomass dominant in April, falling in May, rising slightly in June but becoming of limited overall significance from July onwards. Results also showed that the facultative predators (almost exclusively *Asplanchna priodonta*) played a great role, with

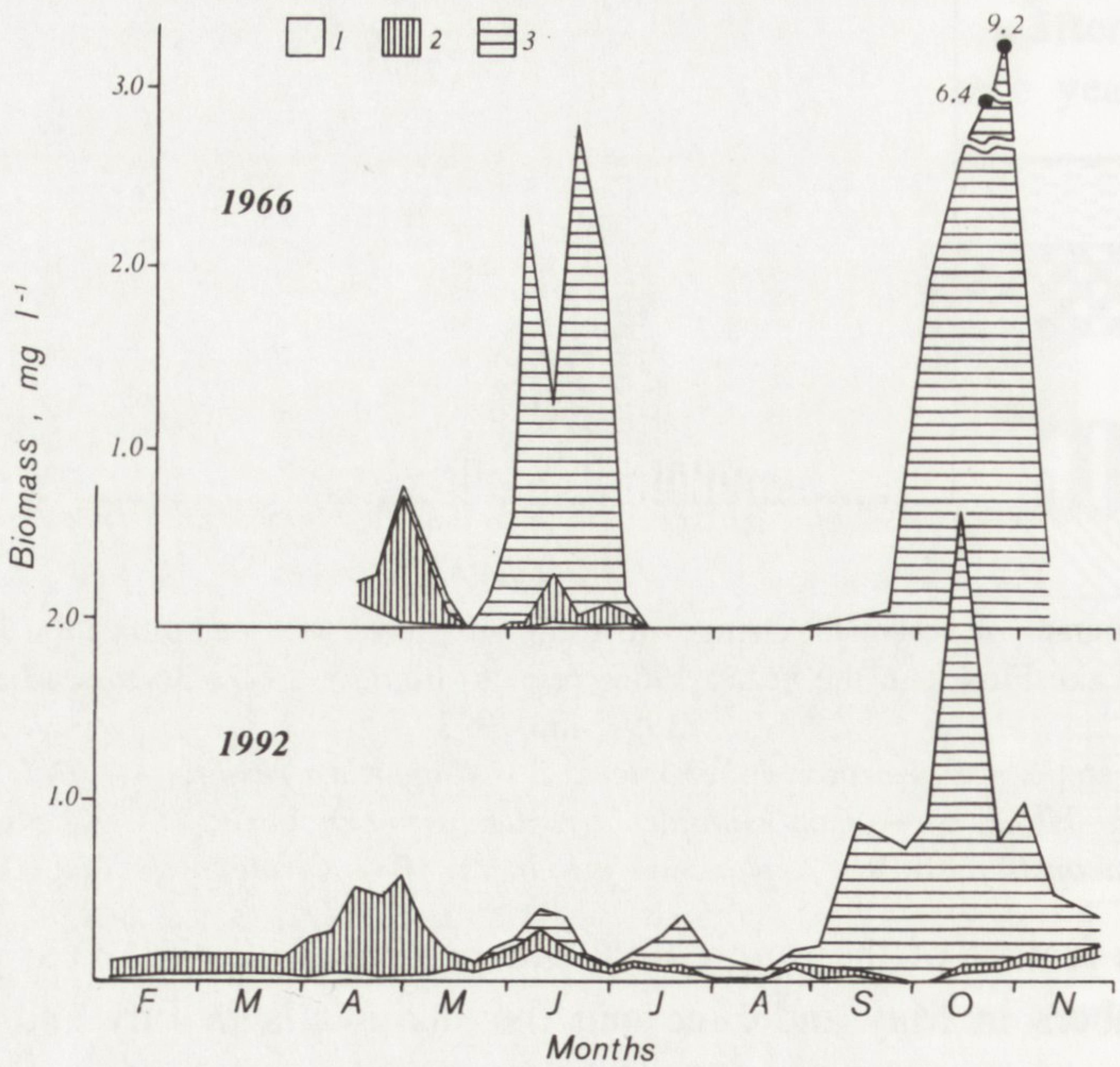

Fig. 3. The course of seasonal changes in the biomass of three trophic groups of rotifers in 1966 (before liming) and 1992 (22 years after liming)
1 – detritivores/bacterivores; 2 – nannophytoplanktonivores; 3 – predators

two peaks of biomass being noted in June and October 1966, but with only one such (October) peak seen in 1992. In general, in spite of different species structure (Fig. 2) the trophic structure of the rotifers biomass was relatively similar in the two years (Fig. 3).

5. DISCUSSION

One of the characteristic features of the rotifer community of Lake Flosek was the lack throughout the study period of species preferring an environment of decidedly low pH. Species like *Keratella serrulata* (Ehrenberg), *Polyarthra minor* Voigt and *Brachionus urceus sericus* Rousselet were absent. These species, appearing mainly near the shore, especially among *Sphagnum*, in some lakes of very low pH, tend also to be noted in large numbers in the pelagial zone (Morling and Pejler 1990). They were not present – even sporadically – in Lake Flosek, which was instead dominated mainly by eurytopic rotifers, as well as by those typical of oligotrophic waters. The Morling and Pejler (1990) list of common eurytopic species met with in abundance in Sweden's acid lakes and relatively insensitive to low pH does overlap with that of the species occurring most abundantly in Lake Flosek. These are *Keratella cochlearis, Trichocerca capucina, Ascomorpha ecaudis, Asplancha priodonta, Polyarthra remata, P. vulgaris* and *Conochilus unicornis.* The former list did not however include *Conochiloides dossuarius, Collotheca mutabilis* and *Gastropus stylifer,* which all occurred in large numbers in Lake Flosek.

On the other hand, the lack of rotifers preferring decidedly acidic waters is understandable because the waters of Lake Flosek have continued to be neutral or weakly alkaline since 1970. Thus, it is difficult to anticipate the direct impact predicted by Arnott and Vanni (1993) for the effect of pH on the structure of zooplankton and especially on its size structure.

It would thus seem that the main factor determining the species composition of the rotifer community of Lake Flosek is most probably the lake's low productivity. Explainable in this way is the dominance of forms typical for mesotrophic conditions or else exhibiting a wide range of tolerance to environmental conditions, including feeding conditions. Similar features characterized the assemblages of rotifers studied in acidified Swedish lakes by Morling and Pejler (1990) and in lakes in Florida by Brezonik, Crisman and Schulze (1984) and Osborne and Jansen (1993).

Also supporting the above conclusion is the high value noted for the mean individual body weight of rotifers. Karabin (1985) noted clearly negative relationship between the trophic status of a lake and the mean body weight of individuals within a community of planktonic rotifers. However, it would seem that the liming of Lake Flosek did not have the kind of significant influence on these aspects of rotifer food which could have led to a change in size structure of the community of these animals. For, as was noted above, there were no directional changes in the biomass/numbers ratio either immediately after liming or in the 22 subsequent years. In contrast, the reverse process, i.e. the acidification of water in experimental enclosures was shown by Havens (1992) to bring about an increase in the significance of small rotifers. It is not easy to assess the degree to which these changes were directly influenced by the fall in pH, since – as Brezonik et al. (1993) and Roff and Kwiatkowski (1977) suggest – it is difficult to separate the direct influence of pH from that of other factors linked with competition, predation and the trophic status of a lake. Brezonik et al. (1993) even suggested that the changes they observed in the zooplankton of experimentally-acidified Little Rock Lake could not be the direct response to the fall in the pH value because they occurred after too long a period. In their opinion, the sharp fall in the species diversity and abundance of the zooplankton studied was the result of changes in trophic relations.

An illustration of such an influence exerted by trophic conditions on structural features of the rotifer fauna may be afforded by the mass appearance of dinoflagellates and the possible influence of this phenomenon on the species structure of rotifers. In the studies by Hornstrom et al. (1993), the occurrence of *Peridinium* and *Gymnodium* was linked with the appearance of *Asplanchna* and *Polyarthra*. In the control year – prior to liming – Lake Flosek's phytoplankton was characterized by a high proportion of dinoflagellates (Hillbricht-Ilkowska et al. 1977) which was associated with high numbers of *Asplanchna priodonta* and species of the genus *Polyarthra*. As the significance of dinoflagellates diminished so did the role of the aforementioned rotifers in the community. It was only in the years 1992/1993 – when the importance of dinoflagellates began to rise again – that numbers of *A. priodonta* also rose. Guiset (1977) held that besides animal food and dinoflagellates, this rotifer clearly prefers other (Chrysophyte) algae which occur abundantly in humic lakes and which are exemplified by species of the genus *Dinobryon* whose significance increased at Lake Flosek in later years. It is not clear to what extent the consumers of dinoflagellates may determine the abundance of these algae. Studies by Havens and De Costa (1985) showed that phytophagous zooplankton did not have a major influence on the species structure of the phytoplankton in Cheat Lake, with *Peridinium inconspicuum* not being consumed there. However, the lake in question was devoid of zooplanktonic species capable of feeding on *Peridinium* cells.

In contrast, changes in the abundance of *Asplanchna priodonta* within the study period may account for observed differences in the numbers of *Keratella cochlearis*. Willingly eaten by *Asplanchna* (Ejsmont-Karabin 1974, Guiset 1977), this species only appeared in greater numbers in the years in which *Asplanchna priodonta* was of low significance (Table 3; Fig. 1). Lake Flosek's permanently low biomass of a phytoplankton very simple in terms of species may be a factor deciding upon the structure of the rotifer community and leading to the simplification of this structure on the one hand, and to the favouring of species not eating algae on the other. Bacterioplankton should constitute an alternative source of food in humic lakes, because – according to Hornstrom et al. (1993) – the humic compounds supplying a substrate for the bacteria increase their productivity. This should favour dominance by such detritovorous/ /bacterivorous species as *Keratella cochlearis, Filinia* sp. or *Anuraeopsis fissa.* However, these are generally small species easily consumed by *Asplanchna.* Control over the abundance of this trophic group by planktonic predators could explain its relatively limited numerical role in the zooplanktonic biomass (Fig. 3). Studies of the vertical distribution of the zooplankton in Lake Flosek revealed the periodic mass appearance of *Filinia* and *Anuareopsis* in the layers just above the lake bottom (and hence in conditions of the significantly weakeped pressure of *Asplanchna* on these rotifers, as well as the simultaneous great abundance of bacterioplankton).

The strong influence of predators on rotifers should be compensated for by the development of forms able to avoid predation. Lake Flosek did witness strong development of the population of *Conochiloides dossuarius coenobasis*, which may be a result of such adaptation, since the species in question is partly surrounded by a mucus sheath. Research by Guiset (1977) showed that *Asplanchna priodonta* did not eat a single rotifer equipped with such a mucus coating. Studies at Lake Ruby by Osborne and Jansen (1993) also showed the dominance of another mucus-coated rotifer *Conochilus hippocrepis* in the face of the abundant occurrence of the predator *Asplanchna herricki.* Experimental laboratory studies have indicated that mucus sheaths are very effective structures against predation by predatory copepods (Stemberger 1985) and *Asplanchna* (Stemberger and Gilbert 1987).

The changes in the rotifer community observed in Lake Flosek between 1966 and 1993 would thus seem to be a direct consequence of changes in the phytoplankton on the one hand, and in the essential need to avoid predators on the other. Equally, the liming-linked increase in pH would not seem to have had a direct influence on the rotifer community. It is possible to predict a certain direct influence of this measure *via* changes in the biotic environment of rotifers.

6. SUMMARY

The research was carried out at Lake Flosek, a 4 ha forest lake with a mean depth of 3 m.

Analysis of changes in the structure and abundance of the Lake's rotifer community did not reveal a significant direct influence on the fauna as a result of the change in pH of the water. In the control year, in the course of liming and in the 20 subsequent years, between 93 and 100% of the community was made up of species preferring water of low pH (Table 1). The assemblage also differed little in terms of species throughout the period (Table 2).

The basic similarity of the lists of species compiled in all years should not be allowed to disguise the fact there were important changes in the group of dominants through the study years.

These changes were more marked for the spring periods than for the summer periods (Table 3). The most characteristic change in the species composition of the rotifer community was the more abundant occurrence of *Conochiloides dossuarius coenobasis* in the years 1992–1993 (Figs 1 and 2), a phenomenon which may however have been a response to enhanced predation pressure upon small zooplankton species.

Lake Flosek lacked species typical for highly acidic waters and had high values for the ratio of biomass to numbers in the rotifer community. These features attested to the fact that the quantitative and qualitative poverty of the rotifer fauna is most probably determined by the low productivity of the lake. It is probable that the strong domination of phytophagous species in rotifer biomass is a reflection of the strong pressure exerted by predators on the smaller detritivores/bacterivores, rather than of their abundance *per se.*

The liming-associated rise in pH would thus not seem to have had a direct influence on the rotifer assemblage, although it is possible to anticipate an indirect influence acting through changes in the biotic environment, trophic conditions and the level of predation pressure.

7. POLISH SUMMARY

Badania prowadzono na niewielkim (4 ha), płytkim (głębokość średnia – 3 m), śródleśnym, humusowym jeziorze Flosek.

Analiza zmian struktury i obfitości zespołu Rotifera nie wykazała istotnego bezpośredniego wpływu zmiany odczynu wód jeziora na faunę wrotków. Zespół ten, zarówno w roku kontrolnym, jak i w trakcie wapnowania i w ciągu 20 lat po nim, tworzyły w 93–100% gatunki preferujące wody o niskim pH (tab. 1), był on też w ciągu całego tego okresu mało zróżnicowany gatunkowo (tab. 2).

Mimo zasadniczego podobieństwa listy gatunków we wszystkich latach badań, grupa dominantów uległa w ciągu okresu badawczego istotnym zmianom, większym w okresie wiosennym, mniejszym – w okresie letnim (tab. 3). Najbardziej charakterystyczną zmianą w składzie gatunkowym zespołu wrotków było pojawienie się w latach 1992–1993 w większych liczebnościach *Conochiloides dossuarius coenobasis* (rys. 1 i 2), co mogło być jednak reakcją na zwiększony nacisk drapieżników na drobny zooplankton.

Brak w jeziorze Flosek gatunków typowych dla silnie kwaśnych wód oraz wysoka wartość stosunku biomasy do liczebności w zespole wrotkowym, świadczy, iż ubóstwo ilościowe i jakościowe fauny wrotków jest najprawdopodobniej determinowane niską żyznością jeziora. Silna dominacja gatunków roślinożernych (rys. 3) w biomasie wrotków wynika prawdopodobnie nie z ich obfitości, lecz raczej z silnego nacisku drapieżników na drobniejsze gatunki detrituso-bakteriożerne.

Związany z wapnowaniem wzrost wartości pH nie wydaje się więc wpływać bezpośrednio na zespół wrotków. Można spodziewać się natomiast pewnego pośredniego wpływu tego zabiegu poprzez zmiany w biotycznym środowisku wrotków, warunkach troficznych oraz poziomie nacisku drapieżników.

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