

8. LONG TERM CHANGES IN COMPOSITION, DIVERSITY AND ABUNDANCE OF ZOOPLANKTON

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When compare the control (preliming) period, liming period, and two subsequent post-liming periods (1–4 and 20–23 years since the treatment), it may be noticed that two basic zooplankton groups, rotifers and crustaceans, exhibited a clear response regarding species occurrence, diversity and community abundance (Figs 15–18, Tables 6, 7). This might be indirect responses to changes in food abundance and availability and in predation pressure rather than direct responses to raised pH and calcium content in Lake Flosek.

Of 33 species of planktonic rotifers reported by Ejsmont-Karabin (1996) for the entire study period (considering periods from April to August), occurrence of only two species (Table 6,

group I), i.e. *Polyarthra vulgaris* (herbivore species) and *Asplanchna priodonta* (predator) have not shown any changes attributable to liming. *Asp. priodonta* was reported to occur in large numbers prior to liming and 20–23 years afterwards, with sporadic occurrence meanwhile. According to Ejsmont-Karabin (1996) and Węgleńska *et al.* (1996), seasonal dynamics of this predator is periodically connected with abundance of other small-sized rotifers, particularly *Keratella cochlearis*. *Pol. vulgaris* occurred during the entire study period, sometimes in large (seasonally and/or annually) or even very large numbers (Table 6).

Sixteen species (II group, Table 6) exhibited markedly higher abundance

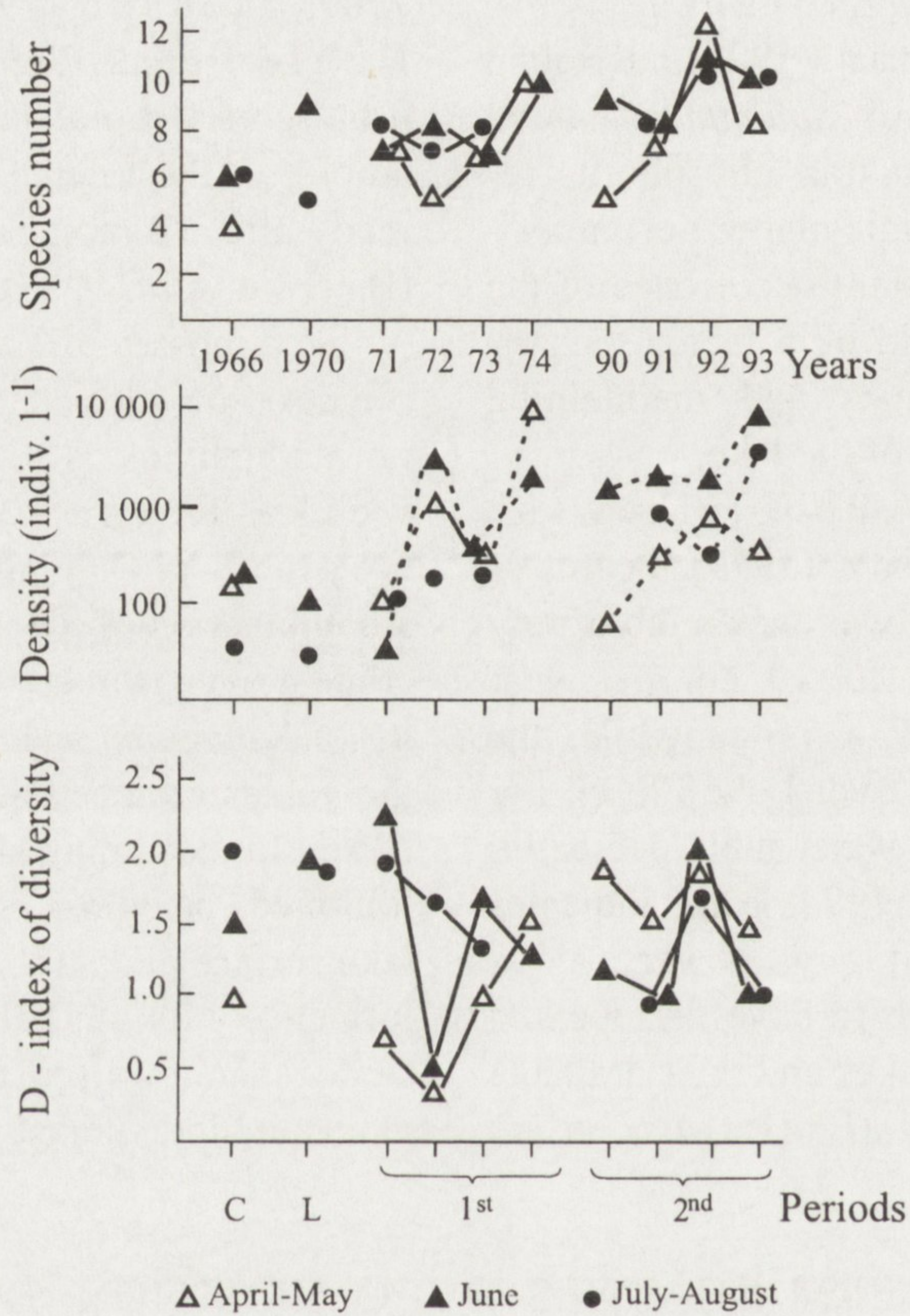


Fig. 15. Changes in rotifer community characteristics in Lake Flosek (after Ejsmont-Karabin 1996). C, L, 1st, 2nd-periods – see fig. 11.

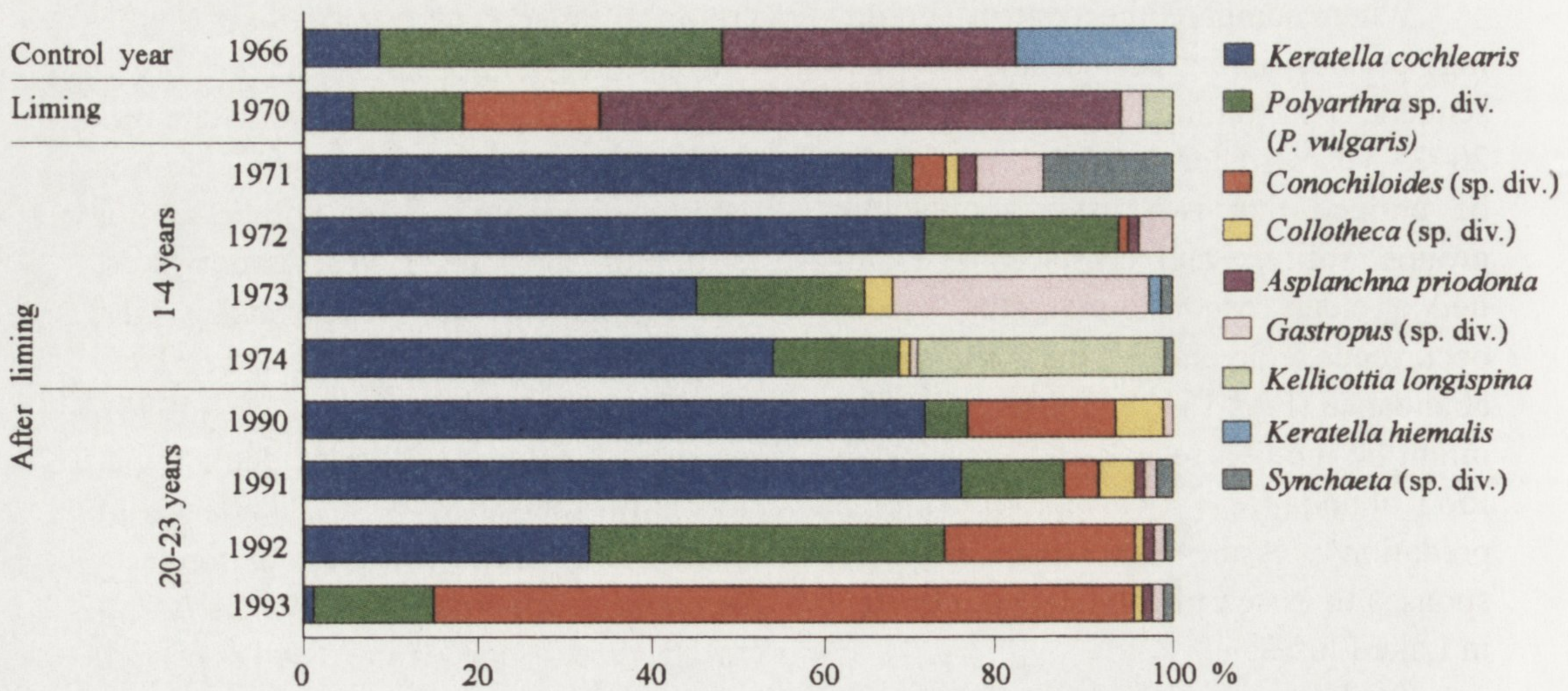


Fig. 16. Changes in dominance structure of planktonic rotifers (percentage participation in total number of individuals) in Lake Flosek in 1966–1993

Table 6. Occurrence of plankton rotifers in Lake Flosek in successive periods. Species are arranged in groups I–IV depending on frequency and abundance

| Group | | Control 1966 | Liming 1970 | 1–4 years after liming | 20–23 years after liming |
|----------------------------------|------------------------------------|-----------------|----------------|---------------------------|-----------------------------|
| I | <i>Polyarthra vulgaris</i> | +++ | + | ++ | +++ |
| | <i>Asplanchna priodonta</i> | +++ | * | * | ++ |
| II | <i>Keratella cochlearis</i> | + | + | +++ | +++ |
| | <i>Pol. dolichoptera</i> | | | ++ | ++ |
| | <i>Gastropus stylifer</i> | * | * | +++ | + |
| | <i>Conochiloides d. caenobasis</i> | | + | + | +++ |
| | <i>Collotheca mutabilis</i> | | | + | ++ |
| | <i>Synchaeta pectinata</i> | | | + | + |
| | <i>Syn. kitina</i> | | | * | + |
| | <i>Gast. hyptopus</i> | | | | + |
| | <i>Pol. remata</i> | | | | +++ |
| | <i>Anureopsis fissa</i> | | | * | * |
| | <i>Chromogaster ovalis</i> | | | * | * |
| | <i>Trichocerca similis</i> | | * | * | * |
| | <i>Syn. oblonga</i> | | | | * |
| | <i>Conochilus unicornis</i> | | | * | * |
| | <i>Bipalpus hudsoni</i> | | | | * |
| | <i>Conochilus hippocrepis</i> | | | | * |
| <i>Macrochaetus subquadratus</i> | | | | * | |
| III | <i>Ker. hiemalis</i> | ++ | * | + | * |
| | <i>Filinia longiseta</i> | + | * | * | * |
| | <i>Trich. longiremis</i> | * | | | |
| | <i>Trich. capucina</i> | * | | + | * |
| IV | <i>Ker. quadrata</i> | | | ++ | |
| | <i>Coll. pelagica</i> | | ++ | * | * |
| | <i>Pol. major</i> | | | +++ | |
| | <i>Fil. terminalis</i> | | | * | |
| | <i>Ascomorpha ecaudis</i> | | | + | |
| | <i>Asc. saltans</i> | | | + | |
| | <i>Kellicottia longiseta</i> | | | +++ | |
| | <i>Lecane luna</i> | | * | * | |
| | <i>Pompholyx sulcata</i> | | | * | |
| | <i>Notholca squamula</i> | | * | | |

* seldom or single individuals (= 10 indiv. l⁻¹)

+ seldom but less than 100 indiv. l⁻¹

++ frequent but usually not numerous, seasonally more numerous – about 100 indiv. l⁻¹

+++ frequent and numerous and/or very numerous; between 100 and 1000 indiv. l⁻¹

and/or frequency in post-liming periods (in relation to the control year) already in the 1st post-liming period or in the 2nd one (20–23 years after treatment). A group consisting of 10 species occurred temporarily in first years after liming and/or in the liming year, while 20–23 years after liming the species were not noted. Four species seem to diminish in the study period. This means that they were relatively more abundant in the control year (III group), and scarce afterwards. *Keratella*

hiemalis may serve as an example (Table 6).

Thereby, the most numerous was II group, i.e. species that appeared or distinctly increased their frequency and/or abundance after liming. These are mainly: *Ker. cochlearis*, *Pol. dolichoptera*, *Pol. remata*, *Gastropus stylifer* and *G. hyptopus*, *Collotheca mutabilis*, three species of the genus *Synchaeta* (with *Syn. pectinata* being most numerous) and *Conochiloides dossuarius caenobasis* (Table 6). The latest species was very

Table 7. Occurrence of crustacean species in Lake Flosek. Species are arranged in groups I–IV depending on frequency and abundance

| Group | Species | Control 1966 | Liming 1970 | After liming | |
|-------|-----------------------------------|-----------------|----------------|--------------|-------------|
| | | | | 1–4 years | 20–23 years |
| I | <i>Bosmina longirostris</i> | + | + | + | + |
| II | <i>Daphnia longispina</i> | | * | + | +++ |
| | <i>Daphnia cucullata</i> | | * | + | * |
| | <i>Chydorus sphaericus</i> | | | + | * |
| | <i>Diaphanosoma brachyurum</i> | | | + | * |
| | <i>Eudiaptomus graciloides</i> | + | +++ | +++ | +++ |
| | <i>Cyclops vicinus</i> | | | | ++ |
| III | <i>Bosmina coregoni thersites</i> | | | + | |
| | <i>Alona quadrangula</i> | | | + | |
| | <i>Mesocyclops hyalinus</i> | | | + | |
| | <i>Cyclops kolensis</i> | | + | ++ | |
| IV | <i>Ceriodaphnia quadrangula</i> | +++ | +++ | ++ | + |
| | <i>Cyclops strenuus</i> | + | + | + | |
| | <i>Thermocyclops oithonoides</i> | + | + | + | * |
| | <i>Mesocyclops leuckarti</i> | + | + | ++ | * |

* seldom, single indiv. l⁻¹

+ frequent but not numerous, periodically numerous up to 10–20 indiv. l⁻¹

++ frequent and numerous up to 50 indiv. l⁻¹

+++ frequent and numerous, periodically very numerous (> 20% of total number) up to 100 indiv. l⁻¹

abundant 20–23 years after liming. All the 16 species together with two next, occurrence of which does not relate to the lime application, constitute a core of planktonic rotifer community of Lake Flosek. Overall number of species recorded in comparable phenological periods was 4–6 in the control year, 4–8 in the treatment year, and 5–10 and 5–12 in the two post-liming periods, respectively (Fig. 15).

A detailed analysis of rotifer tolerance for pH range of 4–10 proposed by Berzins and Pejler (1987) have revealed that nearly all the species noted in the control year, as well as 20–23 years after liming belong to species tolerant of pH shifts from 5 to 9, i.e. the range reported for Lake Flosek in the whole study period. There were no typically acidophilous species such as *Ker. taurocephala*, a common planktonic rotifer of acidic lakes in North America (MacIssac *et al.* 1986, Wright *et al.* 1996), *Ker. serrulata*, *Pol. minor*, *Branchionus urceus sericus* (Berzins and Pejler 1987,

Pejler 1995) nor many other littoral species connected with *Sphagnum* habitat, but able to penetrate water mass of a humic, acidic lake. Some of them, such as mentioned *Ker. serrulata* or *Pol. minor* prefer low pH together with high humus content (Berzins and Pejler 1987).

It is noteworthy that some species have been especially abundant at different pH values of the above given range (Berzins and Pejler 1987), like for example *Ker. hiemalis* – pH = 5–6, and *Filinia longiseta* – at pH = 6, i.e. such as noted in the control year (Table 6). In the remaining years, the species were less numerous. On the other hand, species of the genera *Keratella* (excluding *K. hiemalis*, *K. quadrata*), *Synchaeta*, *Gastropus*, *Anureopsis*, *Collotheca*, *Polyarthra* and *Conochilus* occurred in larger numbers when pH approximated 7. All the above species appeared after liming of Lake Flosek. Other species, such as *Pompholyx sulcata*, *Lecane luna*, *Ker. quadrata*, *Syn. kitina* are abundant in slightly alkaline habitats (pH ~8).

Generally, the community of plankton rotifers of Lake Flosek pelagial consists of species relatively resistant to pH changes noted in the lake. A possible exception is *Ker. hiemalis*. A conclusion may be drawn from the above that a long term variability in rotifer occurrence cannot be explained by a direct effect of raised pH.

Similar opinion have been expressed by MacIssac *et al.* (1986), Morling and Pejler (1990), Olem (1991), Gonzales and Frost (1994), Wright *et al.* (1996). The authors have claimed that such genera and species as those common after Lake Flosek liming, namely *Ker. cochlearis*, *Ascomorpha ecaudis*, *Chromogaster ovalis*, *Conochiloides natans*, *Conochilus unicornis*, *Asp. priodonta* and *Polyarthra* sp. div. are resistant to pH shifts, but these are often found in larger numbers during recovery of a limed lake. In Swedish lakes, the genera *Ascomorpha*, *Collotheca*, *Trichocerca* and *Ker. quadrata*, i.e. species of the groups I and IV from Table 6, increased after liming (Appelberg *et al.* 1995). The species are believed to respond to changed trophic relations, as well as to a decline of abundance of acidophilous species in zooplankton.

The increase in species number of pelagic rotifers was accompanied by a considerable increase in mean abundance in respective seasons of successive years (Fig. 15). In the control and liming years, an average number of rotifers did not exceed a few hundred of individuals per litre, whereas in each phenological season of the post-liming periods it ranged from several hundred to several thousand of individuals l^{-1} (a mean value for water column 0–5 m).

The simultaneous increases in number and abundance of the species caused Shannon-Weaver index of species diver-

sity (Margalef 1957) to vary without any clear tendency. The index values ranged from 0.5 to nearly 2.0 and were similarly variable for every period and season (Fig. 15). According to Ejsmont-Karabin's opinion (1996), these are generally low values indicating low species diversity (the most frequent values occurred in a range 1.0–1.5). This relates to exceptionally much variable seasonal dynamics and a rapid seasonal succession of dominants. These are typical properties of the plankton rotifer community.

The long term changes in abundance and species numbers were accompanied by changes in dominance structure of the rotifer community, i.e. their percentage participation in total abundance of the community (Fig. 16). The most distinct changes were found for a common eurytopic species, *Keratella cochlearis*, abundance of which was responsible for the increase in total rotifer numbers in nearly whole post-liming period. The species belongs to the trophic group of microfiltrators-sedimentators which are feeding on the finest (1–5 μm) bacterio-detrital suspension (Karabin 1985a). These rotifers filtrate and deposit the suspension of the particles directly into mouth opening. For this reason *Ker. cochlearis* is a common indicator of high trophic state of water (eu- and hypertrophic) and progressive eutrophication of non-humic lakes (Karabin 1985b). In 1992 and 1993, the species co-dominated along with mucus-sheath *Conochiloides d. coenobasis* (Table 6). The latter species also belongs to microfiltrators-sedimentators. According to Berzins and Pejler (1987), it is regarded to be a species typical of polihumic habitats. This trophic group also consists of periodically abundant and dominating *Collotheca* sp. div., as well as to less abundant species of the genera

Anureopsis, *Conochilus* and *Pompholyx* (Fig. 16).

On the other hand, species of the genus *Polyarthra* (especially *Pol. vulgaris*) occurring in the entire study period, periodically numerous and dominant (Fig. 16), belong, according to Karabin's analysis (1985a), to macrofiltrators-raptors, i.e. species able to catch larger particles (to 20–30 µm) owing to a mixed (filtering and grasping) way of feeding. Hence, the species constitute a separate trophic group of zooplankton, and nanoplankton may constitute a considerable part of its food. Additionally, the group, i.e. macrofiltrators preferring larger particles, consists of periodically dominating and abundant species of the genus *Gastropus*, and mainly various species of *Synchaeta* able to catch particles up to 50 µm. According to Karabin's analysis (1985a, b), the species dominate rather in mesotrophic lakes where food

era *Trichocerca*, *Ascomorpha*, *Chromogaster*. Hence, fairly large algal cells (30–50 µm) often constitute their food. Among the latter trophic group, i.e. raptors catching actively larger algae (e.g. dinoflagellates) and small rotifers and protozoans, there was only one predatory species belonging to rotifers, namely *Asp. priodonta* (Ejmont-Karabin 1974, Guiset 1977, Karabin 1985b).

Ejmont-Karabin (1996) analysed dominance structure of rotifer communities during spring mixing (May), in the beginning of summer stagnation (June) and during permanent summer stagnation (July, August) in successive years. She has noticed that different species were responsible for the observed increases in species number and abundance of the community in these three seasons. Succession pattern of dominant ($\geq 20\%$ of the total number) species is given below:

| | control period and liming year | 1 st and 2 nd post-liming periods (1–4 and 20–23 years after treatment) |
|------------------------|--|---|
| spring community | <i>Pol. vulgaris</i> <i>Ker. hiemalis</i> | <i>Pol. vulgaris</i> <i>Pol. dolichoptera</i> <i>Ker. cochlearis</i> |
| early-summer community | <i>Asp. priodonta</i> <i>Pol. vulgaris</i> <i>Coll. pelagica</i> | <i>Ker. cochlearis</i> <i>Con. dossuarius coenobasis</i> <i>Pol. vulgaris</i> <i>Pol. remata</i> <i>Pol. dolichoptera</i> |
| late-summer community | <i>Ker. cochlearis</i> | <i>Con. d. coenobasis</i> <i>Pol. vulgaris</i> <i>Coll. mutabilis</i> |

suspension contains fairly large cells of algae (e.g. dinoflagellates).

Majority of low-abundant species of the groups II and IV from Table 6 occurring permanently or temporarily after liming belong to microfiltrators preferring larger particles (e.g. *Ker. quadrata*) or macrofiltrators-raptors actively catching larger particles, such as those of the gen-

The above described long term tendencies in the pelagic rotifer community of the limed humic lake seem do not result from altered composition of species having different tolerance for pH change nor corresponding changes in water chemistry but primarily from changes in type and abundance of suspended food that arose after the lake liming. The

change in food abundance is twofold. On one hand, it consists in higher abundance of bacterio-detrital mass, i.e. suspension of the finest particles. This was brought about by enhanced decomposition of organic matter (DOM and POM accumulated in the lake) and higher production of bacterial biomass. The latter factor was an indirect effect of neutralised acidity. The overall effect consisted in higher abundance and permanent dominance of eurytopic microfiltrators, particularly *Ker. cochlearis*. After liming, abundance of this rotifer group as well as the species mentioned approximated values characteristic of eutrophic lakes. On the other hand, phytoplankton production of the lake was constantly low, which was manifested by low algal biomass (1–3 mg l⁻¹). Among the algae, large dinoflagellates dominant in the control period decreased in numbers after liming in favour of chrysophytes and small flagellates (cf. Chapter 6). Such groups as green algae, chloromonads and other unicellular edible (for rotifers) algae occurred sporadically, and nanoplankton contribution, especially after 20–23 years since liming, was particularly low (cf.: Chapter 6). This seems to result in low abundance of raptor species, such as *Polyarthra*, *Gastropus* and *Synchaeta* preferring nanoplanktonic algal cells.

To generalise, the long term changes of the rotifer community resulted mainly from modifications in bottom-up controlled food web. This was especially pronounced soon after liming, and noticeable 20–23 years afterwards. Attention should be paid to 22nd and 23rd year after liming, when *K. cochlearis* was replaced by *Conochilus d. coenobasis* – another microfiltrator feeding on fine suspension. The change seems to have resulted from changing predator pressure, e.g. *Cyclopiidae*, predatory *Asp. priodonta* and larvae

of *Chaoborus* (see: Chapter 9) readily eating small rotifers (Karabin 1978). Ejsmont-Karabin (1996) has claimed that the above was indirectly related to elimination of small-sized *Keratella* and avoidance of *Conochilus d. coenobasis* (due to its gelatinous sheath) (Guiset 1977) by *Asplanchna priodonta* (occurring numerously in those years). In the control period, *Asp. priodonta* fed mainly on large dinoflagellates (*Gymnodinium*, *Peridinium*), the group diminished after liming. Osborne and Jansen (1993) have additionally noted that mucus-sheath *Conochilus hippocrepis* dominates in presence of predatory *Asp. herricki*. The former species have recently occurred in Lake Flosek (Table 6). Ejsmont-Karabin (1996) has given results of many experimental studies revealing that the presence of gelatinous sheaths efficiently restricts elimination of fine rotifers by their predators.

It may be assumed that both top-down and bottom-up type of control affected the community of pelagic rotifers in Lake Flosek in the 2nd post-liming period, i.e. 22–23 years after the treatment.

Of 15 planktonic crustacean species noted in Lake Flosek during the whole study period (Table 7), 6 species appeared or clearly increased their frequency and numbers in the post-liming periods (Table 7). This was mainly manifested by occurrence of a few larger species of daphnids, particularly *D. longispina* and *D. cucullata*, which, together with *Chydorus sphaericus* and *Diaphanosoma brachyurum* were very numerous 20–23 years after liming (Table 7). These large daphnids belong to efficient microfilter feeders as they feed on particles $\leq 20 \mu\text{m}$ (Gliwicz 1974, Karabin 1985a). According to size-efficiency hypothesis (Dodson 1974), these species are usually successful in ex-

exploitative competition with small crustaceans and rotifers. The abundance of a macrofiltrator *Eudiaptomus graciloides* (preferring particles from 5 to 50 μm) (Karabin 1985b) also increased. On the other hand, declining species included e.g. small (to 600 μm) bacterio-detritivore *Ceriodaphnia quadrangula*. This species was very numerous in the control year and directly after liming, but clearly scarce in the 2nd post-liming period (Table 7). Small-sized (< 1 mm) predatory species of *Cyclopidae*, like *Cyclops strenuus*, *Thermocyclops oithonoides* and *Cyclops kolensis* were also declining. Three species of predatory copepods co-occurred (temporarily and periodically) in a clear sequence: small *Cyclops strenuus* (in the control period and a few years after liming), slightly larger *C. kolensis* (temporarily in the 1st post-liming period), and large cold-resistant *C. vicinus* (20–23 years after the treatment) (Table 7). Contrary to this, a small microfiltrator *Bosmina longirostris* occurred throughout the whole period, although usually in low numbers.

Consequently, number of co-occurring species and species diversity index (D-index) for corresponding phenological seasons were highest in the case of 1st post-liming period (Fig. 17). Species number increased from 5–6 to 6–12, and diversity index from 0.5–1.0 to 1.5–2.7 in comparison with the control year. Likewise, abundance increased from 100 to 250 indiv. l^{-1} in spring (May, April) and early summer (June), although no clear tendency was observed in the remaining phenological seasons (summer stagnation and autumn) (Fig. 17). Mean individual weight of crustaceans increased substantially due to occurrence of large *Daphniidae* and numerous *Diaptomidae* (Fig. 17).

The above parameters describing the crustacean community changed in the 2nd

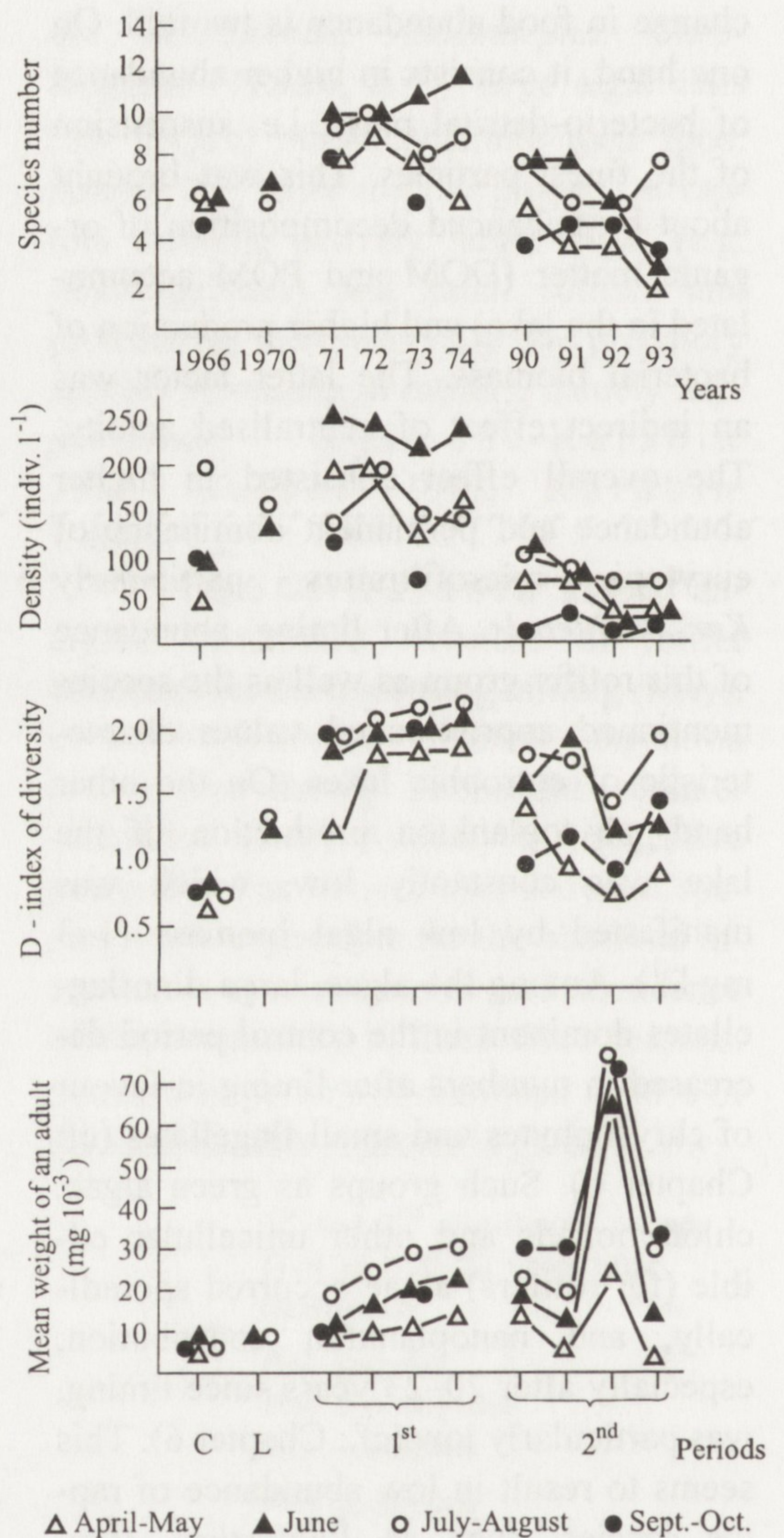


Fig. 17. Changes in crustacean community characteristics in Lake Flosek. C, L, 1st, 2nd-periods – see Fig. 11

post-liming period, i.e. 20–23 years after the treatment (Fig. 17). Number of co-occurring species declined to 2–7 depending on phenological season. Abundance of the community was reduced by half (to the level characteristic of the control year), and diversity index dropped to 0.8–1.2 (Fig. 17). This was accompanied by very rapid fluctuations in mean individual weight. The individual biomass was even several times higher (0.025–0.09 mg) in

1992 than the average values (0.01–0.03 mg) for the remaining years (Fig. 17). This was an effect of abundant occurrence of large *Daphniae*.

The above changes in structural parameters result from changes in both occurrence of particular species and dominance structure of the crustacean community. Contribution of small *Ceriodaphnia quadrangula* was progressively decreasing and, at the same time, large crustaceans like *Daphnia* sp. and *Eudiaptomus graciloides* increased their participation. As a consequence, large filtratory species predominated in the 2nd post-liming period, whereas predatory *Cyclopidae* accounted for as little as 10–25%. This is a value several times lower than that found in the 1st post-liming period and similar to that in the control year (Fig. 18).

The rate and character of the changes were slightly different for different seasonal communities of crustaceans. This is expressed by the following cross-comparison of more abundant species:

| | control period and/or liming year | 1 st post-liming period (1–4 years after treatment) | 2 nd post-liming period (20–23 years after treatment) |
|-------------------------------------|--|--|--|
| spring circulation (April, May) | <i>Ceriodaphnia</i> <i>Diaptomidae</i> <i>Cyclopidae</i> | <i>Diaptomidae</i> <i>Cyclopidae</i> <i>Daphnia</i> | <i>Diaptomidae</i> <i>Cyclopidae</i> |
| early stage of stagnation (June) | <i>Ceriodaphnia</i> <i>Diaptomidae</i> <i>Cyclopidae</i> | <i>Cyclopidae</i> <i>Daphnia</i> <i>Ceriodaphnia</i> <i>Diaptomidae</i> | <i>Diaptomidae</i> <i>Daphnia</i> <i>Ceriodaphnia</i> |
| stagnation peak (July, August) | <i>Ceriodaphnia</i> | <i>Ceriodaphnia</i> <i>Cyclopidae</i> <i>Daphnia</i> | <i>Diaptomidae</i> <i>Daphnia</i> |
| autumn circulation (October) | <i>Ceriodaphnia</i> | <i>Diaptomidae</i> <i>Cyclopidae</i> | <i>Daphnia</i> <i>Diaptomidae</i> |

While the rotifer community did not exhibit any considerable structural differences between the two post-liming periods, the crustacean community was essentially different 20–23 years after

liming when compare with the period shortly after the treatment (1–4 years).

Both zooplankton communities seem to have responded differently to liming – induced modifications in abundance and composition of food. In contrast to rotifers, some crustaceans occurring numerously in the control period diminished. This comprised small detrito-bacterivores (such as *C. quadrangula*). The small filtrators, including some cladocerans occurring periodically (*B. coregoni*, *Alona* sp., *Chydorus sphaericus*) or permanently (*B. longirostris*) in low numbers, did not play any role in the liming-affected crustacean community. The cladocerans seem to have been replaced by efficient filtrators, like large *Daphnia* species (Karabin 1985b). *Daphnia* species are believed to be sensitive to lowered pH (Raddum *et al.* 1986, Olem 1991, Locke and Sprules 1993, Stenson *et al.* 1993). Therefore, acidity neutralisation enables *Daphnia* species as well as *Diaphanosoma* to occur. In limed lakes

Raddum *et al.* (1986) and Olem (1991) have observed a decline in *B. longirostris* and other bosmins in favour of *Diaphanosoma brachyurum*. Stenson and Svensson (1994) reported the

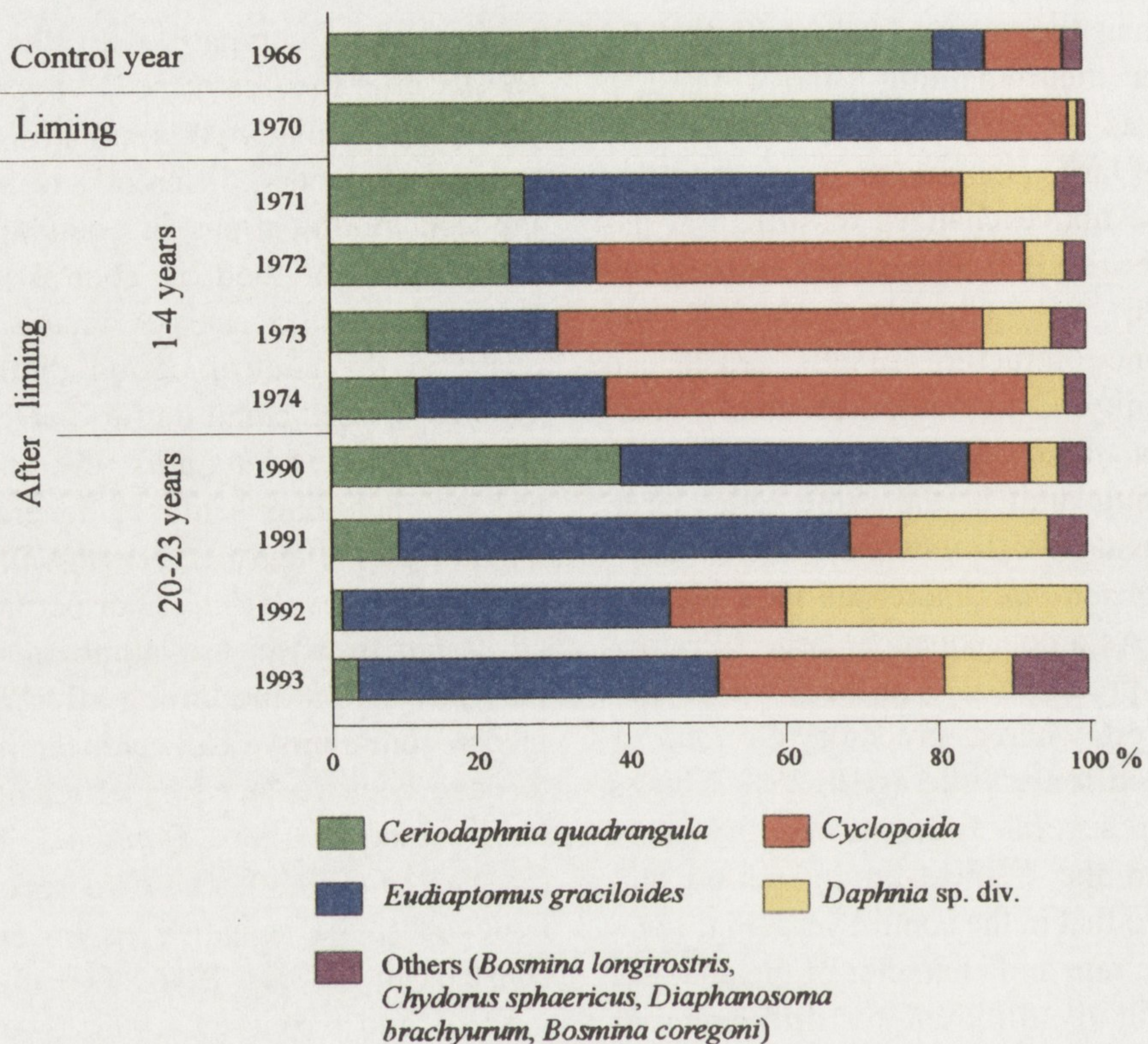


Fig. 18. Changes in dominance structure of planktonic crustaceans (% participation in total number of individuals) in Lake Flosek in 1966–1993

similar decline in favour of *D. longispina*. Beklioglu and Moss (1995) have found *Ceriodaphnia* spp. and *Bosmina longirostris*, and even *Cyclops* spp. to be replaced by *Daphnia hyalina* when pH rose to 9–10. A similar tendency, i.e. an increase in large cladocerans after liming has been found by Ekström and Hörnström (1995). According to size-efficiency hypothesis (Dodson 1974), replacement of small filtrators by larger ones belonging to the genus *Daphnia* through exploitative competition between the two groups is particularly effective when algal food is scarce. Such a situation was observed in Lake Flosek in the whole study period (see: Chapter 6), but particularly 20–23 years after liming when algal biomass amounted to 3–4 mg l⁻¹, but participation of small "edible algae" was low (see: Chapter 6). On the

other hand, the wider size range of food particles and the way of their filtrating by macrofiltrator *Eud. graciloides* did not result in competition with large cladocerans. Thereby, the two filtrators may co-exist after Lake Flosek liming through resource partitioning.

It seems that occurrence of *Daphnia* sp. susceptible to pH shifts and further effects of food competition type may elucidate transformations in the crustacean community, particularly in the 1st post-liming period. Then, in the 2nd post-liming period (20–23 years after liming), cladocerans were strongly top-down controlled, though year-to-year variability was apparent. This was associated with mass occurrence of *Chaoborus* larvae (see: Chapter 9) and changing pressure of planktivory fish (roach, bleak). The latter factor resulted from variable fish stocking

and fishing, less intensive in 1992, and more intensive in 1993 (Table 1). Considerable variability in predator pressure in that period is testified by changes in overall abundance of filtratory crustaceans, *Daphnia* genus in particular, and differences in their mean individual size. The high value of individual weight was found in 1992 at weak fish pressure, while much lower value in 1993 at higher fish pressure (Fig. 17). It was assumed that these phenomena were response on the predators pressure including *Chaoborus larvae* (reaching density up to $13 \cdot 10^3$ indiv. m^{-2}), *Cyclops vicinus* (density up to $20 l^{-1}$) and fish (fry of roach and bleak). Diurnal vertical and horizontal movements and temporary aggregations of the non-predatory crustaceans and rotifers above the bottom were observed also (Węgleńska *et al.* 1996). These movements are affected by the fact that Lake Flosek being a shallow lake, offers a limited possibility of prey to escape predators.

To generalise the long term changes of zooplankton directly or indirectly related to liming of the humic lake, it may be concluded that:

- species diversity was increased in the case of both rotifers (permanently) and crustaceans (periodically, with a clear decrease 20–23 years after liming). This corresponds well with other reports from acidic lake liming (e.g. Olem 1991);

- eurytopic and pH insensitive rotifers responded essentially to enlarged bacterio-detrital suspension and thus were primarily bottom-up controlled; However, 20 years after liming more pronounced indirect and direct influence of

predatory invertebrates (*Asplanchna*, *Chaoborus*, *Cyclops*) were noticed;

- appearance of several pH-sensitive species of the genus *Daphnia* initiated exploitative competition. This resulted in a decline in small cladocerans and resource partitioning, with numerous co-occurring macrofiltratory copepod *Eudiaptomus graciloides*. At the same time, planktonic food web was more intensively top-down controlled by fish (variable pressure) and invertebrates (constantly heavy pressure), *Chaoborus larvae* in particular. The above system regulating structure of the planktonic crustacean communities, and partially planktonic rotifers, seems to characterise well the ecosystem of Lake Flosek 20–23 years after liming;

- on the background of the above described long term changes, and despite presence of species tolerant of lower pH and lack of many others (such as large *Daphnia*), the structure characteristic of the control year (prior to liming) may be regarded as a system controlled by essentially one key-stone predatory invertebrate, namely *Chaoborus* occurring in low numbers (to several indiv. m^2). On the basis of direct observations it may be assumed that possible pressure of planktivory fish in Lake Flosek was low. Predatory *Chaoborus* affects structure of poorly diversified and not numerous community of filter feeders (rotifers, *Ceriodaphnia*) dependent mostly on scarce edible algae. *Chaoborus* is known as a main factor affecting zooplankton structure in fishless acid lakes (Nyman *et al.* 1985, Stenson and Oscarson 1985).