6. LONG TERM CHANGES OF PHYTOPLANKTON COMPOSITION AND BIOMASS

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Annual mean biomass of phytoplankton (a mean value for the layer 0–4 m and the period May – October) amounted to several mg l^{-1} irrespective of the study year or period (Fig. 11). This is generally a low value rather characteristic for mesotrophic lakes. No clear tendency was found attributable to liming although some year-to-year variability was apparent (Fig. 11). Biomass usually attained maximum in summer and spring, and was highest (about 20 mg l^{-1}) in the liming

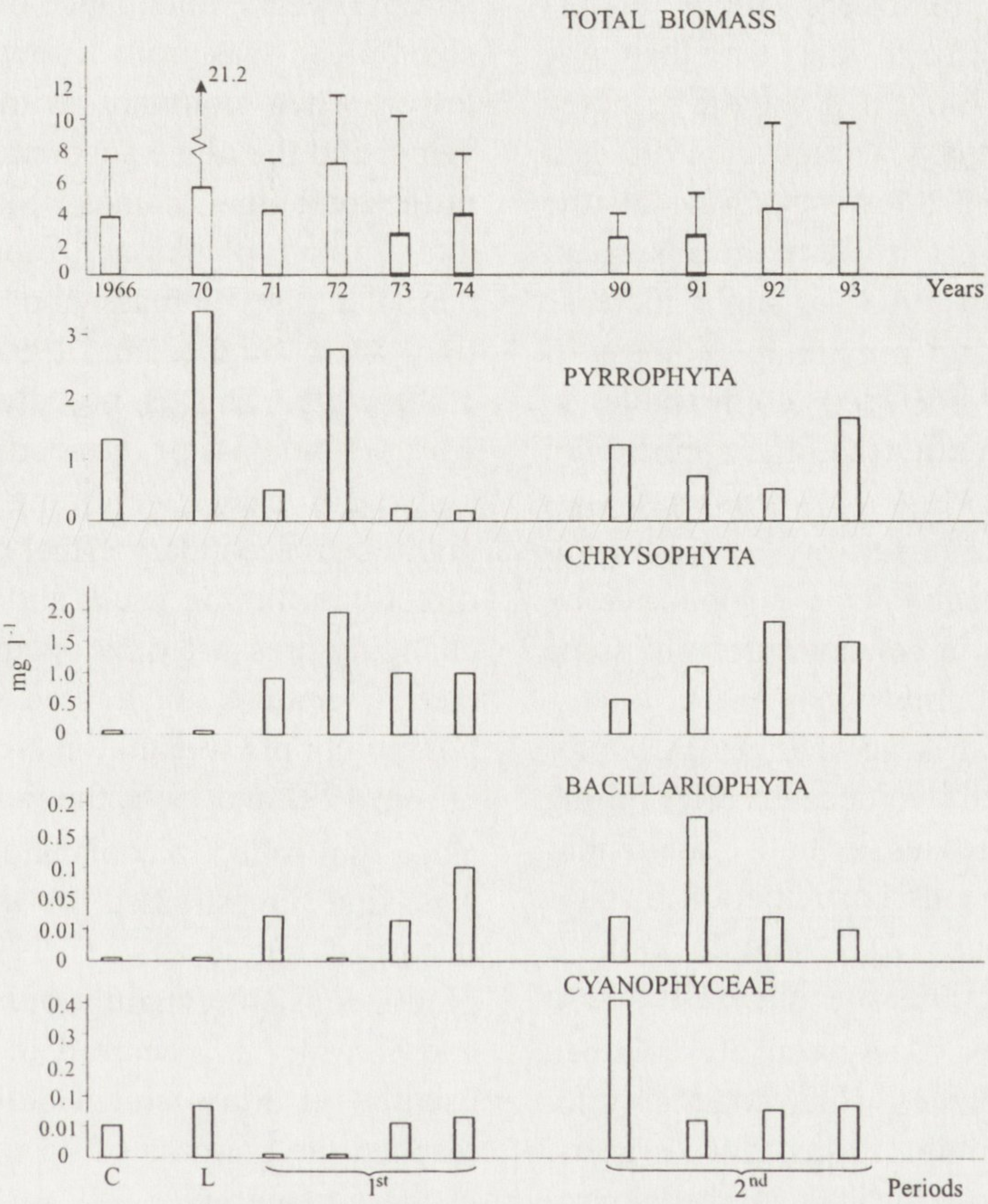

Fig. 11. Mean (0–4 m, May–October) biomass of phytoplankton[3] and its main groups in Lake Flosek in C(ontrol) (1966)[1], L(iming) (1970)[1] and two post-liming periods (1971–1974[1], 1990–1993[2])

[1] acc. to Hillbricht-Ilkowska *et al.* 1977

[2] unpublished data of I. Spodniewska

[3] vertical lines – maximal values

(Note different scales for particular groups!)

year, and lower (of about 10 mg l^{-1}) in some years of the 70-ties and 90-ties (Fig. 11).

Biomass maximum of as much as 20 mg l^{-1} reported for the liming year (1970) was reached early in September (according to Figs 7 and 9 in Hillbricht-Ilkowska *et al.* 1977), i.e. after application of fourth lime dose. This biomass peak was related to development of dinoflagellates, particularly *Peridinium* sp. and *Ceratium hirundinella.* This seems to reflect an immediate but temporary response to calcium addition, and is opposite to the functional phytoplankton response described in Chapter 4 i.e. the decrease of production. Thus, phytoplankton has not increased nor decreased its abundance for a long time following Lake Flosek liming.

No clear tendency in total biomass (or chlorophyll *a* content, or phytoplankton production), has been reported by other authors in case of progressive water acidification (Findley and Kasian 1990, 1991), Muniz 1991, Schindler *et al.* 1991) or pH rise due to liming (Olem 1991), provided that the changes were relatively minor at pH shifts confined to 5.8–7.0, i.e. to the range found in Lake Flosek. It should be noted that mean biomass values in 1990 and 1991 were almost lowest among all the study years (Fig. 11). Then, in subsequent years (1992 and 1993), a slight increase in both mean and maximum biomass of phytoplankton occurred comparable to that found soon after the lime application, i.e. 1971–1974 (Fig. 11). This may suggest an increase in fertility, i.e. eutrophication, to has begun. This is supported by slight increases in concentrations of some chemical compounds (Chapter 4).

The most striking changes in phytoplankton noticed two decades after liming comprised decreases in both nanoplankton biomass and its participation in phytoplankton (Fig. 12). Nanoplankton is composed of various fine algae (from 2 to 20 μm), usually blue-green algae, green algae and flagellates which together constitute the edible forms for grazers. Biomass of those groups in the control (liming) year and several subsequent years was, on average, about 2–3 mg l^{-1} and accounted for at least a half of the phytoplankton biomass (cf.: Figs 11, 12). After 20 years, abundance of those small-sized algae was from a few to ten times lower when compare with the former years, and the algae accounted for 5–20% of the total algal biomass. Similarly to the total phytoplankton biomass, both nanoplankton biomass and its participation were higher in 1992–1993 than 1990–1991. This is not clear, however, why the biomass of these edible algae declined 20 years after liming. The decline might be a secondary effect dependent indirectly on liming itself, and directly – on changing pressure of zooplankton grazing (see: Chapter 8) or altered species composition of phytoplankton (see below).

In 1992 and 1993, the finest fraction of algae, so called picoplankton (1–3 μm), was first investigated in the long run. It turned out (J a s s e r 1996) that the group, consisting mainly of blue-green algae *Sinecoccus*, occurred in Lake Flosek usually in May and October when it reached the biomass of up to 0.55 mg l^{-1} in the surface layer 0–1 m, and thus accounted for as much as 20% of total algal biomass. However, when annual mean biomass is considered, this is a few per cent of the total phytoplankton biomass,

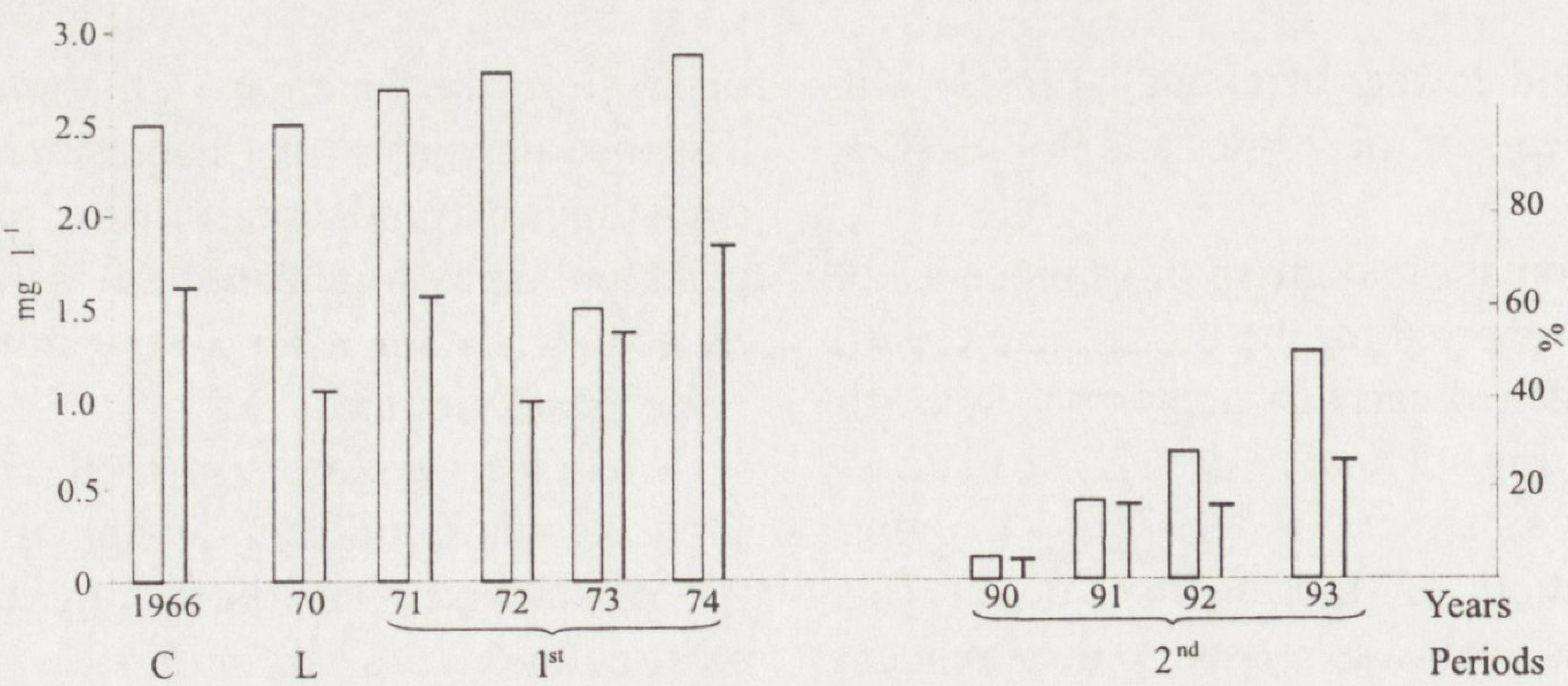

Fig. 12. Mean (0–4 m, May–October) biomass of nanoplankton (≤ 20 μm size) (bars) and its contribution (vertical lines) to total biomass (%) in Lake Flosek in different years and periods (See Fig. 11 for explanations).

and several times less than the biomass of nanoplankton (J a s s e r 1996).

When long term data series are analysed, the changes in composition, biomass and occurrence of particular fractions, genera and species of phytoplankton seem to be attributable to liming (Fig. 11). This may be generalised as follows. Dinoflagellates, the biomass of which decreased soon after liming, tended to be scarce. This was especially true for *Peridinium* sp. and *Ceratium hirundinella*, dominating in that group prior to and in the year of liming. However, biomass of this group increased again in 1993 due to a higher contribution of *Gymnodinium sp.* (occasionally to 64% of biomass), a small-sized species (of about 20 μm), most likely *Gymnodinium luteofaba*.

A pattern of changes in total biomass and participation of chrysophytes was somewhat different. Furthermore, an evident succession of the species could be observed during the 20-year period (Table 5). Annual mean biomass of the group was very low before and at liming, and then soon after the treatment it increased by one or two orders of magnitude reaching, on average, about 1–2 mg l^{-1} in 1971–1974 and 20 years afterwards (Fig. 11.). This was especially true for the genus *Dinobryon*, constituting in some seasons as much as 50% of the phytoplankton biomass. This is a fairly long term effect of liming and consequent increases in calcium and water pH on phytoplankton composition. The increase was evident for species of low abundance in 1966 and 70-ties (*Dinobryon divergens, D. sociale* or *D. sertularia*) (Table 5), as well as more for species rarely noted in those years, i.e. *D. pediforme, D. acuminatum, D. bavaricum* and *Syncrypta* sp. Thus, diversity of this phytoplankton group increased (Table 5).

Biomass of other groups, namely diatoms, blue-green algae or green algae was generally low, and their overall participation not exceeded, on average, a few percent, although periodically it could account for as much as 50% of the total biomass (Fig. 11, Table 5). However, mean biomass of diatoms tended to be higher after liming and genera typical for eutrophic lakes, such as *Asterionella, Synedra, Melosira, Stephanodiscus*, appeared in both postliming periods (Table 5). Despite scarcity of blue-green algae in Lake Flosek, alike tendency was detected in 1990 when *Gleocapsa limnetica* reached very high biomass (Table 5). Twenty years after liming (1991), biomass of green algae (*Ankistrodesmus falcatus, Botryococcus braunii, Scenedesmus* sp.) was also much higher (in summer up to 0.29 mg l^{-1}, i.e. about 20% of the total algal biomass). In 1992 and 1993, mass occurrence of chloromonad *Vacuolaria viridis* took place. In summer 1992 biomass of this species amounted to 1.18 mg l^{-1}, and accounted for as much as 90% of the total phytoplankton biomass. After liming, flagellates such as *Cryptomonas* and *Trachelomonas* were also more abundant (H i l l b r i c h t - I l k o w s k a *et al.* 1977).

The above changes in abundance of more important phytoplankton taxa in Lake Flosek may be attributed to the raised calcium content and pH. They correspond fairly well with those reported for limed acidic, humic lakes, although the rate of structural changes and their further persistence depend on the shifts in pH. Disappearance of dinoflagellates (*Gymnodinium, Peridinium, Ceratium*) and cryptophytes in favour of chrysophytes (the genus *Dinobryon*), and first of all, green algae and diatoms, usually accompanies pH and calcium increases, whereas a reverse tendency occurs when

Table 5. Occurrence of selected phytoplankton taxa in Lake Flosek for which the marked changes in abundance were noted in successive years

Year, period Taxon	Control [1] 1966	Liming [1] 1970	Postliming 1971–1974 [1]	 1990–1993 [2]
Pyrrophyta:				
Peridinium sp.	+++	+++	++	+
Ceratium hirundinella	++	++	+	+
Gymnodinium sp.	+	+	+	++
Chrysophyta:				
Dinobryon divergens	+	+	+	+++
D. sociale	+	+	+	+
D. sertularia	–	–	+	+++
D. pediforme	–	–	+	+
D. acuminatum	–	–	+	+
D. bavaricum	–	–	–	+
Syncrypta sp.	–	–	–	++
Chloromonadophyta:				
Vacuolaria viridis	–	–	–	+++
Chlorophyta	–	–	+	++
Ankistrodesmus falcatus	–	–	–	+
Scenedesmus sp. div.	–	–	–	+
Botryococcus braunii	–	–	–	+
Bacillariophyta:				
Asterionella formosa	–	–	+	+
Synedra acus	–	–	+	+
Melosira islandica	–	–	+	++
Stephanodiscus astrea	–	–	+	+
Cyanophyta:				
Gleocapsa limnetica	–	–	–	++
Flagellata:				
(*Cryptomonas*,	–	–	+	+
Trachelomonas)	–	–	+	+

(–) very seldom
(+) frequent but not numerous
(++) frequent and occasionally numerous
(+++) constant and numerous
[1] data compiled from H i l l b r i c h t - I l k o w s k a *et al.* 1977
[2] data elaborated by I. Spodniewska (unpublished data)

pH falls to about 5.0. The latter tendency has been found in various lakes and *in situ* experiments (O l e m 1991), e.g. in Lake Gardsjön (H ö r s t ö n and E k s t r ö m 1986, B u k a v e c k a s 1988, 1989, S t o k e s *et al.* 1989, M o r l i n g and W i l l e n 1990) and in experimentally treated Canadian lakes (F i n d l e y and K a s i a n 1990, 1991, M u n i z 1991, S c h i n d l e r *et al.* 1991, H a v e n s 1992a, b). M o r l i n g and W i l l e n (1990) have revealed an apparent succession of species of the genus *Dinobryon* after liming, which resembles that found in Lake Flosek. All the authors have pointed out that full reconstruction of phytoplankton diversity and abundance to the pre-acidification level in a short recovery period must not be possible, even if pH does not fall previously below 5.0. It is often the case that species less sensitive to lowered pH may survive, and even dominate temporarily, at higher pH, which is exemplified by e.g. some dinoflagellates (Schindler *et al.* 1991). Under acidic conditions, non-nitrogen fixing blue-green algae such as *Anabaena spiroides* may disappear (Morling and Willen 1990), while such genera as *Merismapaedia* sp. may sustain lowered pH (Fleisher *et al.* 1993), and disappear after liming.

The above alterations in species composition and size distribution of phytoplankton after liming are crucial for matter transformations in an ecosystem, because the change generally consists in replacement of non-edible algae (dinoflagellates) by algae (mainly chrysophytes) available to filtrating apparatuses of grazing zooplankters (Dickson 1989, Blömqvist *et al.* 1993).

In a limed lake, edible algae are controled by zooplankton grazing rather than nutrient availability. However, Jones (1992a) has pointed out that the dominance of chrysophytes (*Dinobryon*, *Ochromonas*) and other flagellates (*Cryptomonas, Mallomonas*) may be associated with their response to enlarged pools of particulate organic matter and bacterial plankton. Although the author has collected a lot of data on phagotrophy and bacterivory of those groups of phytoplankton, he warns that opinions vary, and a question whether chrysophytes and cryptophytes are obligatory or occasional heterotrophs is still a matter of speculation. However, it seems that in the case of Lake Flosek where liming was responsible for higher decomposition rate and abundance of microbial plankton soon after the treatment (cf.: Chapter 4) and thereafter, the increase in that algae group is more likely to reflect their response to enlarged pool of particulate organic matter. This is also supported by high concentrations of chrysophytes (and chlorophyll *a*) found in deeper layers (4 – 5 m) of Lake Flosek, including winter period, as well as in lakes examined by Jones (1992a).

Generally, qualitative and quantitative changes of phytoplankton observed in 90–ties, i.e. 20 years after liming, seem to indicate a lack of stability in composition and dynamics of this group. Phytoplankton is a mixture of co-occurring or seasonally exchanged species and groups. The most abundant and diverse group were chrysophytes influenced by liming. This group represents heterotrophic or mixed type of feeding, and they are probably the important component of microbial loop in a lake. There were also small dinoflagellates, including species so typical of humic lakes (according to Salonen *et al.* 1992a) such as *Gymnodinium*. Their presence may indicate re-occurring symptoms of Lake Flosek dystrophication. Eventually, occurrence of numerous species of green algae, chloromonads, diatoms, and occasionally blue-green algae may indicate eutrophication, i.e. a response to external nutrient input or elevated internal supply (recycling) of these compounds. It seems that intensive zooplankton grazing due to changing fish pressure in recent years (1992, 1993) might also influence size fractions distribution of phytoplankton (see: Chapter 8).