11. DISCUSSION: EFFECTS OF MODERATE LIMING OF A HUMIC LAKE
(Anna Hillbricht-Ilkowska)

Lake Flosek typically represents small mid-forest lake formed from melted ice block. This lake type is characteristic of biomes of coniferous and mixed forest and peatmoss communities responsible for its biogenic acidification. It does not belong to so called clear-water lakes lying on granite bedrocks and containing little humus, highly acidic (pH below 5.0) and susceptible to anthropogenic acidification. This weakly acidic (pH 5.5–6.5) soft-water and humus-rich lake with no outflow, and surrounded by conifer catchment was subject to application of lime. The treatment raised water and sediment pH to 7–8. Calcium content of water was lifted up by several times, and that of sediments – doubled. This was noticeable even 20 years after the treatment.

Single lime application did not lead to a continuous nor significant change in trophic type of the lake (at least in 23 years following the treatment). The lake is still low-productive, has low mean TP concentration ($\leq$ 50 μg l^{-1}) and algal biomass ($\leq$ 3 mg l^{-1}), high water transparency (SD to 4 m in summer), exhibits oxygen deficit near the bottom (wind sheltering effect) however without hydrogen sulphide. Peatmoss surrounding the lake (*Sphagnum* mats) remained intact, and very low pH of water among plants (about 4.0) was kept up, although the mat expansion over the lake table was restrained. Conditions favourable for appearing of periphyton and metaphyton algae, including filamentous green algae characteristic of low-productive waters, were maintained. Furthermore, certain planktonic algae typical of humic lakes and recorded in pre-treatment period reoccurred between ten and twenty years after liming.

A principal factor providing low fertility of the lake seems to be bottom sediments. The humic and aluminium compounds deposited therein cause phosphorus to be relatively firmly retained and resistant to being released (i.e. recycled) even under anaerobic conditions. It seems that liming-induced transformations of sediments (acidity neutralisation, elevated calcium content) were insufficient as to permanently change site conditions toward a greater mobility of phosphorus confined to sediments. Such a situation causes internal eutrophication to be restricted. The internal loading of phosphorus could be undesirable effect of liming, as it was reported by Dickson *et al.* (1995) who have analysed fate of numerous Swedish lakes subjected to heavy and frequent lime application.

Preservation of unique features of lakes of this type (oligotrophic character of the lake itself with its spatial division into the lake and *Sphagnum* habitats) may be explained by a relatively minor interference of liming in respect to conditions prevailing in the lake. These conditions mitigate the physiological influence of pH change after liming. They are primarily: a high content of organic matter able to neutralise toxic aluminium even at low pH (e.g. Havens 1993b and references cited in Chapter 1) and a relatively little pH change (by about 2 units) starting from an initial value of about 5.5–6.0. At such pH found in the pre-liming period, toxic aluminium was unlikely to reach concentrations lethal to ichtyofauna of the lake. Consequences of liming are relatively less serious in the case of weakly acidic lakes (like Lake Flosek) than clear-water lakes on granite shields, the latter ones having pH of about 4.5 and hence being fishless prior to liming (Malley and Chang 1994, Jarvinen *et al.* 1995). Moderate liming applied in Lake Flosek allowed to avoid problems generated by liming of numerous peatbogs and wetlands. Deleterious changes observed in those habitats are regarded as mistakes made during recovery of limed lakes (Brandrud and Roelofs 1995, Henricksen *et al.* 1995, Svenson *et al.* 1995).

Liming performed has not led to permanent and significant change in the Lake Flosek trophic state. However it has provided the lake waters and sediments with a chemical system able to counteract possible effects of further acidification, at least for a few decades. The acidification may be of biogenic (*Sphagnum* surroundings) or anthropogenic origin. The latter one may result from low pH of precipitation (of about 4.0–4.5) in the north-eastern region of Poland. Liming made habitat of Lake Flosek more favourable for ichtyofauna in a sense that in-lake sites having low pH lethal for fish were eliminated. Such sites could include near-bottom and near-shore habitats where pre-liming pH values were found to be lower than 5.5 (Hillbricht-Ilkowska *et al.* 1977). A possible influence of planktivory fish on zooplankton structure, due to random introduction of roach, perch and others, was revealed as late as in the post-liming period. However the above single–dose and moderate liming appeared to be sufficiently strong to initiate changes in food web and thereby changes in functioning of the lake ecosystem.

The food web structure in the control (pre-liming) period can be characterised as follows (Fig. 22A). A few species of filter feeders were dependent on low biomass (of a few mg l^{-1}) of edible algae and scarce bacterio-detrital suspension. This trophic system combined with the low pH is favourable for small planktonic cladocerans and rotifers occurring in low numbers. Equally scarce and not numerous deposit-feeders occur in benthos. Certain large algae such as *Ceratium, Peridinium* together with small filter-feeders support the poorly diversified community of predators, particularly *Asplanchna priodonta* (a large predatory rotifer), scarce predatory *Cyclopidae* and larvae of *Chaoborus flavicans*. It may be concluded that the lake system had a food web simplified due to lowered pH, low predation pressure, low efficient mechanisms of in-lake nutrient recycling and slow decomposition of organic matter resources due to inhibited bacterial activity. Generally, the food chain is primarily of grazing type where food web is controlled by low algal production and slowly decomposed detritus resources. This is the system of entirely bottom-up control.

Liming altered considerably the above system. On the basis of the long term observations it can be seen that the system was completely different in the period following directly the treatment and 20 years afterwards (Fig. 22B, C). A fundamental change in the former period comprised abatement of low pH stress and enhanced species diversity and trophic relations within planktonic and benthic communities. Functioning of food web was based on increased abundance of available bacterio-detrital suspension. This, in turn, was an effect of intensive bacterial decomposition of organic matter resources accumulated previously in the water and sediments (Fig. 22B). The food resources mobilised in the lake ecosystem – in turn stimulated the development of various suspension feeders such as roti-

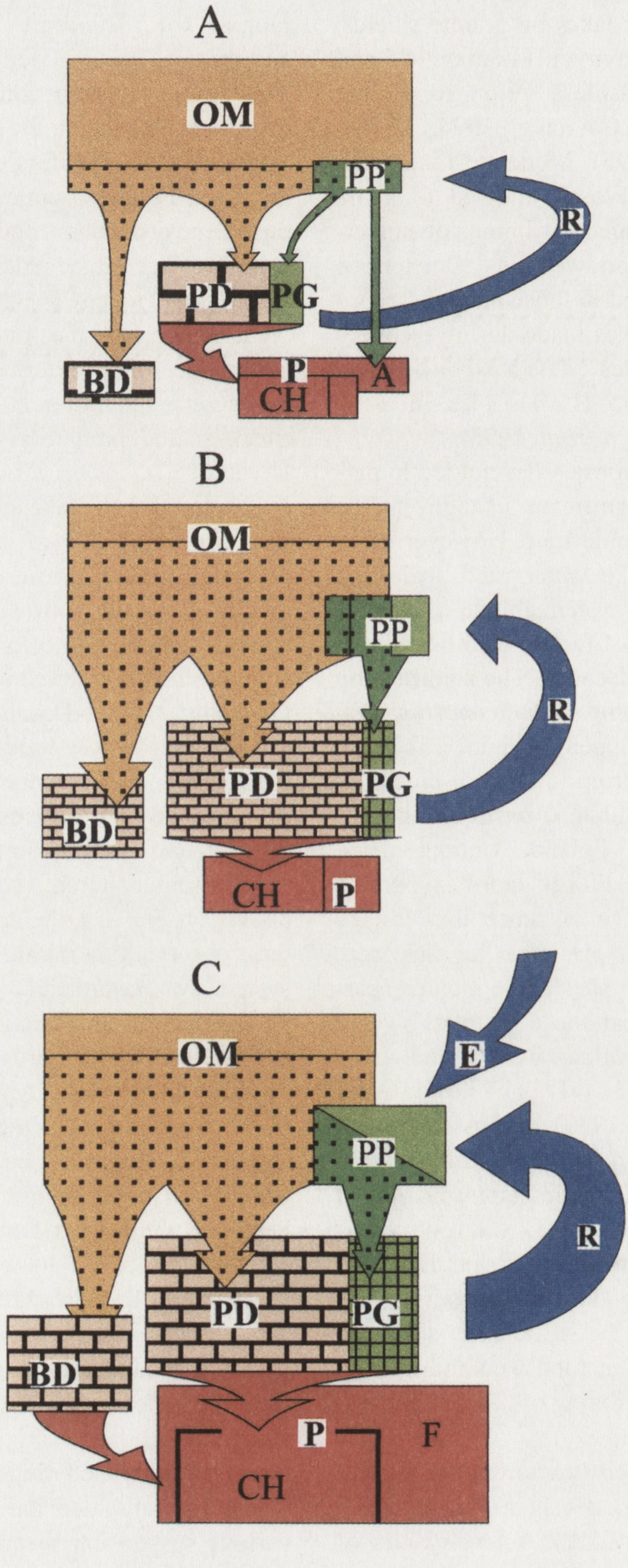
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Fig. 22. Scheme of main trophic path-ways in a humic Lake Flosek before liming (A), during liming period and a few years after (B) and 20–23 years after treatment (C).

Size of successive boxes and arrows roughly equal the character of long term changes of biomass of trophic links and the flux of matter between them. Pointed parts mean the food suspension available to filter feeders (bacterio-detrital and nanoplankton i.e. edible algae. The density of in-box pattern means the low or high biodiversity (species richness). Note the unrealistic, vertical relation between size of boxes (trophic links)! Diagram is aimed to stress the longitudinal changes in respect to trophic links in lake in different periods connected with treatment. The vertical orientation of scheme is deliberately chosen to visualise the main trophic path-way from the food reserves occurring in the water to the predatory component (mainly *Chaoborus* larvae) occurring mainly on lake bottom.
Orange area – microbial production and reserves of OM in lake
Brown area – bacterio-detritus feeders
Green area – primary production, phytoplankton and grazers
Red area – predators
Blue – flux of nutrients
OM – organic matter (dissolved and particular) together with bacterial biomass (pointed area)
PP – pelagic producers: phytoplankton, edible algae (pointed area)
PD – planktonic detrito-bacterivores (mainly small rotifers and cladocerans)
PG – planktonic grazers (diatomids, larger rotifers, daphnids)
BD – benthic detrivores and deposit-feeders (chironomids, oligochaets)
P – predators: CH – *Chaoborus*, F – fish, also cyclopoids and predatory rotifers like *Asplanchna* – A
R – remineralization (mainly via zooplankton)
E – eutrophication: possible external input of nutrients

A. Only a small part of OM is available (detrito-bacterial suspension) for filter feeders because of slow decomposition rate under acid condition. The biomass and diversity of plankton (PD) and benthic-detrivores (BD) are low due to low pH. A part of the low algal biomass (PP) is grazed by predatory rotifer (*Asplanchna*) and some diatomids. The biomass of predators (P) including larvae *Chaoborus* is low. Remineralization is inefficient (R). The system seems to be mainly bottom-up controlled and limited by low pH.

B. After liming a larger fraction of OM became available for filter and deposit feeders (pointed orange area) because of microbial decomposition and development of microbial loop (chrysophytes in phytoplankton). The biomass and the diversity of plankton bacterio-detrivores (PD) (especially rotifers) and benthic ones (BD) (chironomids) are higher. A bit higher algal biomas (PP) is probably more effectively grazed by "new-comers" PG, like daphnids. It is why the contribution of edible algae (nanoplankton) is lower (pointed green area). Predator biomass especially *Chaoborus* is higher. Remineralization is more efficient.

C. Higher biomass of plankton grazers (PG) like daphnids and diaptomids in grazing food chain and much higher biomass of *Chaoborus* (CH) larvae together with introduced fish (F) among predators (P) make the whole food web strongly top-down controlled. Effective in-lake remineralization (R) (via bigger zooplankton) as well as possible input of nutrients from outside of the system (E) affect primary producers. A higher algal biomass (PP) but lower contribution (due to grazing) of edible algae (pointed green area) was noted in 22 and 23 years after treatment.

fers or benthic detrivores. Also they were probably responsible for dominance of heterotrophic chrysophytes in phytoplankton. In that period, abundance of bacteria increased, and phosphate phosphorus concentration dropped considerably as phosphates were possibly utilised by intensive microbial production competing with phytoplankton production (the latter one being almost unchanged). Development of consumer chain exploiting microbial food web (rotifers, cladocerans) led to alterations of predatory community, i.e. an increase in abundance of *Cyclopidae* (including colonisation of new species of the genus *Cyclops*) and *Chaoborus* larvae.

In-lake recycling mechanisms seem to be more effective. It should be expected that activation of microbial production also brings about development of microbial food web (bacterivores, like nanoflagellates) in the first place. Probably due to intensive bacterial uptake of nutrients, biomass of edible algae was maintained on low level but sufficient for grazing by *Diaptomidae* and large *Daphnia*. These bigger components of zooplankton effectively replace small microfiltering cladocerans. According to Salonen *et al.* (1992a, b) *Daphnia* may graze not only edible algae, but also components of microbial food web such as fine nano-flagellates or chrysophytes.

To generalise, much diverse system in the first years following liming still was strongly bottom-up controlled although grazing pressure of big daphnids and diaptomids on lower links was also significant (Fig. 22B).

Twenty-twenty three years after liming, food web functioning in Lake Flosek shows clear symptoms of top-down control although increase in biodiversity initiated by liming is maintained. This results from abundance increase of predatory invertebrates such as *Cyclops vicinus, Asplanchna priodonta*, and particularly *Chaoborus* larvae, as well as presence of planktivory fish (roach, bleak, perch). The joint pressure of predators determines overall decline in numbers of planktonic crustaceans and variability in their individual sizes, constrains diurnal migration and differentiates predator pressure in the central and near-shore parts of the lake, and selects species avoided by predators (e.g. rotifers with a gelatinous sheath) to be dominants. Numerous *Daphnia* and *Eudiaptomus* populations seem to have been responsible for over-grazing of phytoplankton as in the period considered edible algae were constantly scarce (Fig. 22C).

Twenty years after the treatment, the food web of Lake Flosek began to turn into the consumer system of strong top-down control. It seems that the system recycles nutrients more efficiently owing to a greater contribution of large grazers and predators. It may be presumed that statistically significant increases in total phosphorus, phosphate phosphorus and organic nitrogen, and consequent increase in algal biomass observed recently, i.e. in 22 and 23 year after liming, are symptoms of a higher efficiency of recycling mechanisms. However, another possible explanation of the phenomenon, namely "normal" symptoms of eutrophication, so called "new production", (i.e. a response to external nutrient supply), cannot be excluded. The supply may result from e.g. fish feeding, touristic attractiveness of the lake due to its location near a road where access by car is easy (though illegal), and forest clearance in a further surrounding of the lake.

Food web structure and functioning of the limed Lake Flosek in the period considered, i.e. after more than 20 years since the treatment, are thus generally different from those observed in the pre-liming or liming periods. An opinion expressed by Stenson (1985), Locke and Sprules (1994), Jarvinen *et al.* (1995) and Stenson and Svensson (1995), who have compared food webs between limed and non–limed lakes or (as in the case of Lake Gardsjön) between pre-liming and post-liming periods, has been confirmed. The above authors have claimed that the main factor responsible for full recovery of acidic lakes is reconstruction of top-down control of food web by using fish and predatory invertebrates. They have also noted that liming results solely in increased biodiversity, whereas abundance or dominance structure are regulated by predation and competition.