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The recovery of Vesijärvi, a lake in southern Finland: water quality and phytoplankton interpretations

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The recovery of formerly heavily eutrophicated Vesijärvi from noxious cyanobacterial blooms is described in terms of changes in phytoplankton and water quality. Substantial water protection and restoration measures were introduced since 1975. Two main turning points in the phytoplankton community structure occurred: a shift from *Planktothrix agardhii*- to *Aphanizomenon flos-aquae*-dominant blooms in the early 1980s and the total collapse of the cyanobacterial blooms in 1990. Both shifts were closely connected to the decrease in the nutrient concentrations (total N decreased from 800 mg m⁻³ to 600 mg m⁻³ and total P from 60 mg m⁻³ to 30 mg m⁻³), to the increase in water transparency, and to the elimination of extremely high pH values (> 9). In the mid-1990s the water quality as well as the species composition and the biomass of phytoplankton in Vesijärvi resembled the situation in the late 1950s.

Introduction

Eutrophication of freshwater lakes is frequently accompanied by blooms of cyanobacteria, which significantly lower the recreational and fishery value of the water body. In the restoration of lakes one goal is, thus, often to raise the recreational value of the lake by removing these noxious blooms. The reasons for the mass occurrence of cyanobacteria in eutrophicated lakes are manifold. Cyanobacteria have the ability to outcompete other species at low light intensities (Pearl and Ustach

1982, Zevenboom *et al.* 1982) and low maximal growth rates (Reynolds 1984). They are also capable of regulating their buoyancy and have low loss rates (e.g. Reynolds and Walsby 1975, Klemer *et al.* 1982), as well as often high affinities for N (Tilman *et al.* 1986) and/or the ability to fix atmospheric N (e.g. Zevenboom and Mur 1980). While the occurrence of cyanobacterial blooms is a very popular field of study, the mechanisms responsible for the disappearance of cyanobacterial blooms in the course of lake restoration have been studied rather less (Sas 1989, Kairesalo *et*

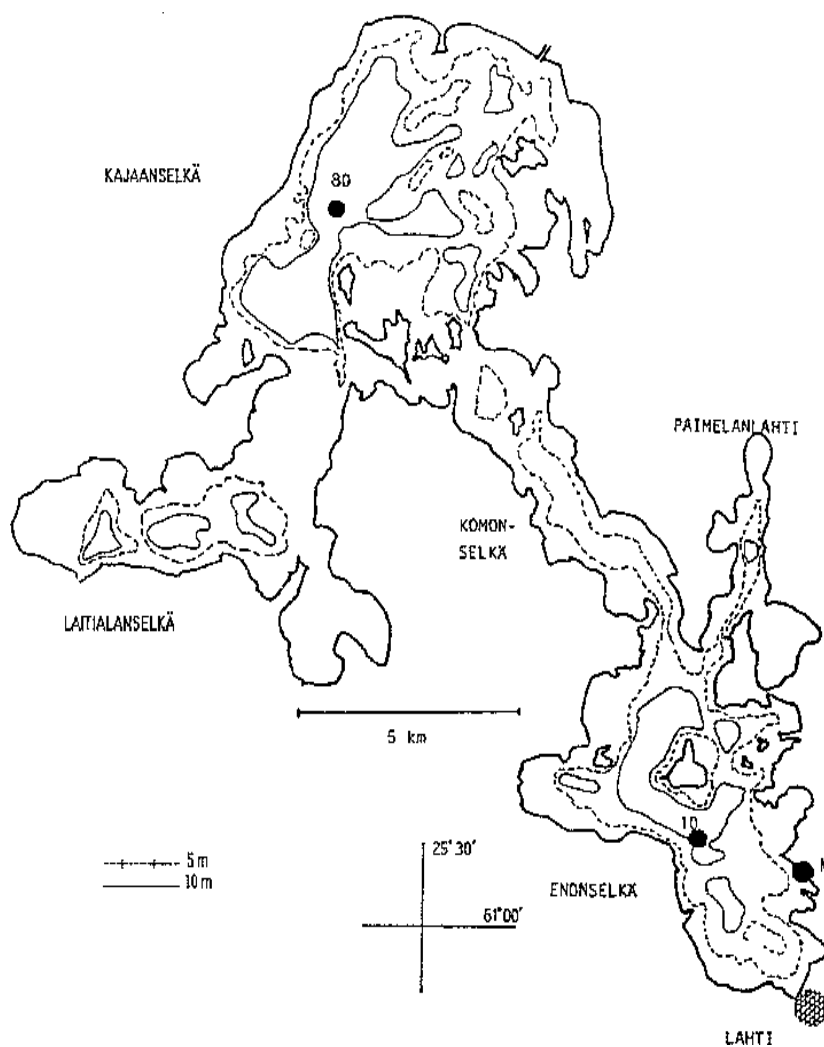


Fig. 1. Vesijärvi. The samples were taken from the deeps of Kajaanselkä (80) and Enonselkä (10) and from the community beach in Mukkula (M). The 5 m and 10 m depth curves are also shown.

al. 1999). Although it has been shown that cyanobacterial blooms tend to disappear as the P concentration of the water decreases (e.g. Sas 1989), the mechanisms and time-scales involved in different types of lakes as well as the role of internal loading are still fairly unknown. The occurrence of different species of cyanobacteria and their interaction with other phytoplankton groups is another interesting aspect in the often-observed successional decrease of noxious cyanobacterial blooms in lakes recovering from eutrophication.

Vesijärvi (Fig. 1) is a formerly heavily eutrophicated lake in southern Finland (61°00'N, 25°30'E) with a surface area of 110 km² and a mean depth of 6.0 m. After decades of urban sewage pollution, the sewage inflow to the lake was

diverted in 1976. The Enonselkä basin (area 26 km², mean depth 6.8 m) in particular was heavily eutrophicated by the sewage pollution through its nearness to the city of Lahti, while the Kajaanselkä basin in the northern part of the lake suffered less. The Enonselkä basin was artificially aerated during stagnation periods in 1979–1984 (Keto and Sammalkorpi 1988). The initially promising recovery of the lake (Keto 1982) was disturbed by the return of noxious cyanobacterial blooms in the beginning of the 1980s, due to roach-stock mediated internal nutrient loading (Keto and Sammalkorpi 1988). The internal loading maintained and even intensified the eutrophication and restricted the recreational and fishery use of the lake in the late 1980s through the mass development

of cyanobacterial blooms (Keto and Sammalkorpi 1988, Horppila and Kairesalo 1990, Horppila 1994).

The Vesijärvi Project was initiated in 1987. The goals of the program were to stop the eutrophication, to eliminate the toxic blooms and mass developments of cyanobacteria, to rehabilitate the recreational values and to re-establish a sustainable fishery in the lake. The project combined the goals of water quality control and fishery management in an ecological management strategy. Over 1 200 tonnes of coarse fish (mainly roach and smelt) were removed from the lake (described more closely in Horppila 1994 and Kairesalo *et al.* 1999). Pikeperch and other predatory fish stocks were introduced beginning in 1984. These measures have resulted in increases in the natural stocks of predatory fish (pike and pikeperch) and in economically important planktivorous fish (species of vendace and whitefish). A considerable decrease in the external loading of the lake was reached by establishing protection zones between the watercourses and cultivated areas.

This article is an overview of the development of the water quality and phytoplankton community in the lake in the course of the recovery from the man-induced eutrophication and, especially, biomanipulation process. In particular, we try to illustrate the causes involved in the phase-out of the noxious cyanobacterial dominance in the lake phytoplankton.

Materials and methods

The water quality and phytoplankton data series consists of water quality monitoring data collected from Vesijärvi mainly between 1982 and 1995. The water quality samples (total nitrogen (N), total phosphorus (P), iron (Fe), manganese (Mn), pH, conductivity, secchi depth, O₂ and temperature) were taken monthly, whereas phytoplankton and chlorophyll *a* samples were collected 5–8 times between May and October each year. Samples were collected from the deepest part of two basins: Enonselkä (maximum depth 30 m) and Kaajaonselkä (40 m). In addition, pH measurements from the littoral zone of Enonselkä (Mukkula) were included. The water samples were analysed in the laboratory of the City of Lahti as described

in Keto (1982) and Horppila and Kairesalo (1990). The phytoplankton samples were counted according to Utermöhl (1958). The nomenclature follows Tikkanen (1986) and Krammer and Lange-Bertalot (1991).

The statistical analyses were performed with the Detect and Exceed software, version 2.0. Firstly, the nature of any existing trends (monotonic, i.e. steadily increasing or decreasing, or stepwise, i.e. sudden) was preliminarily investigated with the cumulative sums function (CUSUM, Cluis 1988). Thereafter, the data were analysed for Markovian persistence, i.e. the structure of the autocorrelation within them was analyzed (Kettunen 1989), after which the data were checked for seasonality with Bartlett's test (Neter and Wasserman 1974) according to Cluis (1988). Thereafter, an appropriate non-parametric test (*see* Cluis 1988 or Kettunen 1989) was chosen to detect significant ($p < 0.05$) monotonic trends or stepwise changes in the trends of the data series. These procedures were performed on the whole data series (1979–1994) and on the earlier (1979–1988) and later (1989–1994) periods separately. Further information about the tests used can be found in Lettenmeier (1976), Hirsch *et al.* (1982), Hirsch and Slack (1984), Van Belle and Hughes (1984) and Kettunen (1989).

Results

Water quality

The main trend in the recovery of Vesijärvi can clearly be seen in the conductivity values since the 1960s (Fig. 2). In Enonselkä, the conductivity attained its highest point in 1975. As the lake recovered, the values decreased to the level of those measured in the late 1960s. The overall development of the water quality of Vesijärvi is also reflected in the water transparency (secchi depth) in the lake. After the diversion of the sewage loading the transparency in Enonselkä improved considerably to around 2 m, but by the beginning of the 1980s it had started to decline again. The winter blooms of cyanobacteria in the early 1980s lowered the transparency all over Vesijärvi, but as the winter blooms declined in 1985 the transparency of Vesijärvi increased, only to decrease

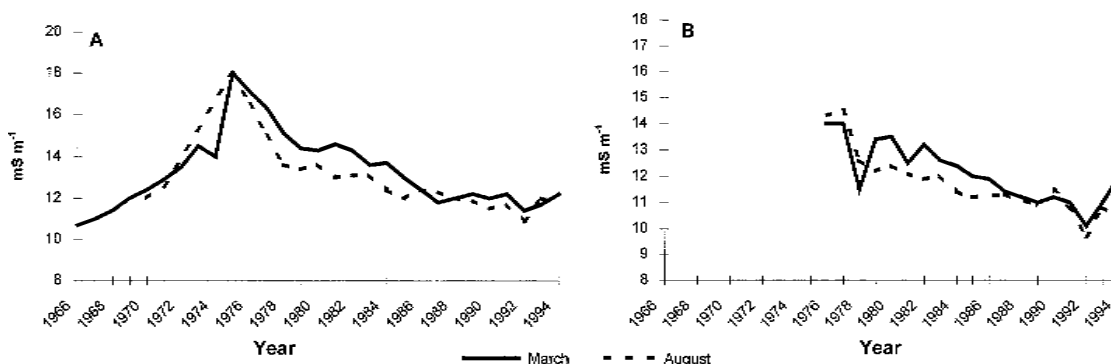


Fig. 2. The conductivity (mS m^{-1}) in (A) Enonselkä (1966–1994) and (B) Kajaanselkä (1976–1994).

again during the productive season through the summer-blooming cyanobacteria in the mid-late 1980s. In the beginning of the 1990s the clarity of Vesijärvi water improved, and especially in June and July the transparency in Enonselkä increased (Fig. 3A). When only the period after 1989 is considered, a significant positive step was found for the secchi depth in Enonselkä in 1992 and in Kajaanselkä in 1991 (Fig. 3A and E). On average, the transparency of the water during the growth season doubled between 1989 and 1994.

The dissolved oxygen concentration (DO) has increased slightly in the Enonselkä basin during the biomanipulation (statistically significant difference, Fig. 3B), while there have been only minor changes in the DO concentrations in Kajaanselkä (Fig. 3F). In Enonselkä, the DO concentration in the hypolimnion in particular has improved, most notably in March, so that it approaches the level of that in Kajaanselkä (Fig. 4).

Since 1982, when the regular phytoplankton monitoring began, the total N level in Enonselkä has decreased statistically significantly, from around 800 mg m^{-3} in 1982 to 500 mg m^{-3} in 1994 (Fig. 5A), and the total P correspondingly from $50\text{--}60 \text{ mg m}^{-3}$ in the early 1980s to below 30 mg m^{-3} in the mid-1990s (Fig. 5B). The clearest step downwards took place in 1989 (N) and 1990 (P). In Kajaanselkä, the initial levels were lower and the decreases less steep; both total N and total P decreased statistically significantly, however, from around 500 mg m^{-3} to about 400 mg m^{-3} (N; Fig. 5D), and from 20 mg m^{-3} to 15 mg m^{-3} (P; Fig. 5E). A stepwise trend was detectable in 1987 for N and in 1990 for P. The N:P ratio fluctuated

between 10 and 40 in Enonselkä while there were more high values in Kajaanselkä. When only the period after 1989 is considered, a new step downwards emerged for N in Enonselkä, in 1992 (Fig. 5A). If only the beginning of the 1980s are considered, the N values as well as the N:P ratio in Enonselkä showed positive stepwise trends in the early 1980s (1983 and 1984, respectively). The increase in the N:P ratio is partly due to the increase in the external N:P loading ratio (1973: 5.9, 1979: 12.2, 1987: 19.5, 1992:20).

The chlorophyll *a* concentrations (Chl *a*, Fig. 5D and H) tended to increase in the late 1980s but have decreased afterwards more rapidly than the respective phosphorus concentrations.

The water of Vesijärvi is slightly alkaline; during the winter stagnation period the pH is typically 7.2–7.4 (epilimnion) and 6.8–7.0 (hypolimnion) in both basins. In the 1980s, the pH often exceeded 8 during the diatom blooms in May, and during cyanobacterial blooms from June till late summer pH was 8.5–9 in the the upper part of the epilimnion in Enonselkä (0–5 m; Fig. 3C). In August 1989, for instance, the surface water pH was 10.5–11.0 during a two-week massive cyanobacterial bloom. In the 1990s the mid-summer pH values have not exceeded 8, but in August or early September slight blooms of cyanobacteria have elevated the pH to 8.5–9 for a few days. The overall trend in the surface pH in Enonselkä has been rising; however, it rose slightly throughout the 1980s (Fig. 3C), with a step up in 1983. If only the beginning of the 1980s are considered the pH values also increase, continuously in Enonselkä and stepwisely in Kajaanselkä (1983; Fig. 3C and G).

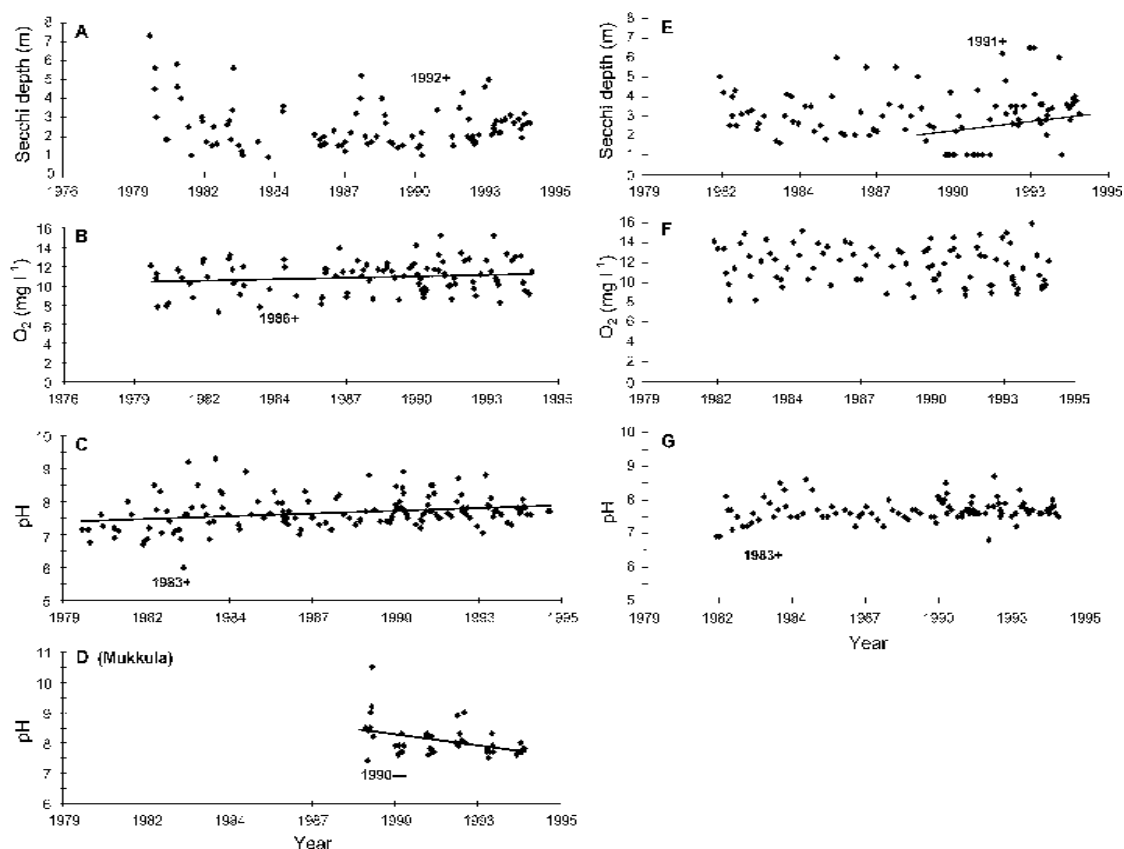


Fig. 3. The secchi depth (water transparency; m), dissolved oxygen concentration (mg l^{-1}) and pH in Enonselkä (left-hand side panels) and Kajaanselkä (right-hand side panels). Significant ($p < 0.05$) monotonic trends are shown as increasing or decreasing lines. Significant ($p < 0.05$) stepwise increasing or decreasing trends are indicated by the year in question with a + or – sign attached. If the stepwise trend was significant for the entire period, the year is underlined. A non-underlined year indicates a significant stepwise trend during a shorter period (1984–1988 or 1989–1994).

The pH values from the littoral zone (the community beach in Mikkula) showed a decreasing trend from 1989 to 1994, though (Fig. 3D).

Phytoplankton

The total phytoplankton biomass in Enonselkä was very high (yearly average $7\text{--}8 \text{ g m}^{-3}$, maximum values $> 23 \text{ g m}^{-3}$) in the beginning of the 1980s, but decreased sharply in 1984 and has decreased further since then (statistically significant decrease; Fig. 6A). A significant stepwise decrease took place in 1987. Except for a few isolated high values, the total biomass in Kajaanselkä has been on a lower level ($< 3 \text{ g m}^{-3}$) throughout the stud-

ied period (Fig. 6H).

The phytoplankton species composition in Enonselkä has changed dramatically since the early 1980s as the cyanobacteria have been replaced by other groups, mainly diatoms and cryptophytes (Fig. 7A). In Kajaanselkä, the cyanobacterial dominance was marked only for a short period in the beginning of the 1980s, and diatoms have dominated for most of the rest of the period. The chrysophytes' share of the total biomass in Kajaanselkä has increased slightly in the 1990s (Fig. 7B). The decreases in cyanobacterial biomass were significant in both basins, and significant steps down were found in 1984 (Enonselkä) and in 1986 (Kajaanselkä; Fig. 6B and I); if only the period since 1989 is considered, negative stepwise

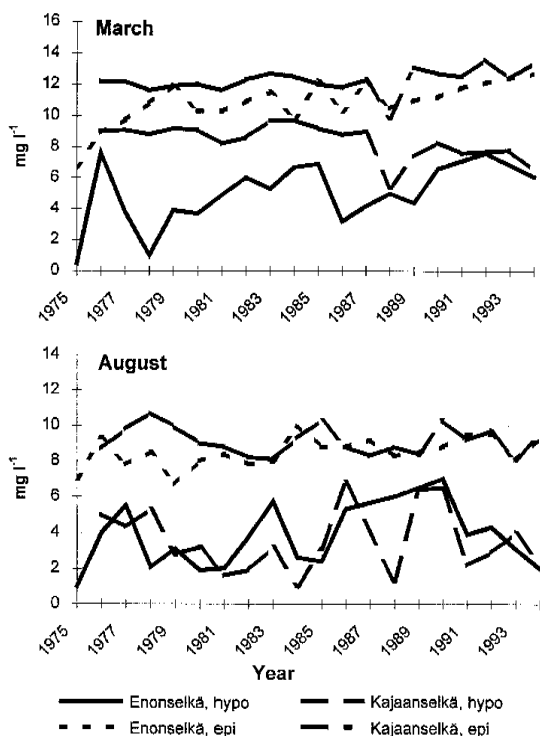


Fig. 4. The dissolved oxygen concentration (mg l^{-1}) of the epi- and hypolimnion in Enonselkä and Kajaanselkä in March and August between 1975 and 1994.

trends are found in Enonselkä in 1993 for the total phytoplankton biomass and in 1989 for the cyanobacteria (Fig. 6A and B).

In Kajaanselkä, the trend has been the same: the dominance of *Planktothrix agardhii* (Gomont) Anagostidis and Komarék (possibly *Planktothrix mougeotii* (T. Finni pers. comm.) and previously referred to as *Oscillatoria agardhii* Gomont (e.g. Keto 1982, Keto and Sammalkorpi 1988)) in the beginning of the 1980s was however briefer, and the mass occurrences of *Aphanizomenon flos-aquae* (Linné) Ralfs between 1985 and 1989 were absent (Fig. 8). Colonial coccal cyanobacteria (*Microcystis* sp., *Woronichinia* sp. and *Snowella* sp.) and *Anabaena* species have replaced the earlier dominant species in the 1990s (Fig. 8). In 1982–1984, a strain of red hepatotoxin-producing *Planktothrix agardhii* caused substantial damage in both Enonselkä and Kajaanselkä by blooms in late autumn and winter (Keto 1982, Keto and Sammalkorpi 1988, Persson *et al.* 1988).

The *Aulacoseira* bloom among the bacilla-

riophytes in Enonselkä in the early-mid-1980s (Fig. 8) consisted of a succession of species (*Aulacoseira italica* (Grunow) Müller, *A. islandica* Simonsen, *Aulacoseira ambigua* (Grunow) Simonsen and *A. granulata* (Ehrenberg) Ralfs. In the 1990s several species have dominated (Fig. 8), but none for any extended period of time (*Aulacoseira* sp., *Asterionella formosa* Hassall, *Fragilaria crotonensis* Kitton, *Tabellaria flocculosa* (Roth) Kützinger). A curiosity is the emergence of the in Vesijärvi previously unknown *Actinocyclus normanii* fo. *subsalsus* (Gregory ex Greville) Hustedt in the 1990s (Liukkonen *et al.* 1997, Kairesalo *et al.* 1999). In Kajaanselkä the *Aulacoseira* maximum in the mid-1980s was smaller. Only when the period after 1989 is considered separately did the diatom biomass increase in Enonselkä (Fig. 6F).

The cryptophyte biomass has increased significantly in Kajaanselkä, with a step up in 1990, while the trend in Enonselkä has been if anything decreasing (negative step in 1991; Fig. 6C). The dinophyte biomass has increased slightly towards the end of the studied period in Enonselkä (Fig. 6D). The chrysophyte biomass has increased statistically significantly in Enonselkä (Fig. 6E). Among the chlorophytes, a mass occurrence of the littoral *Mougeotia* sp. in 1984 in both Enon- and Kajaanselkä is interesting.

Discussion

The changes in the phytoplankton community and the variations in the water quality variables in Vesijärvi during the studied period were clearly interconnected. In Enonselkä, two obvious step-wise changes in the trends of the nutrients and phytoplankton biomass have occurred: in 1984–1985 and in 1989–1990. Both steps were apparently functions of changes in the cyanobacterial biomass and species composition, which were either reflected in, or caused by, respective changes in the water quality and in the food web (Kairesalo *et al.* 1999).

The disappearance of the *Planktothrix agardhii* blooms, which had plagued Enonselkä for two decades (Keto and Sammalkorpi 1988), was the main manifestation of the sudden change in 1984 in Enonselkä and responsible for the sudden drop in the total phytoplankton biomass. The

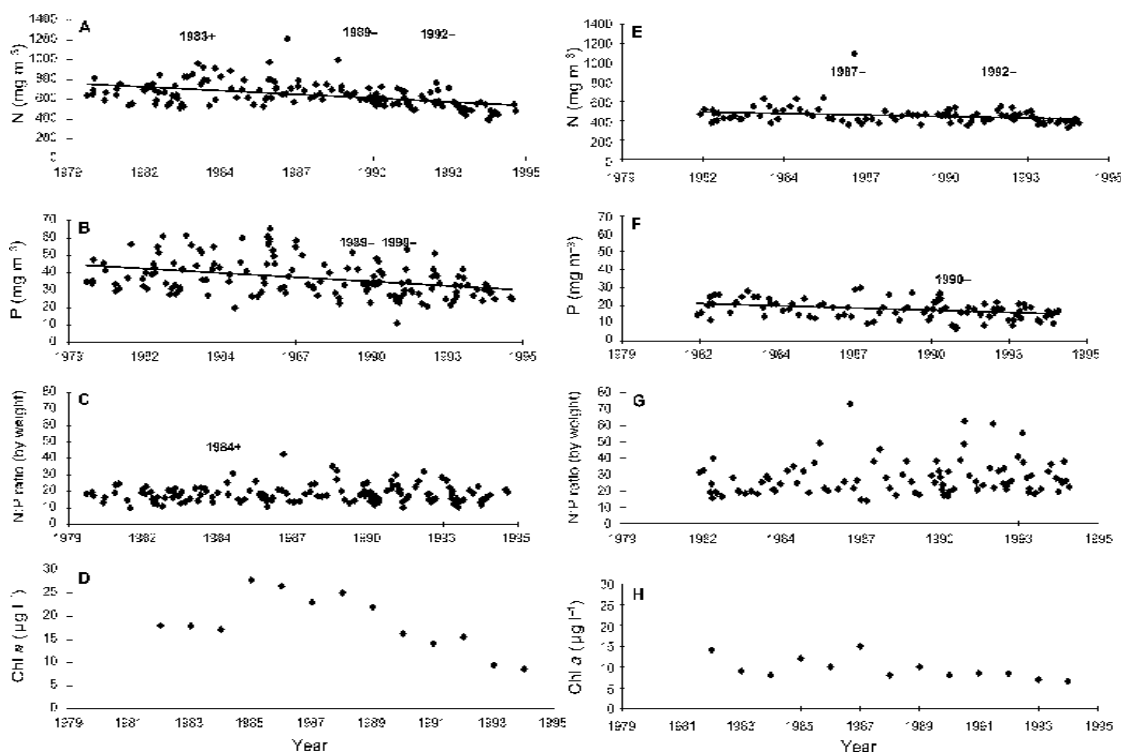


Fig. 5. The N and P concentrations (mg m^{-3}), N:P ratio and chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) in Enonselkä (left-hand side panels) and Kajaanselkä (left-hand side panels) between 1980 and 1994. Significant ($p < 0.05$) monotonic trends are shown as increasing or decreasing lines. Significant ($p < 0.05$) stepwise increasing or decreasing trends are indicated by the year in question with a + or – sign attached. If the stepwise trend was significant for the entire period, the year is underlined. A non-underlined year indicates a significant stepwise trend during a shorter period (1984–1988 or 1989–1994). The chlorophyll *a* concentrations in Enonselkä and Kajaanselkä on average for the growth season from 1982 to 1994.

shift in species composition among the still dominant cyanobacteria was towards *Aphanizomenon flos-aquae*.

The aeration of the hypolimnion in the Enonselkä basin during stagnation periods between 1979 and 1984 ceased in 1984, which may have partially caused the disappearance of *Planktothrix agardhii*. *P. agardhii* grows throughout the productive layer and does not form scums on the surface (Ahlgren 1977, 1978). The additional turbulence induced by the aeration may have favoured the species, since *P. agardhii* and similar, turbulence tolerant species (w-strategists, *sensu* Reynolds 1986) are stimulated by mixing (Reynolds 1984), and thus favoured by comparatively high (2–3; Reynolds and Walsby 1975) mixed layer:euphotic layer depth ratios. The curious mass occurrence of the green, normally exclusively littoral algae *Mougeotia* sp. in the lake in 1984 may

also be an indication of changes in the turbulence patterns in the lake that summer.

P. agardhii is in many respects more of an opportunist than *Aphanizomenon flos-aquae* (e.g. Uehlinger 1981, Zevenboom *et al.* 1982). Apart from the end of the aeration the recovery process of the lake may have reached a new, steadier equilibrium phase eight years after the sewage loading had been diverted, which also favoured the more “stable” cyanobacteria *Aphanizomenon flos-aquae*. The dominance of *P. agardhii* was, namely, also diminished in Kajaanselkä, which had not been aerated, at the same time. There, *Aphanizomenon flos-aquae* did not take the place of *P. agardhii*, however; the cyanobacterial share of the total biomass, which had always been much lower than in Enonselkä, dropped instead.

Aphanizomenon flos-aquae is in addition, as opposed to *P. agardhii*, capable of N_2 -fixation (e.g.

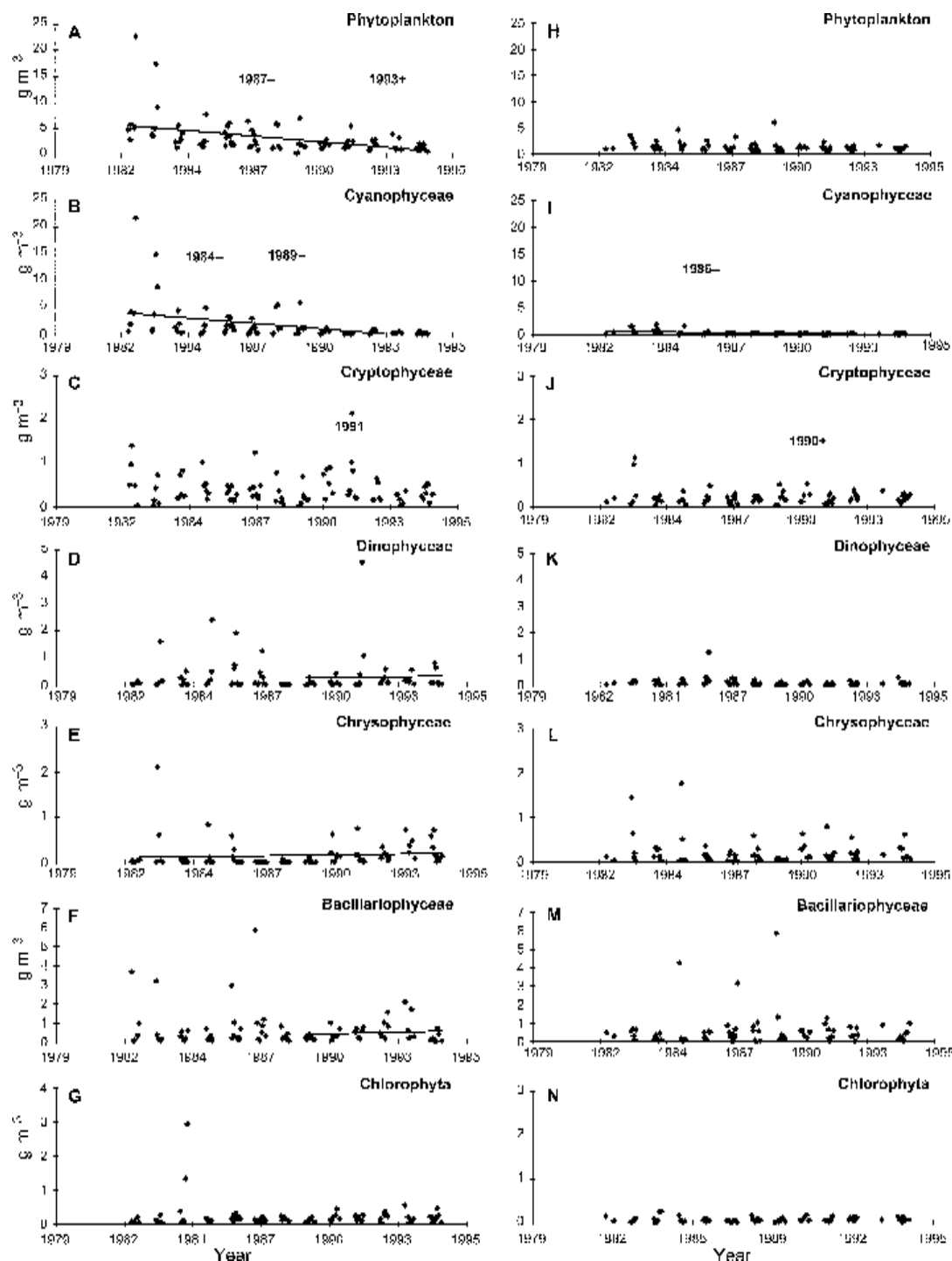


Fig. 6. The total phytoplankton, cyanophyceae, cryptophyceae, dinophyceae, chrysophyceae, bacillariophyceae and chlorophyta biomasses in Enonselkä (left-hand side panels) and Kajaanselkä (right-hand side panels). Significant ($p < 0.05$) monotonic trends are shown as increasing or decreasing lines. Significant ($p < 0.05$) stepwise increasing or decreasing trends are indicated by the year in question with a + or – sign attached. If the stepwise trend was significant for the entire period, the year is underlined. A non-underlined year indicates a significant stepwise trend during a shorter period (1984–1988 or 1989–1994).

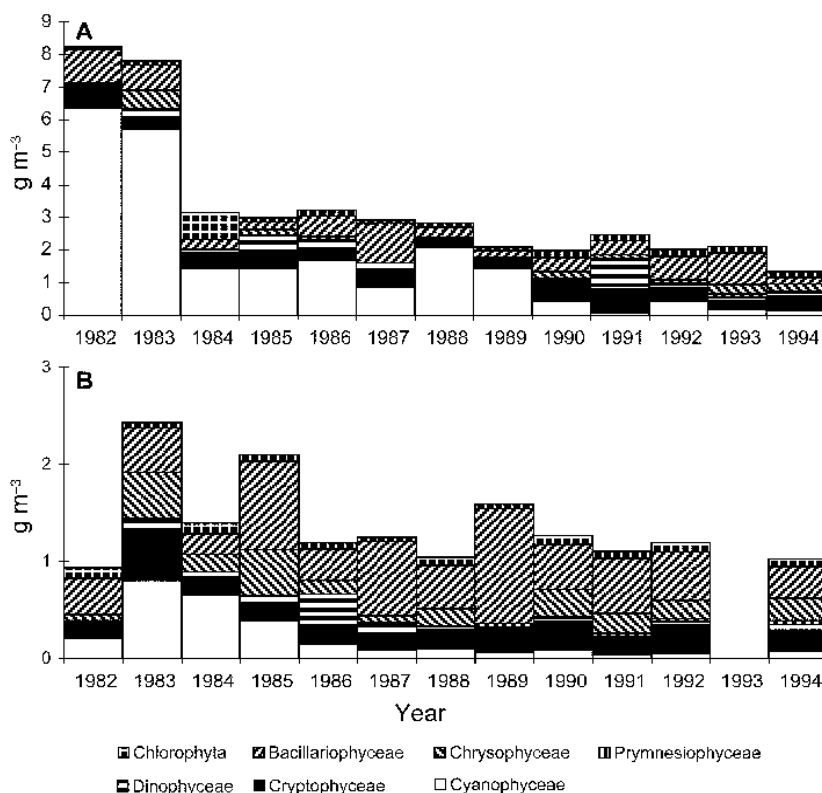


Fig. 7. The yearly average total phytoplankton biomass and its division between different groups from 1982 to 1994 in Enonselkä (A) and Kajaanselkä (B). Note the different scales.

Uehlinger 1981), and the shifts in the nutrient concentrations in Enonselkä contributed to the shift in species. The total N concentration in the water, as well as the N:P ratio, showed an increasing trend in 1984, however, and N fixation may, moreover, be of only minor importance in shallow eutrophic lakes where the internal loading is more likely to compensate for any observed N deficiency (Leonardson 1984). Also, *Aphanizomenon* has been shown to rather depend on nutrient pulses from deeper water layers than on its comparatively uneconomical N fixation (Grönlund *et al.* 1996, Heiskanen and Olli 1996, Kononen *et al.* 1996). Different nutrient affinity is more likely to be the operative factor than N fixation. Whereas *P. agardhii* has a high affinity for nitrate (Zevenboom and Mur 1980), heterocystous cyanobacteria have another competitive advantage over non-heterocystous ones in that they have a higher affinity for P (Leonardson 1984, Jensen *et al.* 1994). At least under *in vitro* conditions, the heterocyst-forming *Aphanizomenon flos-aquae* has a higher affinity for PO_4 than *Planktothrix agardhii* (Ahlgren 1977, Uehlinger 1981).

Whereas the temperature optima of the two species lie in the same range (25–30 °C; Uehlinger 1981), *Aphanizomenon flos-aquae* is more tolerant of high light intensities than is *Planktothrix agardhii* (Uehlinger 1981) — naturally enough, since *Aphanizomenon flos-aquae* forms surface blooms and thus is exposed to very high light intensities. Another of the groups which replaced *Planktothrix agardhii*, *Microcystis* sp., also have high light requirements (Paerl and Ustach 1982). Zevenboom *et al.* (1982) hypothesise that it is namely the higher growth rate of *Planktothrix agardhii* under low light requirements in combination with a higher affinity for nitrate (Zevenboom and Mur 1980) that paradoxically enables it to outcompete the N-fixing *Aphanizomenon flos-aquae* even under conditions when N is the limiting nutrient.

Although the most massive blooms of *Planktothrix agardhii* primarily took place in late summer (July–August), the species was among the dominant phytoplankton almost throughout the year; in Enonselkä, the blooms of red strains of *Planktothrix agardhii* occurred even throughout

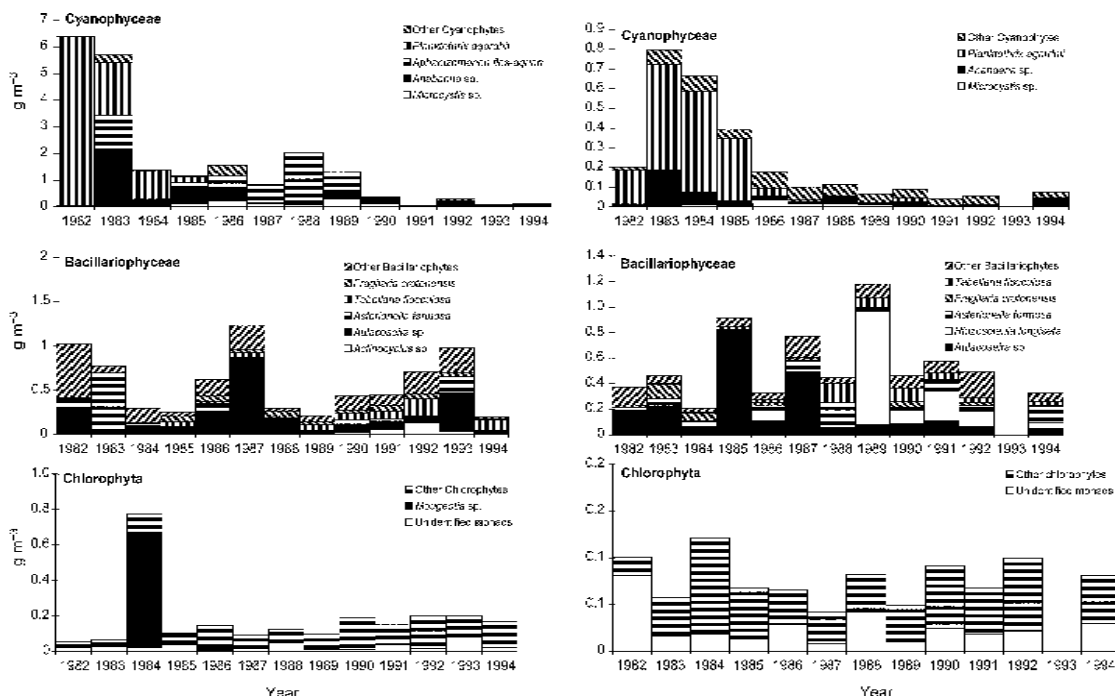


Fig. 8. The yearly average cyanophyceae, bacillariophyceae and chlorophyta biomasses in Enonselkä (left-hand side panels) and Kajaanselkä (right-hand side panels), with the most common taxa in each group shown. Note the different scales.

the winters in 1982–1984. Dominance by *P. agardhii* is usually accompanied by low phytoplankton diversity (Romo and Miracle 1995). *Aphanizomenon flos-aquae*, on the other hand, occurred almost exclusively in late summer. Whether this ecological difference affected the shift in dominance is not clear; it did, however, most certainly affect the overall species composition among the phytoplankton. This shift from *P. agardhii* to *A. flos-aquae* freed a number of ecological niches for the phytoplankton and raised the species diversity. All the *Aulacoseira* species which abounded in Vesijärvi in the mid-1980s were species which thrive in eutrophic waters (Tikkanen 1986, Krammer and Lange-Bertalot 1991), especially the peak-forming *A. islandica*. Apparently the shift among the cyanobacterial species in 1984 freed a niche for the Aulacoseirans in the still eutrophic lake. Among the species which replaced the *Aulacoseira* spp. in Enonselkä both *Fragilaria crotonensis* and *Tabellaria flocculosa* are summer species, which, presumably, to a larger extent compete with the cyanobacteria than the mainly spring- and autumn-species of *Aulacoseira*.

The collapse of the cyanobacterial blooms and the subsequent shift towards dominance by other phytoplankton groups in the early 1990s in Enonselkä (Kairesalo *et al.* 1999) did probably also have multiple causes. Clear downward steps in both the total N and total P concentrations in the surface water were found in 1989–1990. Since cyanobacteria in general are inefficient at taking up nutrients at low ambient concentrations (e.g. Reynolds 1984), it is probable that the additional factor which, apart from the decrease in the total nutrient concentrations, contributed to the shift in 1989–1990 was a change in the rate of cycling of nutrients in the lake.

The mass removal of cyprinid fishes and the subsequent reduction in the roach and smelt stocks (Horppila and Peltonen 1994) is bound to have affected the phytoplankton structure in Vesijärvi. A substantial amount of P was, firstly, taken away from the lake through the removal of the fish, accelerating the decrease in the total P concentration in the water (Horppila 1994). Secondly, the removal of especially the bottom-foraging roaches decreased the internal loading pressure on the lake

(Horppila 1994, Kairesalo *et al.* 1999). The decrease in the roach stock may in addition have been instrumental in causing a shift in the nutrient recycling in the pelagial, too, since migrating schools of roach have been shown to represent a substantial input of nutrients to the pelagial in the form of pulses of easily-degradable faeces, at least in mesocosm experiments (Horppila and Kairesalo 1990, Keto *et al.* 1992, Kairesalo *et al.* 1999). Further, the manipulation of the fish stocks undoubtedly caused some changes in the rest of the food web (e.g. decrease of the cyprinids and improvement in the predator fish stocks), which were reflected in the phytoplankton biomass and species composition (Peltonen *et al.* 1999).

At high pH, especially, when the supply of suitable carbon sources for other phytoplankton (e.g. eucaryotic r-strategists) may become the limiting growth factor, cyanobacteria are favoured by their ability to utilize even low levels of CO₂ (Shapiro 1973, Fogg *et al.* 1973, Paerl and Ustach 1982). Since cyanobacteria thus are less competitive at pHs lower than 8.5 (Shapiro 1990), they probably suffered relatively more than e.g. chlorophytes and diatoms in the recovery process of Vesijärvi. Although the overall pH trend in Enonselkä has been increasing, the littoral values have decreased since 1989, and extremely high (> 10) summer values have no longer appeared in the 1990s. Thus, the lowering of the pH as a result of declining primary production may have been another causative factor in the disappearance of the cyanobacterial blooms from Enonselkä in the 1990s. The lower pH most likely made the shift more dramatical than would have been expected from the changes in the other water quality variables.

Conclusions

The water quality in Enonselkä, especially, has improved substantially since the beginning of the 1980s, particularly since the biomanipulation started in the late 1980s. The noxious cyanobacteria blooms, which were the perhaps greatest obstacle in the recreational use of the lake, disappeared in a stepwise fashion: in 1984–1985, the cyanobacterial biomass dropped and the dominance shifted from *Planktothrix agardhii* to *Apha-*

nizomenon flos-aquae, and in 1989–1990 the mass blooms of cyanobacteria disappeared altogether.

The main factors that caused the shift in species dominance in 1984 were probably the cessation of the aeration of the Enonselkä hypolimnion in combination with the gradual lowering of the total N and, especially, P concentration of the lake water. The collapse of the cyanobacterial blooms in the early 1990s was most likely driven by biomanipulation-induced changes in the recycling rates of the remaining nutrients. The elimination of the earlier extremely high pH values may have further accelerated the change in the phytoplankton community. It is notoriously difficult to point out specific connections between the changes in the phytoplankton and the changes in nutrients and other water quality variables, however. Monitoring data does not reveal the mechanisms behind the observed changes which are results of several biological processes of different spatio-temporal scales. The recovery of the lake has to be viewed as a dynamic, interactive process, where many mechanisms interact and causes and effects are jumbled.

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