LIISA LEPISTÖ

Phytoplankton assemblages reflecting
the ecological status of lakes in Finland

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Liisa Lepistö

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Contents

Summarised publications and the author's contribution

This thesis is based on the following papers, which are referred to in the text by their Roman numerals I–VII:

I Lepistö, L., Räike, A. & Pietiläinen, O.-P. 1999. Long-term changes of phytoplankton in a eutrophicated boreal lake during the past one hundred years (1893–1998). Algological Studies 94: 223–244.

II Lepistö, L. & Saura, M. 1998. Effects of forest fertilization on phytoplankton in a boreal brown-water lake. Boreal Environment Research 3: 33–43.

III Lepistö, L. 1995. Phytoplankton succession from 1968 to 1990 in the subarctic Lokka reservoir. Publications of the Water and Environment Research Institute 19: 1–42.

IV Lepistö, L. & Pietiläinen, O.-P. 1996. Development of water quality and phytoplankton communities in two subarctic reservoirs and one regulated lake. In: K. V. Rao (ed.). Proceedings of international conference on aspects of conflicts in reservoir development & management. Dep. Civil Engineering, City University, London, UK. 553–566.

V Lepistö, L., Antikainen, S. & Kivinen, J. 1994. The occurrence of *Gonyostomum semen* (Ehr.) Diesing in Finnish lakes. Hydrobiologia 273: 1–8.

VI Lepistö, L., Lahti, K., Niemi, J. & Färdig, M. 1994. Removal of Cyanobacteria and other phytoplankton in four Finnish waterworks. Algological Studies 75: 167–181.

VII Lepistö, L. & Rosenström, U. 1998. The most typical phytoplankton taxa in four types of boreal lakes. Hydrobiologia 369/370: 89–97

• Liisa Lepistö has since 1965 participated in the microscopy work of phytoplankton from the monitored lakes in Finland and is responsible for the phytoplankton data in papers I–VII.
• In paper I L. Lepistö was responsible for planning of the examination, for examination of the unpublished data, and for processing the phytoplankton data. All authors took part in the physico-chemical data processing, interpretation of results and writing in their own area of expertise.
• In paper II the examination was planned and the data processed together with Matti Saura. Phytoplankton was analysed by L. Lepistö. Both authors (L. Lepistö and M. Saura) were responsible for the interpretation and writing of results, L. Lepistö having the main responsibility.
• L. Lepistö initiated the treating of data and interpretation of results for paper IV, O.-P. Pietiläinen participated in the writing. L. Lepistö had the main responsibility.
• L. Lepistö and S. Antikainen participated in the planning of the study (V) and in the interpretation and writing of results. S. Antikainen was mainly responsible for data processing. J. Kivinen commented on the manuscript. L. Lepistö had the main responsibility.
• In paper VI the examination was planned together with Dr. Kirsti Lahti who was responsible for the toxicity studies and the data from the water works. L. Lepistö examined the phytoplankton samples. All authors took part in data processing, interpretation of results and writing in their own area of expertise.
• L. Lepistö planned the examination in paper VII, U. Rosenström treated the data and both authors participated in the interpretation of results and writing, L. Lepistö having the main responsibility.

Phytoplankton assemblages reflecting the ecological status of lakes in Finland

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ABSTRACT

A review is presented of studies on phytoplankton reflecting the ecological status of natural and man- made lakes in Finland. Attention is paid to phytoplankton quantity and quality in different lake types, and to changes in phytoplankton assemblages caused by human activities, particularly waste water loads and construction of man-made lakes. The response of phytoplankton in Lake Tuusulanjärvi to eutrophication during the twentieth century and to changes in water quality caused by water protection efforts since the late 1970s was investigated as a case study. Reduction in the nutrient load in 1979 changed the phytoplankton assemblage, as the non-N_2- fixing cyanophytes were replaced by N_2- fixing cyanophytes. The total biomass decreased, and some species indicating more oligotrophic conditions reappeared. The possible response of phytoplankton to the fertilization of the catchment area of a humic forest lake with NP-fertilizers was considered. Only in the subsequent spring was an increase in phytoplankton biomass observed. No other biomass maxima were observed in the lake until five years later, when *Gonyostomum semen* became abundant. After the construction of man-made lakes the phytoplankton develops via several stages; the original river plankton, such as pennate diatoms, is succeeded by centric diatoms, especially during periods of strong water level regulation. Phytoplankton quantity reflected the water quality of the reservoirs. In the meso-eutrophic Lokka reservoir, cyanophytes became abundant, especially during warm weather conditions. The feasibility of phytoplankton monitoring as an indicator of the ecological status of lakes, identification problems of phytoplankton and the need for a methodological tradition are considered. The correct identification of phytoplankton is the basis of all phytoplankton assemblage studies. Species diversity, which is an important indicator of water quality, is gravely influenced by methodological problems in phytoplankton analysis.

Key words: Phytoplankton, eutrophication, trophic status, ecological status, lakes, artificial lakes

1 Introduction

1.1 Phytoplankton

Studies on phytoplankton assemblages of lakes in Finland were initiated in the late 1890s by Kaarlo Levander (1900). In the early 1910s, Heikki Järnefelt (*e.g.* 1932, 1934, 1956a) started his fundamental studies on phytoplankton, covering lakes from southern Finland as far north as Lapland. He classified the trophic status of lakes according to their phytoplankton assemblages (Järnefelt 1952, 1956a). On the basis of Järnefelt's studies, the monitoring of water bodies in Finland was started by the water authorities in the early 1960s. The first monitoring network covered 150 lakes (Heinonen 1980). In addition to the monitoring data of water authorities, several authors have published phytoplankton data from Finnish lakes. For example, Ilmavirta (1980, 1983), Arvola (1983, 1984) and Salonen *et al.* (1984) studied humic lakes and focused on the influence of water colour on phytoplankton assemblages. Eloranta (1976, 1986, 1995) examined the phytoplankton of lakes in central and southern Finland, including lakes situated in the national parks which could be regarded as reference lakes for monitoring. Ilmavirta *et al.* (1984) studied the phytoplankton of 151 lakes in eastern Finland during the summer stratification. Spatial and seasonal variations of phytoplankton of the oligotrophic Lake Pääjärvi, Lammi, southern Finland, was studied by Ilmavirta and Kotimaa (1974). The quantity and quality of phytoplankton of Lake Pyhäjärvi, Säkylä, SW- Finland was briefly discussed by Sarvala and Jumppanen (1988) and of Lake Ala-Kitka, NE-Finland by Kankaala *et al.* (1990). The horizontal distribution of phytoplankton and relationships between phytoplankton, zooplankton and water quality of Lake Saimaa were examined by Holopainen *et al.* (1993) and Karjalainen *et al.* (1996). Furthermore, the influence of a sulphite cellulose factory on phytoplankton of Lake Keurusselkä was studied by Eloranta (1972, 1974), and Granberg (1973) studied the influence of paper mill waste waters on phytoplankton in Lake Päijänne.

Lake ecosystems, with their specific chemical compositions and geographical locations are often characterised by their own phytoplankton assemblages, referred to as plankton formations (Teiling 1916). When phytoplankton occurs in a water body in low densities, it seldom receives attention. However, when eutrophication manifests itself as an increase in biological productivity, phytoplankton becomes more visible. As a result of the process of eutrophication several negative impacts, such as an increase of injurious phytoplankton species, taste and odour problems and prolonged water blooms are observed (Reynolds and Walsby 1975, Paerl 1988).

The dynamics of seasonal succession of phytoplankton in oligotrophic lakes generally differ from those in eutrophic lakes and the phytoplankton is often characterised by typical spring, summer and autumn assemblages (*e.g.* Hutchinson 1967, Ilmavirta 1980, Heinonen 1982, Rott 1984, Trifonova 1986, 1993, Willén 1987, 1992a, Eloranta 1995). In addition to the seasonal variability there are usually also marked interannual variations in the abundance of phytoplankton. The species assemblage from year to year has no exact timing, and hence the occurrence of individual species may vary widely so that the dominant species at any given successional stage will not always be the same. Seasonally the mean population densities may vary within 6-9 orders of magnitude (Reynolds 1986).

The composition of a phytoplankton assemblage (Fig. 1) does not depend only on nutrients but also on physical (*e.g.* temperature, illumination, turbulence and vertical stratification) or chemical factors (*e.g.* vitamins and antibiotics) and on biological factors, such as specific growth and loss rates among the algae, parasitism, predation and competition (Ohle 1955, Hutchinson 1967, Harris 1986, Reynolds 1986, Sommer 1989). These factors should be taken into account when considering the reasons for fluctuation of phytoplankton (Jacobsen and Simonsen 1993), and due to their complex interactions and rapid changes no absolute standards for biological quality can be set (Commission of the European Communities 1999).

1.2 Terminology

1.2.1 Plankton

"Plankton" as a term includes all organisms of microscopical size which float freely and involuntarily in open water independently of shores and bottom, as demonstrated by Hensen (1887).
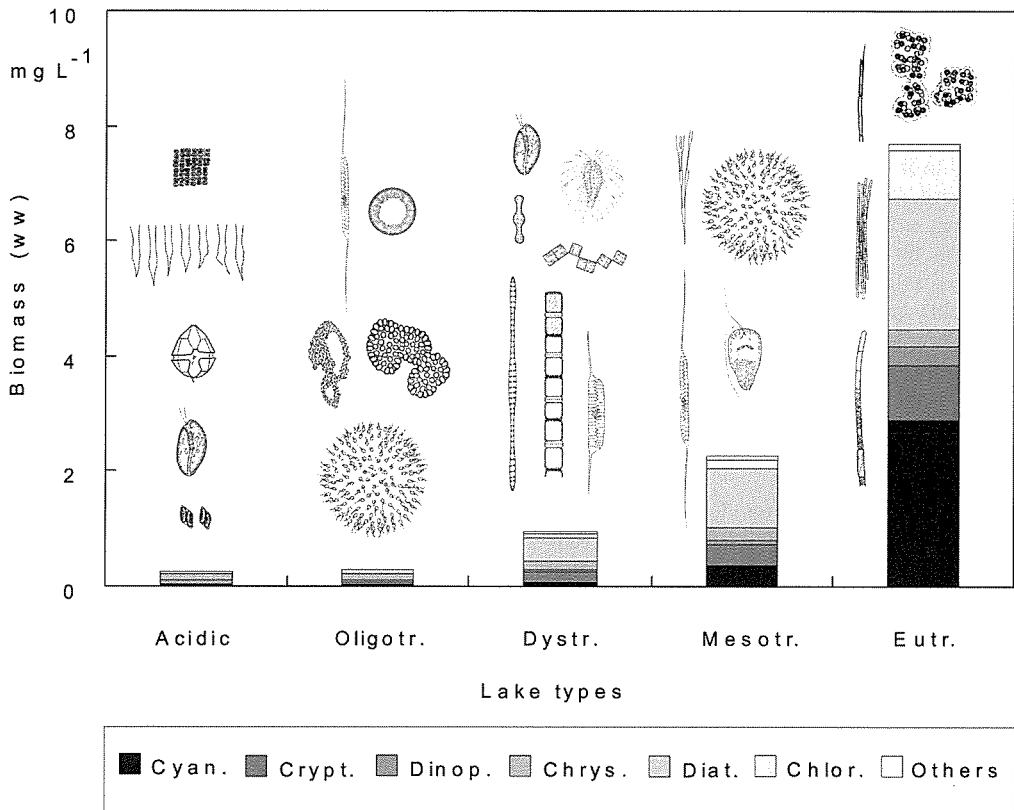
Fig. 1 The composition and quantity (wet weight mg L^{-1}) of phytoplankton (June – August) in different lake types (not hyper-eutrophic) with some typical taxa in 1981–1997 (VII, database of FEI). Cyan. = cyanophyta, Crypt. = cryptomonads, Dinop. = dinoflagellates, Chrys. = chrysomonads, Diat. = diatoms, Chlor. = green algae. E.g. *Gonyostomum semen* (Raphidophyceae) is included in the group others. Figures according to Tikkanen and Willén (1992).

Many of them are only facultatively planktic (Hutchinson 1967, Round 1981). Plankton could be regarded as the community of prokaryotic and eukaryotic organisms, such as bacteria, algae, protozoa and larger zooplankton adapted to suspension in the sea or in fresh waters and liable to passive movement by wind and currents (Reynolds 1986). According to Hutchinson (1967) and Round (1981), the term "community" is used to denote a collection of species living together and linked to a particular habitat. A collection of populations is termed an "assemblage" when there is no attempt to define dominance. In this study the term assemblage is used with this meaning. In terrestrial environments, the plant communities are more fixed entities, whereas plankton communities with short renewal times are less constant.

The plankton of lakes (limnoplankton) can be segregated from plankton in ponds (holoplankton) and rivers (potamoplankton) (*e.g.* Reynolds 1986). The term euplankton (holoplankton) is used to refer to the permanent planktic assemblage of organisms which completes their life cycle suspended in water. Species which spend part of each season resting on the sediments (mainly zooplankton but also several phytoplankton species) comprise the meroplankton. Casual species derived from other habitats (bottom and littoral) are referred to as pseudoplankton (tychoplankton), which is also present as epiphytes or as a loose collection of non-motile organisms, such as *Tabellaria flocculosa* (Roth) Kützing, and some desmids *e.g. Cosmarium*, and *Staurastrum* (Round 1981).

1.2.2 Classification of phytoplankton

Representatives of several groups of planktonic "algae" and bacteria, as well as the infective stages of certain actinomycetes and fungi are suspended in freshwater. "Algae", although a much used term, does not have any exact systematic meaning, and should be regarded as a loose blanket term for "primitive" cryptogamic photoautotrophs, as proposed by Reynolds (1986). Heterotrophic species, such as *Katablepharis ovalis* Skuja, have often also been included in the phytoplankton. Furthermore, several phytoplankton species are considered to be capable of mixotrophy (Ramberg 1979, Salonen and Jokinen 1988, Tranvik *et al.* 1989, Jansson *et al.* 1996, Roberts and Layborn-Perry 1999).

A discrete group among algae are the cyanophytes, also referred to as Cyanophyceae, Cyanobacteria, Cyanoprokaryota or simply "blue-green algae". Cyanophytes share affinities with the prokaryotic organization of bacterial cells; they lack both the structural organization of chromosomes within a separate nucleus and the discrete pigment-containing organelles (plastids or chromatophores) characteristic of many plants. The identification of naturally occurring taxa as a botanical approach is proposed to depend on morphological, physiological, genetic, and ecological data (Anagnostidis and Komárek 1985). As was noted by Reynolds (1986), there are difficulties in matching wild cyanophytes to cultured type-strains, because their morphology may alter under laboratory conditions from that of the initial isolate.

In addition to cyanophytes, fresh waters also carry a mixture of cryptomonads (Cryptophyceae), dinoflagellates (Dinophyceae), chrysomonads (Chrysophyceae), diatoms (Diatomophyceae) and green algae (Chlorophyceae). Xanthophyceae, Prymnesiophyceae and Prasinophyceae are usually less abundant. Euglenids (Euglenophyceae) tend to be abundant in small bodies of water (Round 1981, Tikkanen and Willén 1992). Phytoplankton encompasses a great range of cell size and cell volume, from the largest forms visible to the naked eye to algae less than 1 μm in diameter. The different sizes are classified, according to Round (1981) and Reynolds (1986) as:

picoplankton	(< 2 μm),
nanoplankton	(2–20 μm),
micro- or netplankton	(20–200 μm),
meso- and macroplankton	(> 200 μm).

1.2.3 Water blooms and eutrophication

Naumann (1912) introduced the term "vegetation colouring" for an algal mass occurrence in the whole water column. "Water bloom" was widely understood as the surface accumulation of planktic cyanophytes. In this study the term water bloom is used to refer to such mass occurrences of cyanophytes or occasionally of the green alga *Botryococcus*.

The term eutrophication (nutrient enrichment) describes a trophic change in the aquatic environment due to the high input of nutrients (Reynolds 1986). During the past four decades the enrichment of many of the world's lakes has been a direct consequence of social or cultural advances made by growing human populations with increased waste water loads, diffuse loads and run-off from agriculture (Vollenweider 1968, Holtan 1980, Kauppi 1984, Willén 1987, 1992a, Rekolainen 1989, Ekholm 1998). The important roles of nitrogen and phosphorus in increasing eutrophication were recognized at an early stage of the study of eutrophication (Pearsall 1932, Ohle 1955, Vollenweider 1968).

The term natural eutrophication (maturation) describes very gradual changes in the trophic status of a lake over long periods, which are however short in a geological time scale (Round 1981). As silts derived from the catchment area are inwashed and accumulated as lake sediment, the lake volume diminishes but no change occurs in the amount of nutrient reaching the basin. As a result, the nutrients become more concentrated. However, this concept is not accepted by all researchers (Round 1981, Reynolds 1986). Climatic changes directly influence the weathering rate of rocks in the catchment area, throughflow and leaching of the soils, and consequently the loading of nutrients in the recipient lake system (Järnefelt 1958a).

1.2.4 Ecological status

Ecological status is an expression of the structure and functioning of aquatic ecosystems associated

with surface waters. Good ecological status is defined in terms of the biological communities, the hydrological characteristics and the chemical characteristics. Biological communities with ecological variability but with minimal anthropogenic impact are the target of protection (Commission of the European Communities 1999).

1.3 Lakes

Lakes in Finland have mainly been formed through three events: cracking of the bedrock, transport of boulders and soil by water and ice, especially during the glacial period, and deglaciation, resulting finally in the development of a lake (Järnefelt 1958a,b). The lake type depends in general on the nature of the weathering bedrock in the drainage area, on the loose soil particles: clay and carbonates in the bedrock cause eutrophy; moraine and sand cause oligotrophy. In Finland, naturally eutrophic lakes are mainly situated in coastal areas with wide clay plateaus, but are also found elsewhere in areas where clay is abundant in the soil or where phosphates occur in the bedrock.

Oligotrophic lakes are situated in the vicinity of the Salpausselkä formation, in areas where the soil mainly consists of sand or crust, and in Lapland (Maristo 1941, Järnefelt 1958a). Oligotrophic lakes are more or less rich in humic compounds and are characterized by low phytoplankton biomass and no occurrences of water blooms (Teiling 1916). Dinoflagellates, chrysomonads, some green algae, especially the genus *Botryococcus* and desmids are abundant (Järnefelt 1952, 1958a, Hutchinson 1967, Rosén 1981, Brettum 1989).

A moderate degree of eutrophication is described as mesotrophy (Hutchinson 1967). Mesotrophic lakes are intermediate between oligotrophic and eutrophic waters, with lower concentrations of nutrients and total phytoplankton compared to eutrophic lakes (Hutchinson 1967, Heinonen 1980, Wetzel 1983). In the 1970s, approximately 10 % of the monitored 400 lakes in Finland were mesotrophic on the basis of total phytoplankton biomass (variation from 1.01 to 2.50 mg L^{-1}, Heinonen 1980). Usually the species diversity is high in mesotrophic lakes (Brettum 1980, Økland 1983).

Eutrophic lakes in temperate regions are characterized by high phytoplankton biomass and by dense algal surface accumulations, *i.e.* "water blooms" (Naumann 1917). Cyanophytes and diatoms mainly dominate in these lakes (Teiling 1916). Eutrophic dinoflagellates (*Ceratium* and *Peridinium*) and green algae, *e.g. Pediastrum*, are also often abundant (Hutchinson 1967). Järnefelt (1952) also included euglenids in this eutrophic category. When the degree of eutrophication increases the number of species also first increases (Heinonen 1980, Eloranta 1986), but when the biomass exceeds 10 mg L^{-1} the species number and the diversity may decrease (Brettum 1980, Heinonen 1980, Økland 1983).

Thienemann (1925) added dystrophic lakes to the lake category. Järnefelt (1956a,b) classified the oligotrophic and eutrophic brown-water lakes as dys-oligotrophic and dys-eutrophic or mixotrophic lakes. The latter term has not been generally accepted (Round 1981). Dystrophy characterized by brown or yellow water colour is mainly caused by allochthonous humic compounds originating from the drainage area. These humic compounds are of varying composition (Järnefelt 1958a, Wetzel 1983, Pennanen 1988). Dystrophy is typical in lakes situated in marshy areas and is generally associated with an oligotrophic drainage basin. Many of the lakes in forest areas are weakly exposed to wind, which leads to meromixis during spring and nutrient depletion in the productive layers (Arvola 1983). The rapid development of thermal stratification in spring restricts the availability of nutrients to immobile algae. Consequently these lakes are dominated by cryptomonads and flagellated green algae (Ilmavirta 1983, Smolander and Arvola 1988), able to support their growth by migrating between the nutrient-rich hypolimnion and the illuminated but nutrient-poor epilimnion (Salonen *et al.* 1984). Large dystrophic lakes exposed to winds which cause turbulence and with less dark brown water colour are dominated by cryptomonads and diatoms (Järnefelt 1958a, Ilmavirta and Kotimaa 1974, Eloranta 1995).

In Finland most man-made lakes are constructed by damming a river in its upper catchment area, and therefore young man-made lakes can be considered as systems intermediate between rivers and lakes. During their early stages the decomposition of organic material causes high nutrient levels, high biological production and dark water colour, especially in drainage areas with wide peatlands (Vogt 1978, Kinnunen 1982).

Later on, the biota and the nutrient levels of these lakes change towards oligotrophy (Kinnunen 1982, Krzyzanek *et al.* 1986, Carnier 1992). Water level regulation with strong unidirectional flow affects phytoplankton by displacing the water with suspended phytoplankton assemblages, perennating cells and resting spores downstream. Under these circumstances spring growth may be delayed because the inocula of phytoplankton is small, although nutrients and light are adequate (Reynolds 1986).

Acidification was recognized as a severe environmental problem in the 1980s both in Europe and in North America. In southern Finland, small clear water lakes with catchment areas mainly of infertile forest soil or granite bedrock are particularly sensitive to acid deposition (Kauppi *et al.* 1990). However, many lakes in Finland are naturally acidic and dystrophic or have been so for at least the past 100 years due to dissolved humic substances derived from the surrounding soils (Rask *et al.* 1986).

1.4 Aims of the study

The aims of the present study were:
1) to evaluate the typical phytoplankton assemblages in different lake types
2) to evaluate the response of phytoplankton assemblages to anthropogenic stresses in terms of long-term or short-term nutrient load, as well as to the development of trophic degree in man-made lakes after their construction and to water level regulation
3) to evaluate the feasibility of phytoplankton as a monitored environmental variable, and the significance of single species/ taxa as signs of changes, and finally
4) to evaluate the key problems in the analysis of phytoplankton.

2 Materials and methods

The phytoplankton data included in this study are based on the data set of the most intensively monitored lakes of the Finnish Environment Institute (FEI), with a total of 859 samples from 43 lakes and two reservoirs situated between the latitudes 60° and 69° (I–VII). Phytoplankton records from a brown-water forest lake (II), from two monitored man-made lakes in Lapland (III-IV) and from four lakes examined as raw water sources for water works (VI) are included in the studied lakes. Lakes were classified as acidic, oligotrophic, dystrophic, mesotrophic, eutrophic or hyper-eutrophic using average values of some physical and chemical variables in 1991–1997 (Table 1). The acidic lakes were those examined during the HAPRO project – Acidification in Finland (Kauppi *et al.* 1990) (VII).

Table 1. Some water quality variables (mean, maximum and minimum) in the studied lake groups in 1990–1997 (March–October) from the depth of one metre, n = number of the lakes / and the number of samples. Lake types according to Forsberg and Ryding (1980), in which acidic lakes were not included.

Lake types	n	Total P μg L^{-1}		Total N μg L^{-1}		Water colour mg L^{-1} Pt		pH	
Oligotrophic	9 / 181	6	(3–8)	380	(180–490)	20	(5–30)	7.0	(6.9–7.2)
Acidic[1]	11 / 36	8	(4–16)	280	(170–430)	30	(5–140)	5.5	(4.7–6.0)
Dystrophic	10 / 603	14	(9–23)	460	(320–1100)	70	(50–80)	6.6	(5.8–7.1)
Mesotrophic	6 / 456	18	(13–23)	610	(360–1100)	30	(9–50)	7.0	(6.6–7.5)
Eutrophic	5 / 212	57	(37–70)	1300	(800–2200)	90	(50–140)	7.0	(6.5–7.2)
Hyper-eutrophic	2 / 276	65	(36–93)	1250	(1200–1300)	75	(50–100)	7.5	(7.4–7.5)
Lokka[2]	1 / 36	36	(21–60)	610	(440–770)	80	(60–100)	6.8	(5.7–7.6)
Porttipahta[2]	1 / 38	19	(10–38)	370	(310–460)	70	(40–100)	7.0	(6.1–7.7)

[1] in 1984–1994
[2] man-made lake

Table 2. The sampling time, depth, method and preservatives used in the investigations of phytoplankton (I–VII). Methods are those used in the monitoring programme of FEI, with the exception of (II).

Publ. No.	Date Year	Month	Sampling depth >0–2 m	0–2 m[1]	Sampling method net	Ruttner	Preservatives Form.	Lugol[2]
I	1893–1995	V–IX	0–9 m	x	x	x	x	x
II	1988–1994	V–IX		x		x		x
III	1968–1990	VI–IX	0–10 m	x		x	x	x
IV	1965–1994	VI–IX	0–10 m	x		x	x	x
V	1982, 1986	VII		x		x		x
VI	1991	V–XI	1–12 m		x	x[3]		x
VII	1982–1994	VII		x		x		x

[1] Since 1971 in general
[2] Preserved with acid Lugol's solution; formalhyde (35 %), as 16 % final solution, added afterwards
[3] Sampling from the pipes of raw and treated water

Phytoplankton has been sampled by the Regional Environmental Centres since 1963 (Table 2), and the biomass as fresh weight has been estimated by microscopy using the Utermöhl (1958) technique. During the analyses all the observed taxa of a permanent area of the chamber bottom are counted and the counting results, including those taxa observed in low numbers, are converted to biomass using coefficients. Phytoplankton quantity as chlorophyll *a* concentration (I–V) has been determined since 1973. The data from the study lakes (I–VII) and additional phytoplankton data from the database of FEI were examined to find the average biomass of the most important taxa during spring, summer and autumn, and the seasonal succession of phytoplankton in the different lake groups. Partly unpublished data from the database of FEI were used when considering the long-term changes of cyanophytes, diatoms and total phytoplankton, and the proportion of different algal groups in lakes in Finland. Acidic lakes were not included in this treatment as they were sampled only in July 1987. Qualitative data concerning algal nuisances (water blooms) are included in the biological database of FEI. This database was established in 1992, and also contains earlier information (I, IV, VI). The list of valid species names and synonyms is given in Appendix 1.

3 Phytoplankton in different types of lakes

3.1 Long-term eutrophication of a shallow lake

Lake Tuusulanjärvi is a shallow lake in southern Finland. The naturally eutrophic lake was the raw water source for the city of Helsinki during the 1950s and 1960s. With increasing nutrient concentrations the lake became hyper-eutrophic, phytoplankton biomass increased and long-lasting water blooms of cyanophytes were frequently observed. Several water protection procedures have improved the water quality since the early 1980s (I).

In 1921-1932 the total phytoplankton biomass was on average 1.4 mg L^{-1}, but in the 1970s it had increased to 22.4 mg L^{-1} (I). Phytoplankton was characterized by strong seasonal and year-to-year fluctuations. The maximum biomass value ever recorded, 84 mg L^{-1}, was caused by *Planktothrix agardhii* (Gom.) Anagnostidis & Komárek in the mid 1970s. When the urban waste water load was finished in 1979, the total biomass decreased to an average of 14.5 mg L^{-1}, although the biomass still varied remarkably in the 1980s. In the 1990s, the mean biomass decreased further to 8.7 mg L^{-1}, and peak levels of phytoplankton biomass were clearly lower compared to the maximum values in the 1970s. However, phytoplankton quantity still reflects highly eutrophic conditions (see also Table 3), according to the criteria of Heinonen (1980). During the warm and calm weather condi-

Table 3. Mean and standard deviation of phytoplankton biomass (wet weight, mg L^{-1}) and chlorophyll a concentration (µg L^{-1}) in 1981–1997 (June–August) in the studied lake groups and in man-made lakes. n = number of samples or taxa. SD denotes standard deviation.

Lake types	Samples n	Taxa n	Biomass mg L^{-1}		Samples n	Chlorophyll a µg L^{-1}	
			Mean	SD		Mean	SD
Acidic[1]	11	77	0.3	0.1	-	-	-
Oligotrophic	165	436	0.3	0.2	181	2.7	1.2
Dystrophic	197	519	0.9	0.7	603	6.2	3.0
Mesotrophic	144	556	2.3	2.0	456	8.7	4.8
Eutrophic	35	313	7.6	7.7	212	36.9	30.1
Hyper-eutrophic	146	486	13.2	12.4	276	52.4	44.0
Lokka[2]	37	277	3.0	2.4	39	12.3	7.2
Porttipahta[2]	31	249	1.0	0.9	75	6.7	5.3

[1] in 1987

[2] man-made lake

tions in summer 1997 *Aphanizomenon* spp. caused dense water blooms. This emphasizes that weather is an essential regulating factor in the formation of algal blooms (I).

Soon after 1910, the cyanophytes *Anabaena*, *Aphanizomenon* and *Microcystis* were rather abundant, although no algal colouring of the water was visible (Järnefelt 1937, 1956b). At that time eight species indicating oligotrophy were included in the phytoplankton assemblage. *Dinobryon bavaricum* Imhof and *D. divergens* Imhof were rather abundant, and the cyanophytes *Coelosphaerium kuetzingianum* Nägeli and *Woronichinia naegeliana* (Ung.) Elenkin, both occurring in oligo-mesotrophic waters (Brettum 1989), were also common, as were the oligotrophic diatoms *Cyclotella kuetzingiana* Thwaites and *Tabellaria flocculosa* (I). Water blooms caused by *Anabaena flos-aquae* (Lyngb.) Brébisson, *A. macrospora* Klebahn and *A. spiroides* Klebahn first developed in 1926 (Järnefelt 1937). *Planktothrix agardhii* was observed for the first time in 1921 and abundantly in 1956 (Järnefelt 1956b). The diatom *Acanthoceras zachariasii* (Brun) Simonsen, typical of eutrophic waters (Lepistö 1990, Rosenström and Lepistö 1996), was common at that time but disappeared in the 1960s (I). This alga seems to be sensitive to hyper-eutrophic conditions (Tables 4–6).

In the 1950s water blooms of *Anabaena* resulted in serious taste and odour problems in the tap water of the city of Helsinki which used Lake Tuusulanjärvi as a drinking water reservoir. In 1959 the water was treated with copper sulphate (Kangas 1961). According to Kenefick *et al.* (1993) and Lam *et al.* (1995), such treatment probably causes a leakage of toxins from the decaying cyanophytic cells. Water blooms occurred each summer in the 1960s and in the early 1970s. Especially in the 1970s, when the waste water load into the lake was strong, phytoplankton was alternatively dominated by cyanophytes, such as *Planktothrix agardhii*, and diatoms, such as *Aulacoseira italica* (Ehr.) Simonsen. The diatom *Tabellaria flocculosa*, favouring oligotrophic conditions (Hutchinson 1967), disappeared in 1976 during the highly eutrophic conditions when silicate depletion was also observed. *Tabellaria* was absent until 1985.

Planktothrix agardhii dominated the summer phytoplankton until 1979 when the waste water load was stopped. The species was still observed in 1981, but since then it has occurred only occasionally and in low numbers. *Planktothrix* was succeeded by the N_2 – fixing *Anabaena* and *Aphanizomenon*. However, the non-N_2 – fixing *Microcystis* was occasionally abundant although inorganic nitrogen, the important nitrogen source (Kappers 1980, Blomqvist *et al.* 1994), remained depleted. *Microcystis* is capable of vertical migrations and is able to utilise nutrients present in deeper strata when the N:P ratio decreases (*e.g* Reynolds 1972, Konopka *et al.* 1978, Hyenstrand *et al.* 1998). Changes in nutrient concentrations, especially the decrease of inorganic nitrogen, affected the phytoplankton assemblage. In 1982 no

significant biomass of cyanophytes was observed. Obviously, this was partly due to the exceptionally windy and rainy spring and early summer. During strong turbulence, diatoms are able to outcompete cyanophytes (Reynolds 1980). In the 1980s diatoms were clearly reduced compared to the previous decade of vigorous diatom growth, which obviously depleted the silicate. The large-sized *Aulacoseira granulata* (Ehr.) Simonsen was succeeded by the narrow *A. granulata* v. *angustissima* (O. Müller) Simonsen (I).

In the 1990s, more than 10 years after the end of waste water input to the lake, cyanophytes decreased markedly although they still dominate the phytoplankton. *Aphanizomenon flos-aquae* (L.) Ralfs became abundant (Tables 4–6), but cryptomonads, dinoflagellates, especially chrysomonads and also green algae increased. As a new phenomenon the small-sized *Rhodomonas lacustris* Pascher & Ruttner produced a biomass peak in May 1994. There was a shift from *Microcystis*-dominated, usually hepatotoxic (Watanabe *et al.* 1986, Sivonen *et al.* 1990), blooms to *Aphanizomenon* dominance in the 1990s. Lower phosphorus and nitrogen concentrations not only decrease the intensity of mass occurrences but favour less harmful populations of *Anabaena* and *Aphanizomenon* (*e.g.* Ekman-Ekebom *et al.* 1992, Willén and Mattson 1997, Rapala 1998).

In the 1990s, 22 "new" taxa, mainly of cyanophytes, were identified. Such taxa were *Aphanothece, Cyanodictyon, Radiocystis,* and *Snowella* which form small bacteria-like colonies and are typical for naturally eutrophic shallow lakes (Komárková-Legnerová and Cronberg 1994). Furthermore, *Anabaena mucosa* Kom.-Legnerová & Eloranta and the diatom *Skeletonema potamus* (Weber) Hassle, which earlier was assigned to the green alga *Gloeotila* according to Turkia and Lepistö (1997), were observed. *Dinobryon suecicum* Lemmermann, *Gonyostomum semen* (Ehr.) Diesing (Raphidophyceae) and *Botryococcus terribilis* Komárek & Marvan were also observed in the 1990s. Some taxa, observed in the late 1800s and early 1900s, such as *Coelosphaerium kuetzingianum, Dinobryon bavaricum, D. divergens, D. sociale* Ehrenberg, *Acanthoceras zachariasii* and *Rhizosolenia longiseta* Zacharias were observed again, indicating a lower trophic status of Lake Tuusulanjärvi.

A shift from large to small phytoplankton species has been observed since the early 1980s,

which is considered to reflect the decreased nutrient input (Watson and Kalff 1981, Willén 1987). Large diatoms were succeeded by small-sized diatoms, a phenomenon also caused by decreased silicate concentration (Stoermer *et al.* 1985, Suttle *et al.* 1987). The increase of small-sized algae in the material also depends on the development in taxonomy which made possible the identification of small bacteria-like cyanophytes in the 1990s (I).

The high total phosphorus concentration of Lake Tuusulanjärvi already indicated eutrophy in the 1920s. In fact the lake is situated on a clay area and is naturally eutrophic (Järnefelt 1937). Compared to the median concentrations of phosphorus and nitrogen in Finnish lakes (13 μg L^{-1} and 400 μg L^{-1}, respectively, Henrikson *et al.* 1998), nutrient concentrations in Lake Tuusulanjärvi are still in the 1990s exceptionally high (total median phosphorus 100 μg L^{-1} and total median nitrogen 1200 μg L^{-1}), indicating eutrophy or even hyper-eutrophy. Although oxygen availability in the hypolimnion has improved due to water aeration, the internal loading of the lake is still operative and the phosphorus concentration remains at a high level. After the end of the waste water load to the lake, the decrease or even depletion of inorganic nitrogen in summer strongly suggests that nitrogen may limit algal growth. In fact, the low median DIN:DIP (w/w) ratio, clearly below seven (the optimum ratio for algal growth, Redfield *et al.* 1963), also strongly supports this conclusion.

3.2 Effects of forest fertilization on a brown-water lake

The forests in the catchment area of Lake Kalliojärvi in the Juupajoki municipality, southern Finland, were fertilized by NP-fertilizers in midsummer 1988 (Frisk *et al.* 1997). During the spring flood after fertilization, phosphorus concentrations were high when the fertilizers leached into the lake. During the study period nutrient concentrations increased in the hypolimnion.

Phytoplankton responded to the increased nutrient concentrations by a biomass (3.9 mg L^{-1}) and chlorophyll *a* (32 μg L^{-1}) peak during the first spring. During the subsequent five years total phosphorus concentrations remained relatively high, on average 17–18 μg l^{-1} as annual means. In

the hypolimnion nutrient concentrations, organic matter, water colour and conductivity increased gradually. Five years after the fertilization, in September 1994, *Gonyostomum semen* caused a second maximum, with total biomass 2.9 mg L^{-1} and chlorophyll *a* concentration 10 µg L^{-1}. Phytoplankton biomass and chlorophyll *a* concentration were in agreement with the relatively high phosphorus concentration reflecting meso-eutrophic conditions, according to criteria by Heinonen (1980) and Wetzel (1983). Except for these two maxima, phytoplankton biomass and chlorophyll *a* concentration remained rather low (II).

The fertilization obviously caused an immediate increase of cryptomonads, accounting for *ca.* 60 % of the total biomass. *Cryptomonas* spp. are favoured by N+P addition (Jansson *et al.* 1996) and are potentially mixotrophic (*e.g.* Tranvik *et al.* 1989, Roberts and Layborn-Perry 1999). After the first spring, cryptomonads contributed less than 20 % to the total biomass (II). During the study period small flagellates, such as the prymnesiophycean *Monochrysis parva* Skuja and the green alga *Monomastix* sp., were typical. *Monochrysis parva* is obviously capable of bacterial consumption (Holen and Boraas 1996). The chrysomonads *Mallomonas*, *Pseudopedinella* and *Synura* were also abundant. The large-sized flagellate *Gonyostomum semen* is able to maintain its growth in brown-water lakes by migrating between the epilimnion and the hypolimnion, where nutrients are concentrated (Cronberg *et al.* 1988, Arvola *et al.* 1990, Eloranta and Räike 1995). *Gonyostomum* appears to be able to consume bacteria (Holen and Boraas 1996).

One year after the fertilization *Merismopedia warmingiana* Lagerheim, typical for nutrient-poor, dark and acidic waters (Brettum 1989), was abundant. Other cyanophytes, such as *Anabaena flos-aquae* occurred sparsely, as low pH prevents the mass occurrence of cyanophytes (Reynolds and Walsby 1975).

The quantity and quality of phytoplankton in Lake Kalliojärvi, with average total biomass 0.9 mg L^{-1} and chlorophyll *a* concentration 6.4 µg L^{-1}, is rather similar to that of the dystrophic lake group (Tables 3, 4–6) as *Cryptomonas* spp., *Pseudopedinella* spp., *Mallomonas crassisquoma* (Asmund) Fott and *Tabellaria flocculosa* are the generally dominating taxa and *Merismopedia warmingiana* is abundant. Less common in Lake Kalliojärvi are *Rhizosolenia longiseta* and *Asterio-*

nella formosa Hassall, typical species of the dystrophic lake group (Tables 4–6). However, *Aulacoseira italica*, rather common in the dystrophic lake group, is rare in Lake Kalliojärvi (II).

3.3 Development of the trophic degree in two man-made lakes

3.3.1 The Lokka reservoir

The reservoirs Lokka and Porttipahta were constructed by damming the rivers Luiro and Kitinen of the Kemijoki watercourse, the second largest watercourse in Finland. Due to the northern location, the reservoirs are ice-covered from the end of October to the end of May or even into early June. The filling of the reservoirs takes place during the spring and autumn floods and the water volume is at its minimum in late winter. The regulation of the reservoirs was especially strong in 1977–1981.

The Lokka reservoir is the largest reservoir in terms of surface area in western Europe (Vogt 1978). It remains lake-like even during the minimum water level, although it is moderately shallow (mean depth 5 metres, maximum 10 metres). The reservoir is constructed on peatland with large swamps, and the abundant organic compounds make the water colour dark brown (Nenonen and Nenonen 1972, Virtanen *et al.* 1993). Oxygen depletions release phosphorus from the bottom sediment. However, only a minor part of the nutrients are in a bioavailable form as they are bound in humic compounds (Boström *et al.* 1988).

In May 1968 the phytoplankton biomass was rather similar in the recently filled Lokka reservoir to that in September 1965 in the River Luiro before any reservoir constructions. The low biomass of 0.03 mg L^{-1} reflected oligotrophy. Ten years later, after a period of strong water level regulation, phytoplankton biomass was increased, and a record high biomass of 11.3 mg L^{-1} was measured in July 1981. The summer chlorophyll *a* concentrations remained high during 1977-1983. Due to the increased erosion and nutrient leaching high silicate concentrations were recorded, favouring diatoms (III, IV). The average phytoplankton biomass remained high in the 1980s, *i.e.* 3.6 mg L^{-1}, reflecting eutrophy according to the criteria of Heinonen (1980), although the silicate and chlorophyll *a* concentrations slightly de-

creased when the extent of water level regulation was diminished in 1981. In the 1990s the average phytoplankton biomass decreased to 1.9 mg L^{-1}, reflecting mesotrophy (Table 3). The interannual biomass variations also decreased (III, IV).

Small colony-forming cyanophytes, *e.g. Eucapsis alpina* Clements et Shantz probably derived from metaphyton in the flooded peaty bogs (Komárek and Anagnostidis 1999), chryso-monads and cryptomonads were the main constituents of the phytoplankton assemblage in the recently filled reservoir. The heterotroph protist *Desmarella moniliformis* Kent was also a typical species (III, IV). This species prefers waters with high concentrations of organic compounds and abundant bacteria (Järnefelt 1961, Tikkanen and Willén 1992). Furthermore, the commonly observed *Dinobryon bavaricum* is closely linked to mixotrophy (Bird and Kalff 1987, Straškrabová and Šimek 1993). Many cryptomonads, such as *Rhodomonas lacustris,* are also mixotrophs (Haffner *et al.* 1980), and are effectively grazed by zooplankton (Porter 1973). The green alga *Monoraphidium contortum* (Thur.) Kom.-Legnerová was very abundant, obviously as a "relict" from the River Luiro (III, IV). Reynolds (1988) classified *M. contortum* as a true river phytoplankton (potamoplankton) which tolerates high-frequency hydraulic disturbances (III, IV). Arvola (1980) described it as a pioneer species able to survive in a new labile ecosystem. With the passage of time, diatoms increased and strong water level regulations favoured species, such as *Aulacoseira ambigua* (Grun.) Simonsen and *A. italica* v. *tenuissima* (Grun.) Simonsen (III, IV). Silicate depletion in summer 1988 obviously caused thin and bent valves of the cells of *Aulacoseira* (Fig. 2). Stoermer *et al.* (1985) and Kling (1993) reported similar thinly silicified and distorted valves of diatoms during silicate depletion in Canadian lakes. Diatoms were occasionally replaced by cyanophytes at the end of the very warm summer of 1988. *Planktothrix mougeotii* Skuja became abundant, causing clogging of nets, but was soon succeeded by *Aphanizomenon flos-aquae* which caused water blooms. However, diatoms still dominate the phytoplankton assemblage.

3.3.2 The Porttipahta reservoir

The Porttipahta reservoir (mean depth 6m, maximum 34m) is situated in an area of moraines and
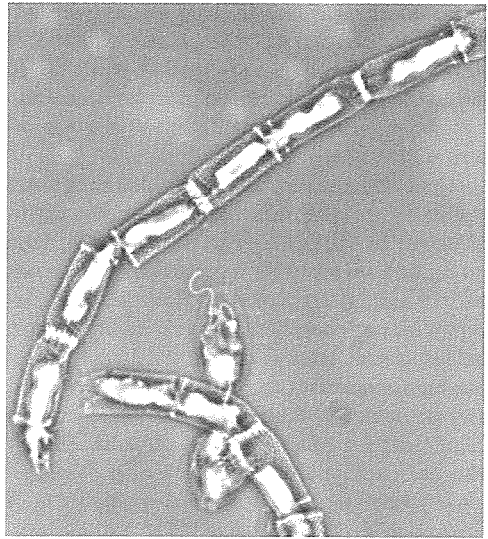

Fig. 2 *Aulacoseira italica* from the Lokka reservoir (5.7.1988).

its shape is oblong and labyrinthic. When the water level is at its minimum it is river-like (Nenonen and Nenonen 1972, Virtanen *et al.* 1993), and there is little organic material in the water. Although the Lokka reservoir drains into the Portti-pahta reservoir, the water quality and also the phytoplankton composition and quantity of Porttipahta differ to some extent from that of the Lokka reservoir. The N:P ratio is high, which is typical for lakes in Finland, and phosphorus appears to be the limiting nutrient for phytoplankton production.

In the early history of the Porttipahta reservoir, which was constructed some years later than the Lokka reservoir, phytoplankton biomass reflected oligotrophy but increased simultaneously with the strong water level regulation (III, IV). When regulation was diminished the phytoplankton quantity began to reflect oligo-mesotrophy. In the 1980s the average biomass was 1.1 mg L^{-1}, and decreased in the 1990s to 1.0 mg L^{-1}, which was one half of that in the Lokka reservoir. Cyanophytes were moderately rare.

During the period of intense water level regulation (1977-1981) diatoms, *e.g. Aulacoseira italica* and *Asterionella formosa,* were abundant, although less so than in the Lokka reservoir. Diatoms are still abundant in the Porttipahta reservoir. Typical are *Aulacoseira italica, Tabellaria flocculosa* and *Rhizosolenia longiseta* which

seems to be abundant in deep waters with adequate nitrogen and low phosphorus (database of FEI). Cyanophytes are less abundant partly due to the consistently high mineral nitrogen concentration. No mass occurrence of cyanophytes was observed in 1988 (III, IV).

The different morphology and different water quality of the two reservoirs affects the phytoplankton. In the Lokka reservoir, phytoplankton production seems to be regulated by both nutrients (P and N) alternatively. However, the concentrations of phosphorus, which are higher than in mesotrophic lakes (Table 1), maintain a phytoplankton assemblage typical for mesotrophic conditions. In the Porttipahta reservoir, nitrogen concentrations are relatively high and consequently phosphorus regulates the growth of phytoplankton. Phosphorus concentration is equal to that of mesotrophic lakes on average (Table 1) but phytoplankton biomass reflects oligo-mesotrophy. The strong water level regulation promotes the occurrence of diatoms. Especially in the Lokka reservoir warm weather periods may favour mass occurrences of cyanophytes.

3.4 Problems caused by increased phytoplankton

Oligotrophic lakes are suitable as raw water sources for waterworks using a minimum of only sand filtration. The chemical quality is not changed during treating of the raw water (VI). Microscopical phytoplankton analyses indicate the reduction of total phytoplankton biomass in the treated water to be on average 76 % and that of cyanophytes 14 %. However, occasionally cells of cyanophytes, such as *Snowella* spp., are flushed from the sand filter with the treated water. Probably the filters are overloaded when phytoplankton is abundant. The algal cells in the treated water are in good condition as observed by microscopy.

In mesotrophic raw waters vernal mass occurrences of chrysomonads and diatoms cause odour and taste problems in treated water, as the odour-causing compounds or the algal cells easily pass intact through the water treatment process (VI). Hyper-eutrophic conditions promote mass occurrences of cyanophytes such as *Microcystis wesenbergii* Kützing and *M. viridis* (A. Br.) Lemmermann in summer, and of *Planktothrix agardhii* in autumn (I, VI). Despite the efficient water treat-

ment with almost total reduction of phytoplankton, cells of *Microcystis* and trichomes of *Planktothrix agardhii* are also observed in treated water during the peak occurrence in raw water. Cells of the euglenid *Trachelomonas* spp. are also inefficiently removed by the water treatment. However, the abundant cyanophytes are not necessarily toxic (VI).

The patchiness of phytoplankton is often significant during a water bloom. Due to this patchiness the species composition of phytoplankton, especially of cyanophytes, may greatly differ from that of the bloom formation in the vicinity of the water intake. The water bloom may be toxic and simultaneously the raw water at the waterworks non-toxic or vice versa (VI). It is also possible that no water bloom can be observed but *Planktothrix* is abundant at a depth close to that of the raw water intake. *Planktothrix* seldom forms water blooms but is known to form depth maxima (Lindholm 1992).

A simple water treatment requires raw water of high quality. Sand filtration is not efficient enough if the lake used as raw water source gradually changes to more eutrophic status. Incipient changes of phytoplankton assemblage in a raw water body are already evident before eutrophication becomes a problem. These changes should be considered as warning signals, as proposed by Davis (1964), who studied the phytoplankton data from the incoming raw water of waterworks in Lake Erie in 1919–1963.

3.5 Phytoplankton as an indicator of the status of lakes in Finland

3.5.1 General

In the 1990s, mass occurrences of cyanophytes appeared to increase in lakes in Finland. In general, these lakes with water bloom observations are moderately small and shallow, but some of them are fairly large and deep (Lepistö *et al.* 1998). However, the data set of the monitored phytoplankton in 1963–1996 only partly support these observations, as cyanophytes decreased in all lake groups in the 1990s, contrary to the water bloom observations. Furthermore, in the 1990s the total biomass level in oligotrophic and oligo-mesotrophic lakes appears to have decreased slightly (Fig. 3) compared to the previous decade.

In fact the 1980s was on average characterised by rather heavy precipitation (Finnish Meteorological Institute 1991). Only in mesotrophic lakes did diatoms increase the total biomass, obviously as a result of slight eutrophication. In eutrophic lakes phytoplankton biomass has clearly decreased due to water protection procedures (I). According to the database of the Finnish Meteorological Institute, June was on average colder and more windy in 1990–1996 compared to the previous decade, which might have influenced phytoplankton development. Due to the cold June the summer stratification development might be delayed as well as the development of phytoplankton spring maxima, or the maxima could be even totally pre-

vented especially in deep lakes (Reynolds 1986). However, weather conditions are only one of the variables affecting phytoplankton (I).

In the studied lakes, the average total phytoplankton biomass generally varied from 0.3 mg L^{-1} to 4 mg L^{-1} but in eutrophic lakes it was approximately 10 mg L^{-1}, with considerable variation. A Swedish investigation of 1250 lakes showed equal phytoplankton quantities in lakes with different trophic status (Rosén 1981), as did the investigation of 40 Tyrolean low- and mid-altitude lakes (Rott 1984).

3.5.2 Oligotrophic lakes

In the studied oligotrophic, moderately deep lakes (VI, VII, database of FEI), phytoplankton biomass is low, on average 0.3 mg L^{-1} (SD % = 67) and varies mainly in May and June (Fig. 4, Table 3). In keeping with this, chlorophyll a concentrations are low, on average 2.7 µm L^{-1} (SD % = 44). Phytoplankton is composed mainly of similar quantities of chrysomonads (32 %), cryptomonads (21 %) and diatoms (21 %). Cyanophytes are of minor importance in oligotrophic lakes as are $e.g.$ members of the classes Prasinophyceae, Raphidophyceae or Tribophyceae (group others in Figs. 1, 5, 6).

The total number of phytoplankton taxa was 436 taxa in 162 samples (Table 3). Chrysomonads, such as the unidentified Ochromonadales, $Bitrichia$ $chodatii$ (Rev.) Chodat, $Chrysolykos$ $planctonicus$ Mack, $Dinobryon$ $borgei$ Lemmermann, $D.$ $divergens,$ $D.$ $sociale$ and $D.$ $suecicum$, are typical for oligotrophic waters. No single taxon of chrysomonads was dominant, although they were abundant as a group (Tables 4–6). Some of the chrysomonads which are considered to indicate oligotrophy, such as the genus $Dinobryon,$ (Järnefelt 1952, 1956a, Brettum 1989), are mixotrophs (Bird and Kalff 1987, Straškrabová and Šimek 1993). It seems that mixotrophy is a competitive advantage in nutrient-poor conditions. The genus $Dinobryon$ is observed in slightly acidic surroundings (Rawson 1956), and according to Eloranta (1989) $D.$ $borgei$ prefers oligotrophic waters whereas $D.$ $divergens$ may be found in more eutrophic waters (I).

The diatoms $Aulacoseira$ $distans$ (Ehr.) Simonsen and especially $Rhizosolenia$ $longiseta$, reflecting oligotrophic and oligo-mesotrophic conditions (Järnefelt 1952, 1956a, Hutchinson 1967, Heinonen 1980, Brettum 1989), are
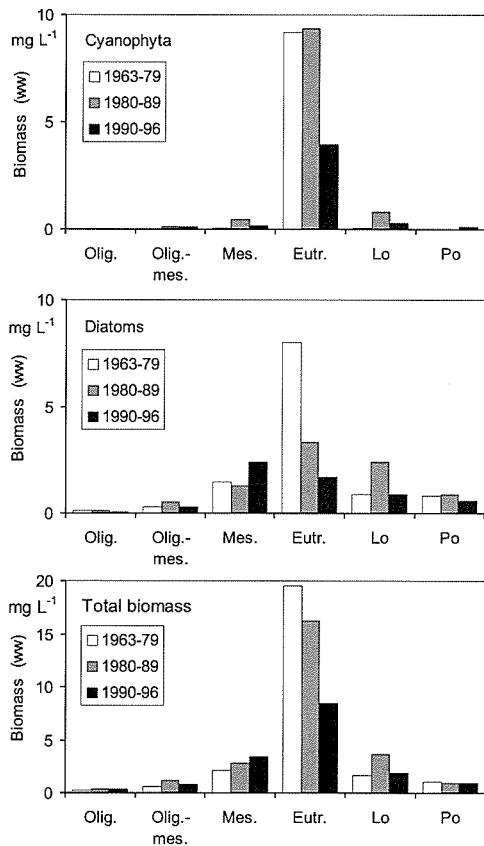
Fig. 3 The long-term changes of cyanophyta, diatoms and total phytoplankton biomass (wet weight, mg L^{-1}) in lakes of different productivity during 1963–1996 as mean biomass of June-August presented in three periods (database of FEI). Olig. = oligotrophic, Olig.-mes. = oligomesotrophic, Mes. = mesotrophic, Eutr. = eutrophic, Lo = the Lokka reservoir, Po = the Porttipahta reservoir. Note the different scale in the figure of total biomass.

Table 4. The dominant spring taxa in different lake types in 1981–1997 given as average biomass (wet weight, mg L^{-1}), + = observed, - = not observed, n = number of samples. The two dominant taxa shown in bold face. Note the eutrophic lake group with only one sample.

Spring

Taxon	Oligotrophic 9 lakes, n = 3	Dystrophic 4 lakes, n = 21	Mesotrophic 9 lakes, n = 10	Eutrophic 1 lake, n = 1	Hyper-eutrophic 2 lakes, n = 30
Aphanothece chlathrata	-	+	-	-	0.12
Cryptomonas spp.[1]	-	**0.10**	-	-	-
Cryptomonas spp. [1,2]	**0.02**	-	-	-	-
Cryptomonas spp.[2]	-	-	-	0.39	**1.57**
Cryptomonas spp.[2,3]	-	-	**0.29**	-	-
Rhodomonas lacustris	0.02	0.02	0.06	0.74	**1.06**
Gymnodinium spp.	0.01	0.02	0.04	-	0.12
Chrysochromulina spp.	+	-	0.02	0.03	-
Mallomonas akrokomos	+	0.02	0.02	-	0.56
Mallomonas allorgei	-	0.03	-	-	-
Mallomonas caudata	+	0.03	+	0.01	+
Ochromonadales	**0.06**	0.02	0.01	-	0.07
Mallomonas crassisquama	+	**0.11**	+	-	+
Pseudopedinella spp.	-	0.05	0.03	-	0.08
Synura spp.	+	0.03	+	0.18	0.40
Aulacoseira ambigua	-	+	**0.17**	-	0.21
Aulacoseira granulata	-	-	-	-	0.19
Aulacoseira alpigena	-	-	-	(7.19)	+
Aulacoseira islandica	0.01	0.03	0.12	0.03	+
Aulacoseira italica	-	0.01	0.09	0.44	0.80
A. italica v. tenuissima	+	+	0.04	(7.15)	0.61
Cyclotella spp.	-	-	0.07	-	+
Rhizosolenia longiseta	0.02	0.02	0.02	-	+
Stephanodiscus spp.	+	-	+	0.65	0.57
Asterionella formosa	+	0.05	0.01	0.01	0.09
Diatoma tenuis	0.01	+	+	-	0.04
Fragilaria crotonensis	+	+	+	0.06	0.11
Fragilaria (Synedra) spp.	0.01	+	+	0.05	0.05
Tabellaria flocculosa	0.01	0.08	0.02	0.02	+
Gonyostomum semen	+	+	0.01	0.02	-
Euglena proxima	-	+	-	0.24	+
Lepocinclis steinii	-	-	-	0.74	-
Trachelomonas hispida	-	-	-	0.17	0.02
Chlamydomonas spp.	+	0.01	0.01	0.41	0.10

[1] small Cryptomonas spp. (8x18 μm)
[2] medium Cryptomonas spp. (13x26 μm)
[3] large Cryptomonas spp. (16x38 μm)

Table 5. The dominant summer taxa in different lake types in 1981-1997 given as average biomass (wet weight, mg L^{-1}),
+ = observed, - = not observed, n= number of samples. The two dominant taxa shown in bold face.

Summer

| Taxon	Oligotrophic 9 lakes,n=162	Dystrophic 10 lakes,n =197	Mesotrophic 6 lakes,n=152	Eutrophic 5 lakes,n=35	Hyper-eutrophic 2 lakes,n=143
Aphanocapsa reinboldii	0.01	0.02	0.03	0.51	0.34
Microcystis aeruginosa	+	+	+	0.29	0.82
Microcystis flos-aquae	-	-	-	0.11	+
Microcystis viridis	+	+	+	0.03	0.73
Microcystis wesenbergii	-	-	+	0.02	0.83
Microcystis sp.	-	-	+	-	0.42
Snowella lacustris	+	+	+	0.21	0.07
Anabaena flos-aquae	+	+	0.03	0.62	0.52
Anabaena lemmermannii	+	+	0.01	0.06	0.48
Anabaena solitaria	+	+	+	0.09	0.34
Aphanizomenon spp.	+	0.01	0.14	0.39	**2.00**
Planktothrix agardhii	+	+	0.04	0.03	0.09
Cryptomonas spp. [2]	**0.03**	**0.13**	**0.24**	**0.70**	0.89
Rhodomonas lacustris	**0.03**	0.05	0.07	0.12	0.13
Ceratium hirundinella	0.01	0.01	0.01	0.09	0.35
Gymnodinium spp.	0.01	0.01	0.03	0.12	0.11
Chrysosphaerella spp.	0.01	+	+	-	-
Mallomonas akrokomos	+	0.01	0.02	+	+
Mallomonas caudata	+	0.02	0.01	0.02	0.11
Ochromonadales	0.02	0.01	0.02	0.12	0.02
Pseudopedinella spp.	0.02	0.02	0.03	0.02	0.01
Uroglena spp.	0.02	0.01	0.02	0.01	0.03
Synura spp.	+	0.01	0.05	0.02	0.01
Acanthoceras zachariasii	+	0.03	0.08	0.15	0.09
Aulacoseira ambigua	+	0.03	0.07	**0.79**	0.31
Aulacoseira distans	0.01	0.02	0.06	0.01	0.01
Aulacoseira granulata	+	-	+	0.27	0.37
Aulacoseira italica	0.01	0.06	0.15	0.34	0.59
Rhizosolenia eriensis	+	0.01	+	+	+
Rhizosolenia longiseta	0.01	**0.10**	0.04	0.04	+
Stephanodiscus spp.	+	+	+	0.09	**2.17**
Asterionella formosa	0.01	0.09	0.09	0.04	0.04
Fragilaria crotonensis	+	+	0.04	0.06	0.23
Tabellaria flocculosa	0.01	0.07	**0.25**	0.04	0.02
Gonyostomum semen	+	0.01	0.09	0.10	+

[1] small Cryptomonas spp. (8x18 μm)
[2] medium Cryptomonas spp. (13x26 μm)
[3] large Cryptomonas spp. (16x38 μm)

Table 6. The dominant autumn taxa in different lake types in 1981-1997 given as average biomass (wet weight, mg L^{-1}), + = observed, - = not observed, n= number of samples. The two dominant taxa shown in bold face.

Autumn

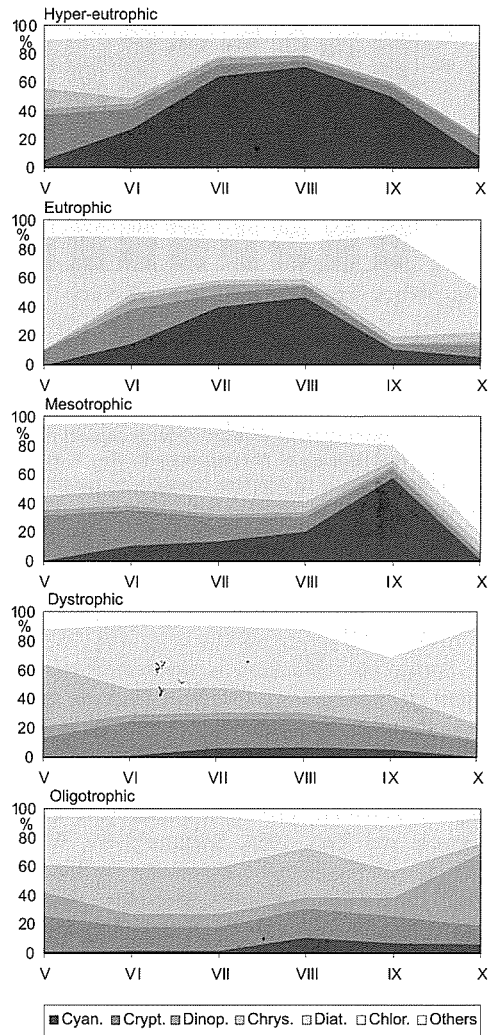| Taxon	Oligotrophic 9 lakes, n= 8	Dystrophic 4 lakes, n = 21	Mesotrophic 4 lakes, n=11	Eutrophic 1 lake, n=5	Hyper-eutrophic 2 lakes, n=41
Aphanocapsa reinboldii	+	+	0.01	0.02	0.17
Microcystis aeruginosa	+	-	+	0.02	0.35
Microcystis viridis	-	-	-	-	0.45
Microcystis wesenbergii	-	-	0.02	-	**1.08**
Snowella lacustris	0.01	-	+	-	0.02
Anabaena flos-aquae	+	+	**1.06**	0.02	0.47
Aphanizomenon spp.	+	+	0.01	0.07	0.42
Cryptomonas spp. [1,2]	-	0.06	-	-	-
Cryptomonas spp. [2]	0.03	-	0.11	0.07	0.41
Rhodomonas lacustris	0.02	0.01	0.03	0.05	0.09
Gymnodinium spp.	**0.03**	+	0.01	0.01	-
Peridinium umbonatum	+	+	0.02	-	-
Dinophyceae	+	0.01	+	-	0.01
Chrysococcus spp.	-	+	+	0.05	+
Mallomonas akrokomos	+	+	0.01	0.05	+
Mallomonas crassisquama	-	0.01	-	-	-
Mallomonas punctifera	0.01	0.01	-	-	+
Ochromonadales	**0.03**	0.01	0.01	-	0.02
Pseudopedinella spp.	+	0.03	0.01	+	0.01
Uroglena spp.	+	0.01	0.02	0.01	-
Synura spp.	+	0.01	0.01	-	+
Acanthoceras zachariasii	+	+	+	**0.46**	0.03
Aulacoseira ambigua	-	+	0.01	0.18	0.60
Aulacoseira distans	0.02	+	0.04	-	+
Aulacoseira alpigena	+	+	+	**0.21**	-
Aulacoseira granulata	-	-	+	0.04	0.26
A. granulata v. angustissima	-	+	-	+	0.19
Aulacoseira islandica	+	0.03	+	0.04	**0.64**
Aulacoseira italica	+	0.08	0.04	0.08	0.07
A. italica v. tenuissima	+	0.02	+	0.01	0.12
Rhizosolenia eriensis	-	0.01	+	0.02	-
Rhizosolenia longiseta	0.02	**0.10**	0.03	0.03	+
Asterionella formosa	+	0.01	0.01	0.07	0.14
Fragilaria crotonensis	+	+	+	+	0.14
Tabellaria flocculosa	+	0.01	0.03	-	-
Gonyostomum semen	+	**0.12**	**0.38**	+	-
Botryococcus spp.	+	0.01	0.01	0.01	0.01
Didymocystis bicellularis	-	+	+	0.05	+

[1] small Cryptomonas spp. (8x18 μm)
[2] medium Cryptomonas spp. (13x26 μm)
[3] large Cryptomonas spp. (16x38 μm)
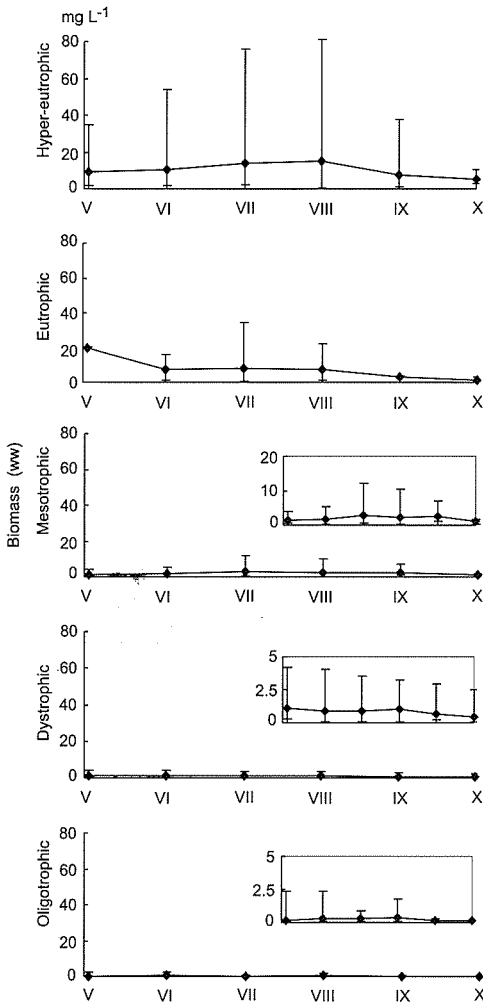
Fig. 4 The seasonal succession (May–October) of phytoplankton as mean, minimum and maximum biomass (wet weight, mg L⁻¹) in 1981–1997 in lakes with different trophic status (I, IV, VI, VII, database of FEI).

Fig. 5 The proportion of different algal groups in May–October (1981–1997) in lakes with different trophic status (I, IV, VI, VII, database of FEI). Explanation of abbreviations in Fig. 1, *Gonyostomum semen* (Raphidophyceae) is included in the group others.

rather abundant (Tables 4–6). Green algae occur only sparsely, accounting on average for less than 10 % of the total phytoplankton biomass. *Botryococcus* is a rather common green alga in oligotrophic lakes but the ecological requirements of the oligotrophic indicator *Botryococcus braunii* Kützing (Järnefelt 1952, 1956a, Hutchinson 1967, Heinonen 1980, Brettum 1989) are not completely understood due to its uncertain identification (Komárek and Marvan 1992). In fact, *B. terribilis* Komárek & Marvan, and *B. neglectus* Komárek & Marvan were included earlier in *B.*

braunii Kützing (Appendix 1). Furthermore, small-celled colony-forming cyanophytes, such as *Aphanocapsa* and *Merismopedia*, are typical for oligotrophic waters but are not important as biomass (Fig. 1). Occasionally some colonies of *Microcystis* and trichomes of *Aphanizomenon*, *Anabaena* and *Planktothrix* are also observed (VI). The tribophycean *Isthmochloron trispinatum* (W.&G.S. West) Skuja occurs in low densities in oligotrophic lakes.
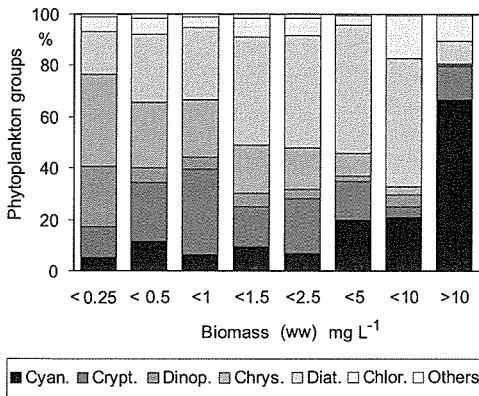
Fig. 6 The proportion of different algal groups in phytoplankton (explanation of abbreviations in Fig. 1) in July 1981-1997 in lakes of different productivity, determined as total phytoplankton biomass (wet weight, mg L^{-1}) (I, IV, VI, VII, database of FEI). The limits, according to the classification of Heinonen (1980) are: < 0.5 mg L^{-1} = oligotrophic, < 1 mg L^{-1} = oligo-mesotrophic, >1–2.5 mg L^{-1} = mesotrophic, >2.5–10 mg L^{-1} = eutrophic and > 10 mg L^{-1} = hyper-eutrophic.

Spring phytoplankton is dominated by diatoms, e.g. Rhizosolenia longiseta, Diatoma tenuis Agardh and Fragilaria spp., and by cryptomonads, mainly Cryptomonas spp. (small and medium), and Rhodomonas lacustris (Table 4, Fig. 5), which are typical for oligotrophic waters (Arvola and Rask 1984, Brettum 1989, Willén 1992a). Chrysomonads, especially unidentified Ochromonadales, are also abundant. Summer phytoplankton is still dominated by chrysomonads, such as Pseudopedinella spp., and Uroglena spp. The cell number of Uroglena, another mixotrophic genus, can sometimes be very high in oligotrophic lakes (VII). Although Uroglena is often considered as a typical spring taxa (e.g. Talling 1993), it appeared to occur in this data set in low densities during spring (Tables 4–6) but to increase during summer. According to Talling (1993), the recent mass occurrences of Uroglena spp. in early summer are connected with increasing eutrophication. Mixotrophy might be a competitive advance especially in early summer when nutrients are often depleted due to the effective growth of phytoplankton. Diatoms, e.g. Aulacoseira italica, Asterionella formosa and Tabellaria flocculosa co-dominate and cryptomonads are also abundant in summer. In October the dinoflagellate genus Gymnodinium dominated the decreased biomass (Fig. 5, Table 6).

3.5.3 Acidic lakes

The phytoplankton biomass in the acidic lake group (VII) is equal to that in oligotrophic lakes, on average 0.3 mg L^{-1} (Fig. 1, Table 3) but varies less (SD % = 33). A total of 70 phytoplankton taxa with eight common species were identified in eleven samples. The low number of taxa is a common phenomenon for many acidic lakes (Arvola et al. 1990). Merismopedia tenuissima Lemmermann is clearly acidophilic, as observed by Morling and Willén (1990). It is abundant in brown-water oligotrophic lakes (II, VII), as was also reported by Ilmavirta (1980). Blomqvist (1996) described the dominance of M. tenuissima as acidification-induced and as a "dead-end" for energy in an acidic, clear water lake. Probably the species is M. warmingiana which has been misinterpreted as M. tenuissima. According to Komárek and Anagnostidis (1999), M. tenuissima is common in fish ponds but less common in lakes.

In terms of biomass, dinoflagellates are the most important group of phytoplankton in acidic lakes (VII). Glenodinium spp. are found in slightly acidic lakes with very low phosphorus concentrations. This genus is rather scarce in other lake types (Tables 4–6). Peridinium umbonatum Stein is most abundant in lakes with the lowest pH. Algae favouring dystrophy, such as Cryptomonas spp., in agreement with observations of Ilmavirta (1983) and Brettum (1989), and Mallomonas akrokomos Ruttner and Uroglena spp. all show indifference to acidity. The identification of cryptomonads, a very heterogeneous group with a wide ecological spectrum, is difficult. Interestingly, Dinobryon divergens is found in lakes which are very acidic and contain only a few other taxa (VII). However, Eloranta (1989) classified D. pediforme (Lemm.) Steinecke as the best indicator of acidic lakes in the genus.

Planktic diatoms together with euglenids are considered to be sensitive to low pH (Kippo-Edlund and Heitto 1990) and to have very low biomass in acidic lakes or to be totally absent. The studied acidic lakes are small in size, which allows only weak turbulence. This normally excludes the non-motile species such as diatoms. Only some of the green algae, such as Sphaerocystis schroeteri Chodat, Botryococcus spp. and Oocystis rhomboidea Fott, appear to prefer acidic as well as oligotrophic lakes (VII). Willén (1992b) classified Eutetramorus nygardii

Komárek, *Monoraphidium dybowskii* (Wol.) Hindàk & Kom.-Legnerová and *Oocystis submarina* v. *variabilis* Skuja as characteristic algae for acidic lakes.

3.5.4 Dystrophic lakes

The dystrophic lakes in this study are rather large and deep (II, IV, VII, database of FEI). Their average phytoplankton biomass, 0.9 mg L^{-1}, is threefold compared to that in oligotrophic and acidic lakes; and varies more (SD % = 78). The average chlorophyll *a* concentration, 6.2 μg L^{-1} (SD % = 48), is twofold compared to the oligotrophic lakes (Table 3). The variation of biomass is at greatest in May–June, after which it gradually decreases (Fig. 4). Lakes may became more dystrophic, as did Lake Kemijärvi, the recipient for the two reservoirs Lokka and Porttipahta, after their construction. Furthermore, the trophic status of Lake Kemijärvi changed slightly towards mesotrophy during the period of strong water level regulation in the reservoirs. This change was mainly caused by increase of cryptomonads and diatoms.

A total of 519 taxa were observed in 197 samples (Table 3). Diatoms clearly dominated the phytoplankton assemblage at *ca.* 40 %. *Aulacoseira italica*, *Rhizosolenia longiseta*, *Asterionella formosa* and *Tabellaria flocculosa,* were the main components (Figs. 1, 5, Tables 4-6). A plausible reason for their occurrence is that the monitored lakes do not have very high humus content and are rather large in surface area, which enables marked turbulence. In the dystrophic, sheltered forest lake, Lake Kalliojärvi, diatoms were observed as abundant only during spring, and flagellated species dominated in the summer months (II). *Aulacoseira italica* has been reported to correlate positively with dystrophy (Pinel-Alloul *et al.* 1990), due to its low light demands (Talling 1957). According to the present material (database of FEI) it appears to prefer eutrophic lakes.

Cryptomonads and chrysomonads occur in equal quantities, each contributing approximately 20 % of the total biomass (Figs. 1, 5). It seems that cryptomonads derive benefit from their pigmentation, equal to that of many cyanophytes (Van den Hoek 1984), in low light conditions in dystrophic waters (Ilmavirta 1980, 1983, Arvola 1984, Rask *et al.* 1986, Salonen *et al.* 1992). Cryptomonads are also able to respond to occasional nutrient depletion by their motility, and by

mixotrophic nutrient uptake (Salonen *et al.* 1984, Salonen and Jokinen 1988, Jansson *et al.* 1996, Roberts and Layborn-Perry 1999). Flagellated chrysomonads survive in very low nutrient concentrations in dystrophic waters (Arvola 1983). The small *Chrysococcus biporus* Skuja and *C. cordiformis* Naumann are typical for dystrophic lakes and the small prymnesiophycean *Monochrysis parva* for dystrophic forest lakes (II).

Green algae, *e.g. Chlamydomonas* spp., and *Botryococcus* spp. contribute on average less than 10 % to the total biomass. Several representatives of Desmidiales originating from the littoral area, such as the large *Xanthidium antilopeum* (Brébisson) Kützing and *Hyalotheca dissiliens* (Smith) Brébisson, typical for dystrophic waters (*e.g.* Tikkanen and Willén 1992), are occasionally observed. Cyanophytes are sparse in dystrophic lakes (Figs. 1, 5, Tables 4–6), contributing only *ca.* 5 % to the total biomass. *Aphanocapsa reinboldii* (Richter) Komárek & Anagnostidis and *Merismopedia warmingiana* are abundant, but these small-sized cyanophytes are of minor importance when considering the biomass. In dystrophic lakes cyanophytes, such as *Anabaena flos-aquae*, are only rarely observed to form visible greenish flakes on the water surface (II).

Spring phytoplankton is clearly dominated by chrysomonads, especially *Mallomonas crassisquoma* but *M. allorgei* (Deflandre) Conrad, *M. caudata* Ivanov em. Krieger and *Pseudopedinella* spp. are also abundant and may contribute more than 60 % of the total biomass (II). In spring small *Cryptomonas* spp. but in summer medium-sized *Cryptomonas* spp. are abundant. In summer, diatoms account for 45 % of the total average biomass, the dominant species being *Rhizosolenia longiseta* and *Asterionella formosa*. The fragile *R. eriensis* H.L. Smith is common only in dystrophic lakes (Tables 4–6).

In autumn, diatoms, chrysomonads and cryptomonads are almost equally abundant, each contributing approximately 20 % of the total biomass. Furthermore, the proportion of *Gonyostomum semen* alone is also *ca.* 20 % (Fig. 5, Tables 5–6). *Gonyostomum semen* is rather rare in large lakes with relatively high water colour (VII), although its occurrence is generally associated with dystrophy. The biomass of *G. semen* correlates only weakly with pH but more strongly with eutrophy (V). In the studied forest lake, Lake Kalliojärvi, *G. semen* obviously benefitted from the

high concentration of nutrients in the hypolimnion (II). A deeper sampling depth than 0–2 metres could be more representative due to the occurrence of this species in deeper parts of the water column (Eloranta and Räike 1995).

3.5.5 Mesotrophic lakes

In the moderately shallow mesotrophic lakes (IV, VI, database of FEI), the average total phytoplankton biomass, 2.3 mg L^{-1}, is eightfold that in oligotrophic lakes, and consists mainly of diatoms (46 %) and cyanophytes (17 %) (Figs. 1, 5). The variability of biomass is also higher (SD % = 87) compared to the less productive lakes. The average chlorophyll *a* concentration, 8.7 µg L^{-1} (SD % = 55), is threefold that in oligotrophic lakes (Table 3). The vernal maximum was not observed in mesotrophic lakes in this study (Fig. 4), due to the late sampling and the varying succession of phytoplankton in the shallow lakes (Trifonova 1993, Knuuttila *et al.* 1994).

Altogether 556 taxa were observed in 152 samples (Table 3). Furthermore, the diversity of phytoplankton increased from oligotrophic to mesotrophic lakes (Figs. 1, 5, 6), which is in agreement with previous observations (Brettum 1980, Økland 1983). The phytoplankton assemblage was clearly dominated by diatoms (46 %), *e.g.* by *Acanthoceras zachariasii, Aulacoseira ambigua, A. islandica* (Müller) Simonsen, all indicators for eutrophic waters (Järnefelt 1952, 1956a, Brettum 1989, Lepistö 1990) and by *A. italica* which Brettum (1989) classifies as typical for mesotrophic waters. However, the abundance of *A. italica* appeared to increase with increasing trophic degree. Furthermore, *Aulacoseira distans* is observed mainly in mesotrophic lakes, especially in summer (Tables 4-6). *Asterionella formosa*, typical for dystrophic lakes, and *Tabellaria flocculosa,* common in the littoral area and favouring oligotrophic conditions (Hutchinson 1967), were abundant in mesotrophic lakes.

Cyanophytes and cryptomonads contribute 17 % and 16 %, respectively, to the phytoplankton biomass. Although water blooms are not very frequently observed (IV, VI), cyanophytes may become abundant under favourable conditions. In mesotrophic lakes mainly the N_2 – fixing cyanophytes, such as *Anabaena flos-aquae* and *Aphanizomenon* spp. are abundant (Tables 5–6). In fact, the genus *Anabaena* accounts for 60 % of water

blooms reported in lakes in Finland (database of harmful algae of FEI). W*oronichinia naegeliana*, a typical cyanophyte in mesotrophic waters (Brettum 1989), was only occasionally observed in the studied lakes (IV, VI). This alga has formed mass occurrences below the ice already in March in the mesotrophic Lake Lappajärvi (Lepistö and Storberg 1995). *Uroglena* spp. might cause occasional fish-like odour during mass occurrences in early summer (VI). This phenomenon is liable to be suppressed with advancing eutrophication (Talling 1993). *Dinobryon bavaricum* and *D. divergens,* generally considered to be oligotrophic indicators (Järnefelt 1952, 1956a, Brettum 1989), are frequently observed in mesotrophic lakes (IV, VI), which is in agreement with the results of Eloranta (1989). *Synura* spp. is the most abundant chrysomonad in this lake group. According to Järnefelt (1952, 1956a), *Synura uvella* (see Appendix 1) belongs to the eutrophic indicators. *Gonyostomum semen* (Raphidophyceae) occurs in high quantities especially in mesotrophic lakes in late summer and in autumn (Tables 4–6). Due to its high photosynthetic pigment content very high chlorophyll *a* concentrations can be measured during its maximum abundance. *G. semen*, if abundant, causes skin irritations in swimmers (Cronberg *et al.* 1988). If abundant in raw water this alga can clog the filters of waterworks during water treatment (Manninen 1987). However, it totally disappears during the water treatment, which destroys the fragile cells (VI).

The spring phytoplankton is dominated by the diatoms *Aulacoseira ambigua* and *A. italica* (VI) and medium and large-sized cryptomonads (Fig. 5, Table 4). The biomass maximum observed in July is caused mainly by *Aphanizomenon* spp. but diatoms, especially *Tabellaria flocculosa*, dominate the summer phytoplankton (Figs. 4, 5). In autumn more than one half of the phytoplankton is composed of cyanophytes, such as *Anabaena flos-aquae* and *Microcystis wesenbergii* (Fig. 5, Table 6).

3.5.6 Eutrophic lakes

In eutrophic lakes (VI, VII, database of FEI) the average phytoplankton biomass is 7.6 mg L^{-1} (Table 3). However, the variability of biomass is very high in these lakes (SD % = 100). The average chlorophyll *a* concentration is also high, 36.9 µg L^{-1} (SD % = 82). A total of 313 taxa were identi-

fied in 35 samples. The proportion of cyanophytes is on average 40 % and that of diatoms 30 % of the total biomass. Cyanophytes belong almost equally to either N_2 – fixing or non-N_2 – fixing taxa. *Anabaena flos-aquae* (Lyng.) Brébisson (earlier also identified as *Anabaena circinalis* Kützing, not *Anabaena circinalis* Rabenhorst) is the most abundant cyanophyte in eutrophic lakes, occurring slightly less in hyper-eutrophic lakes. *Aphanocapsa reinboldii* and *Microcystis aeruginosa* are common and several other species of the genus *Microcystis* are frequently observed in eutrophic lakes. The dominating diatoms, *e.g. Aulacoseira ambigua* and *Acanthoceras zachariasii*, both indicators of eutrophy (Lepistö 1990, Rosenström and Lepistö 1996), clearly prefer eutrophic lakes but are also common in mesotrophic and hyper-eutrophic lakes (Tables 4–6).

Green algae contribute 10 % to the total average phytoplankton biomass (Tables 4–6). This group seldom dominates the biomass, according to Mantere and Heinonen (1983). Eutrophic indicators (Järnefelt 1952, 1956a, Heinonen 1980, Brettum 1989), small in cell size, such as *Actinastrum hantzschii* Lagerheim, *Dichotomococcus curvatus* Korshikov and *Tetraedron caudatum* (Corda) Hanskirg, are numerous. *Pediastrum duplex* Meyen has many modifications, exemplified by *P. duplex* v. *gracillimum* W. & G.S. West and *P. limneticum* Thunmark, obviously reflecting differences in environmental conditions, such as increased concentrations of nutrients. *P. duplex* occurred in almost every eutrophic lake sample (VII).

Euglenids, such as *Euglena proxima* Dangeard, *Trachelomonas hispida* (Perty) Stein and *T. volvocinopsis* Svirenko are abundant in eutrophic lakes, and *T. volvocina* Ehrenberg is typical for the Lokka reservoir (IV, VI, VII). The large-sized *Euglena oxyuris* Schmarda is observed only in eutrophic lakes. This species is classified as a eutrophic indicator (Järnefelt 1952, 1956a, Heinonen 1980) and is often typical in waters receiving sewage effluents (Tikkanen and Willén 1992). In addition, rather sparsely occurring taxa, mainly pseudoplankton of classes Tribophyceae and Conjugatophyceae, are found especially in eutrophic lakes (VII).

Spring phytoplankton consists mainly of rather small diatoms, such as *Aulacoseira alpigena* (Grun.) Simonsen, *A. italica* v. *tenuissima* and *Stephanodiscus* cf. *hantzschii* Grunow. The vernal maximum (Figs. 4, 5) of *Aulacoseira* caused taste and odour in the water (VI), although the number of diatom cells was only half the critical limit (2500 cells/ ml) given in the literature (Seppovaara 1971). Diatoms easily pass through filters in water treatment (VI). In shallow and moderately nutrient-rich waters, diatoms may dominate throughout the growing season (Willén 1992a), when they benefit from mixing of the water column during summer (Lund 1971). In spring the proportion of cyanophytes is rather high, 15 %, with biomass averaging 0.05 mg L^{-1}. Summer phytoplankton is dominated at maximum of 48 % by cyanophytes, such as *Aphanocapsa reinboldii, Anabaena flos-aquae,* and *Aphanizomenon* spp. Diatoms co-dominate, at a maximum of 40 %. *Gonyostomum semen* and the green alga *Pediastrum duplex* are typical summer taxa (Table 5). In autumn, phytoplankton consists mainly of diatom (maximum 71 %), *Acanthoceras zachariasii* occurs in high quantities and *Aulacoseira alpigena* with slightly lower abundance.

3.5.7 Hyper-eutrophic lakes

In hyper-eutrophic lakes (I, VII, database of FEI), in which 486 taxa were identified in 143 samples, the average biomass is 13.1 mg L^{-1} (SD % = 94) and the average chlorophyll *a* concentration 52.4 µg L^{-1} (SD % = 84) (Table 3). Phytoplankton biomass, consisting mainly of cyanophytes (*ca.* 60 %), varies strongly due to the high peak values (Fig. 4, Table 3) and at the same time the diversity may decrease (Figs. 5, 6). The proportion of the N_2 – fixing cyanophytes compared to the non-N_2 – fixing cyanophytes is on average slightly higher. With increasing eutrophication the average summer biomass of cyanophytes increases from 0.4 mg L^{-1} in mesotrophic lakes to 7.5 mg L^{-1} in hyper-eutrophic lakes. The proportion of diatoms is on average only 20 %.

The genus *Aphanizomenon,* including *A. flos-aquae* (L.) Ralfs, *A. issatzschenkoi* (Usac.) Proshkina-Lavrenko, and *A. yezoense* Watanabe, dominates. According to Watanabe (1991), *A. yezoense* is abundant in less eutrophic waters. Furthermore, *Microcystis wesenbergii* and *M. aeruginosa* occur in high quantities in eutrophic and especially in hyper-eutrophic lakes. Due to taxonomical misinterpretations *M. flos-aquae* (Wittr.) Kirchner has been included in *M. aerugi-*

nosa (Kütz.) Kützing. *M. viridis* is abundant mainly in hyper-eutrophic lakes (Tables 4–6). However, *Planktothrix agardhii* is not among the most typical taxa although it is observed occasionally as a very abundant component of phytoplankton in eutrophic lakes (I, VI, VII). *P. agardhii* is typical for eutrophic brackish waters (Niemi 1973, 1979), and can form pronounced deep layer maxima during suitable conditions (*e.g.* Watanabe 1979, Lindholm 1992).

Medium-sized cryptomonads are typical for nutrient-rich lakes, which receive sewage (Rosén 1981), such as Lake Tuusulanjärvi (I). Dinoflagellates produce by far the largest biomass (0.5 mg L^{-1}) in hyper- eutrophic lakes, partly due to the rather large cell size of *e.g. Ceratium hirundinella* (O.F. Müller) Schrank and *Gymnodinium* spp. (VII) (Tables 4–6). Some dinoflagellates, such as *Peridinium bibes* Stein and *P. willei* Huitfeld-Kaas, have been reported as indicators of eutrophy (Järnefelt 1952, Hutchinson 1967, Brettum 1989). In this study *P. bibes* was observed in eutrophic lakes in summer and in hyper-eutrophic lakes it was moderately abundant in autumn (database of FEI).

Spring phytoplankton is dominated by diatoms, mainly *Aulacoseira italica* and *A. italica* v. *tenuissima,* and by *Cryptomonas* spp. (medium-sized) and *Rhodomonas lacustris.* The proportion of cyanophytes is low, less than 10 %, but the average cyanophyta biomass in spring is 0.6 mg L^{-1}. In summer the cyanophytes *Aphanizomenon, Microcystis* and *Anabaena* dominate the biomass with a maximum proportion of 72 % in August, and diatoms (maximum 43 %), *e.g. Aulacoseira italica, A. granulata* and the small *Stephanodiscus* spp. co-dominate. In autumn the abundant cyanophytes, especially *Microcystis wesenbergii, M. viridis* and *Anabaena flos-aquae*, are succeeded by the diatoms *Aulacoseira islandica* and *A. ambigua* in October (Fig. 5, Tables 4–6).

4 Problems in the analysis of phytoplankton

4.1 Sampling

In Finland the monitoring of lake phytoplankton was initiated in the early 1960s. Especially July and August phytoplankton data are extensive, whereas other months are clearly less represented

in the database. However, it seems that in the studied lakes the vernal maximum was partly missed due to the late sampling at the end of May (*ca.* 20th May). The correct timing of sampling depends on the location of the lake, weather conditions and the morphology of the lake basin. During more than thirty years of monitoring some major methodological changes have taken place. The decrease of sampling depth to the two upper metres since 1971 (Table 2) has obviously elevated the phytoplankton biomass (Fig. 3), as phytoplankton is concentrated in the well illuminated upper water layers (Reynolds 1986), especially in humic lakes (Salonen *et al.* 1984). In clear water lakes, phytoplankton may also occur in deeper layers, and in humic lakes flagellated taxa often migrate between the epilimnion and hypolimnion (Eloranta and Räike 1995), and thus are not always covered by sampling. Olrik *et al.* (1998) recommended a sampling depth from the surface to 4–5 metres for lake phytoplankton. However, all changes must be seriously considered. As Harris (1986) noted, data of equal sampling and identification and adequate enumeration of the smaller flagellates are needed in order to obtain a correct picture of long-term changes in phytoplankton abundance.

4.2 Analyses

July samples have been studied with comparable methods to those used by Järnefelt and his co-workers until the end of the 1950s. July samples are considered to give a common picture of the productivity of inland waters during stratified summer conditions (Heinonen 1982), although in July-August the predation of phytoplankton by zooplankton is often very effective and thus may drastically change the community structure of phytoplankton (Lynch and Shapiro 1981).

The qualified identification and counting are to a high degree dependent on the experience and proficiency of the investigator. Intercalibration of phytoplankton counting has demonstrated marked differences between laboratories concerning total numbers of taxa and especially in identification at the species level. This emphasises the need for more exact instructions for phytoplankton counting procedures (Niemi *et al.* 1985).

This need was recently recognised by Olrik *et al.* (1998), who proposed Nordic standard meth-

ods for phytoplankton analysis in fresh waters. The methods include three different levels of quantitative and qualitative analyses of which level 2, a method without analysis of live samples and without electron microscopy (SEM and TEM), should be reached in monitoring studies. Unfortunately, the use of living material as an aid to identification is usually not possible in routine monitoring work. Recommendations for literature on identification are also given. However, an identification procedure only at the genus level as proposed by Blomqvist and Herlitz (1998) does not provide sufficient information if qualitative changes in phytoplankton are considered. The use of the attribute *confer (cf.)* in front of the species name provides more information on the phytoplankton composition together with cell size information, photographs and/or illustrations (I–VII).

The counting of taxa observed in low numbers causes statistical error (Willén 1976) but yields quantitative observations of individual species which might indicate incipient changes in the water body. The simplified method using enumeration of dominant phytoplankton is complemented with a list of species occurring sparsely but not included in the biomass (Willén 1976).

The biomass of phytoplankton estimated as chlorophyll *a* does not necessarily have a strong correlation with biomass on a volume basis (I, IV, V). In this study the best correlation of chlorophyll *a* with total biomass was obtained in the brown- water forest lake (II). According to Tolstoy (1979), chlorophyll *a* concentration generally provides a good measure for phytoplankton biomass, although decreasing chlorophyll content does not necessarily signify decreasing phytoplankton biomass. The composition of the algal assemblage affects the chlorophyll *a* concentration when the chlorophyll *a* content of diatoms and cyanophytes is low compared to that of cryptomonads and green algae (Tolstoy 1979). This is evident when comparing differences between oligotrophic and eutrophic lakes. The total phosphorus concentration increases ninefold and the chlorophyll *a* concentration thirteen-fold, but the phytoplankton biomass in eutrophic lakes mainly consisting of large cyanophytes and diatoms is twenty five-fold compared to that in oligotrophic lakes (Tables 1, 3).

Several new methods in phytoplankton analyses will obviously be useful in the near future, such as automatic identification and cell counting by

image analysers, cell counting by flow cytometry, pigment analyses using HPLC and the identification of species and strains of cyanophytes using the highly advanced tools of molecular biology.

4.3 Lake groups

The consideration concerning typical phytoplankton assemblages in different lake groups is based on the classification of lakes according to certain variables, such as total phosphorus, water colour or pH. However, each classification approach usually produces slightly different lake categories. Different physical, chemical and biological factors influence the phytoplankton assemblages of the lake groups. Furthermore, natural or man-made lakes, even when situated close to each other (IV, V), do not necessarily support similar phytoplankton assemblages due to their different water chemistry and morphometry.

4.4 The importance of tradition

The processing of the old phytoplankton results, the oldest being from the 1910s from lakes in Finland (I, IV, V), has been possible because the identification procedures of professor Heikki Järnefelt have been followed by his students and by his co-workers Toini Tikkanen and Ainikki Naulapää, who in turn have trained the phytoplankton researchers of the Finnish Environment Institute and other limnologists in Finland. Although there are no samples deposited in permanent repositories, as proposed by Stoermer (1984), nor photographs of the taxa in the old data, it is quite easy due to the continuous tradition to interpret the species list influenced by taxonomical changes (Appendix 1) and even to estimate the quantitative values of phytoplankton given by Järnefelt and his co-workers. This tradition in phytoplankton identification should be continued.

5 Summary

Waters of different status all support their own typical phytoplankton assemblages. Due to their small cell size and therefore high potential growth rate, phytoplankton species react quickly to changes in the surrounding environment, such as

Table 7. The variation of the average (June-August) phytoplankton biomass (wet weight, mg L^{-1}) and the chlorophyll a concentration (μg L^{-1}) in lake groups with different total phosphorus concentration (μg L^{-1}) and water colour number (mg L^{-1} Pt). SD % denotes standard deviation percent.

Lake type	Tot. P μg L^{-1}	Water colour mg L^{-1} Pt	Biomass mg L^{-1}	SD %	Chlorophyll a μg L^{-1}	SD %
Oligotrophic	6	20	0.3	67	2.7	44
Dystrophic	14	70	0.9	78	6.2	48
Mesotrophic	18	30	2.3	87	8.7	55
Eutrophic	57	90	7.6	100	36.9	82
Hyper-eutrophic	65	75	13.2	94	52.4	84
Lokka	36	80	3.0	80	12.3	59
Porttipahta	19	70	1.0	90	6.7	79

in water quality. Phytoplankton assemblages are influenced by several factors, of which nutrient concentrations, water colour and pH are generally considered. Furthermore, turbulence, stratification conditions, light conditions and catchment properties as well as the morphology of the lake basin may influence the phytoplankton assemblage. In this study the quantity and quality of phytoplankton reflecting the ecological status of lakes of different types are considered. The classification of lakes is based mainly on the average concentrations of total phosphorus (Table 7). However, when water colour is used as a factor for lake classification the abundance of dominating taxa changes although the nutrient concentrations do not markedly change.

In oligotrophic, mainly clear-water lakes, phytoplankton biomass is low and varies only slightly. Small chrysomonads, some of them capable of mixotrophy, cryptomonads, dinoflagellates, diatoms, but also small-celled colonies of cyanophytes, are the main components of the phytoplankton biomass. In dystrophic lakes and in reservoirs phytoplankton biomass is higher than in oligotrophic lakes, and is composed mainly of diatoms, with the exception of brown-water lakes, and cryptomonads. Mixotrophic flagellates are abundant. Typical species are *Mallomonas crassisquoma* (Chrysophyceae), *Rhizosolenia longiseta* (Diatomophyceae) and *Gonyostomum semen* (Raphidophyceae).

Mesotrophic lakes in this study can be divided into clear-water lakes and moderately brown-water lakes. Diatoms dominate the phytoplankton, and cryptomonads co-dominate. *Gonyostomum semen* (Raphidophyceae) increases in late summer and autumn. Cyanophytes are not very abundant in summer, accounting on average for 10 % of the total biomass, but may increase in late summer and under favourable conditions mass occurrences are possible. Most cyanophytes belong to the N_2 – fixing taxa, such as *Anabaena flos-aquae* and *Aphanizomenon* spp.

In eutrophic lakes the biomass is threefold that of mesotrophic lakes and the variation is considerable. Cyanophytes contribute on average 20 % to the total phytoplankton biomass, but increase after July approximately to 50 % of the total biomass. The N_2 – fixing genera *Anabaena* and *Aphanizomenon* dominate and the non-N_2 – fixing genus *Microcystis* is also abundant. Typical for eutrophic waters are centric diatoms and green algae. In hyper-eutrophic lakes cyanophytes contribute on average 60 % of the total biomass and they become rather abundant already in May, in contrast to the situation in lakes with different trophic status. In hyper-eutrophic lakes *Microcystis* dominates as the genus biomass but *Aphanizomenon* spp. dominates as the individual taxon.

The importance of individual species (taxon) and algal groups as components of total biomass increases with increasing trophic gradient, and the species diversity decreases. The biomass of a single algal group does not necessarily change when the N:P ratio changes but the species composition of the group may change quite drastically. However, almost all taxa are observed in each lake group due to the generally wide ecological amplitude of phytoplankton species, but competition and grazing restrict their occurrence in unfavourable conditions. Exceptionally some algae, *e.g. Microcystis viridis* and *Euglena oxyuris* are observed only in eutrophic waters.

Effective water protection efforts during the past two decades appear to have improved the state of the lakes. Phytoplankton reacts immediately to decreasing waste water load and decreased nutrient concentrations in the water, but the reaction also continues over a long period. Due to the decrease of nitrogen compounds the non-N_2 – fixing *Planktothrix* are soon out-competed, and cyanophytes may totally disappear after some years. The internal loading sustains adequate phosphorus concentration for the N_2 – fixation in water, and the N_2 – fixing *Anabaena* and *Aphanizomenon* occur alternatively with the non-N_2 – fixing genus *Microcystis*, which is an effective competitor for nutrients. Over longer periods of time, taxa typical for less eutrophic conditions, such as the diatoms *Rhizosolenia* and *Tabellaria* and the chrysomonad *Dinobryon* are observed. Simultaneously the species diversity of the phytoplankton assemblage may increase, and it may change towards smaller species accompanied by decrease in the biomass.

The construction, water level regulation, and later the ageing process have all affected the water quality and phytoplankton assemblages in the reservoirs Lokka and Porttipahta. In the young reservoirs river phytoplankton with small cyanophyta colonies, the green alga *Monoraphidium contortum* and flagellated and heterotrophic taxa were abundant. The period of strong water level regulation increased nutrients in the water and water colour also increased due to the organic matter. The high quantity of available silicate benefitted diatoms regardless of the turbidity of water, and especially *Aulacoseira italica* was abundant. Nutrient and organic matter concentrations decreased during the ageing process of the reservoirs.

However, total phosphorus concentration in the Lokka reservoir is still twofold that in mesotrophic lakes, close to the concentrations of eutrophic lakes. Due to the humic compounds, phosphorus is only partly bioavailable for phytoplankton, and perhaps for this reason the phytoplankton biomass is equal to that in mesotrophic lakes. In the Porttipahta reservoir nutrient concentrations are lower, typical for mesotrophic waters, but the biomasses are only one half of those recorded in mesotrophic lakes. *Aulacoseira italica* is typical for both reservoirs but *Rhizosolenia longiseta* is typical for the Porttipahta reservoir. However, during very warm weather conditions cyanophytes may still form water blooms in the Lokka reservoir.

The increase of biological productivity in waters as a consequence of eutrophication often promotes nuisance in the form of mass occurrences of algae. Even in moderately eutrophic lakes the spring maxima of chrysomonads and diatoms may cause taste and odour problems which are inconvenient, especially in surface waters used as raw water for water works. Cyanophytes increase in late summer in moderately nutrient-rich waters but may increase in early summer in very eutrophic lakes, and the possibility of abundant toxic *Microcystis* – species increases. *Gonyostomum semen* increases in late summer even in slightly eutrophic lakes. The slight eutrophication of dystrophic lakes does not increase markedly the quantity of cyanophytes in these lakes.

In general the state of Finnish lakes seems to have improved in the 1990s according to the data of phytoplankton monitoring, although the number of observations of algal blooms has increased. Only in mesotrophic lakes does phytoplankton biomass appear to have increased in the 1990s, mainly due to increase of diatoms. A slow eutrophication process might be the reason for this phenomenon. In highly eutrophic lakes the total biomass, including cyanophytes and diatoms, has strongly decreased in the 1990s, and *ca.* 50 % of cyanophytes are those which only seldom produce toxic strains. The state of the hyper-eutrophic Lake Tuusulanjärvi has clearly improved due to the effective restoration efforts.

The estimation of phytoplankton quantity by analysing the chlorophyll *a* concentration is an effective method and provides much data, but routine chlorophyll analyses do not provide information about the composition of phytoplankton. Information about water quality is provided by monitoring of the occurrence of cyanophytes by microscopy, even at a qualitative level, which is recommended in surface water used as a raw water source for waterworks. The reason for unpredicted increase of chlorophyll *a* might be *e.g. Gonyostomum semen,* an alga with many chloroplasts.

Phytoplankton volume and chlorophyll *a* values show relatively good correlation if plotted against each other in oligotrophic and dystrophic lakes, because the phytoplankton composition consists of small cryptomonads and other algae with high chlorophyll *a* contents. Eutrophic lakes, however, are dominated by large cyanophytes and diatoms, often with rather low chlorophyll *a* con-

tents. Thus the chlorophyll *a* concentrations in these lakes are rather low compared to the total phytoplankton volume. Total phytoplankton volume may be overestimated due to difficulties in estimating the volume of large cyanophyta colonies and also due to errors in microscopic analyses.

In long-term monitoring the seasonal and interannual variability of phytoplankton, *e.g.* due to weather conditions, is often remarkable. The variability appears to increase with increasing trophic degree. The distinction between changes caused by eutrophication and the natural variability is one of the basic challenges for monitoring. "New" members in the phytoplankton assemblage might at an early phase predict changes in ecological status of a water body. However, progress in the taxonomy of phytoplankton also causes the appearance of "new" species and the disappearance of some other species during long-term monitoring. Furthermore, in an ideal situation the long-term monitoring based on microscopical analyses should be performed by one person or by one group with close cooperation and unbroken tradition. Regularly repeated intercalibrations between different phytoplankton researchers are therefore important, because otherwise the changes observed in the phytoplankton assemblage may only reflect changes beside the microscope, not in the environment.

In conclusion, the results show that phytoplankton reflects the ecological status of lakes and also responds both qualitatively and quantitatively to changes therein. The average phytoplankton biomass increases with increasing eutrophy, as does the variation of biomass. This variation is highest in eutrophic lakes but decreases slightly in hyper-eutrophic lakes. In oligotrophic lakes different algal groups are almost equally abundant as biomass but chrysomonads are abundant as cell numbers. Typical for dystrophic lakes are diatoms and cryptomonads but in small brown-water forest lakes diatoms are rare. Mesotrophic lakes are also clearly dominated by diatoms, and the average biomass of cyanophytes consisting mainly of N_2 – fixing Nostocales is moderately low until late summer. In eutrophic lakes and especially in hyper-eutrophic lakes cyanophytes become abundant already in the early summer. Finally, diatoms appear to be the most important group in the studied lakes, and cryptomonads co-dominate. Only in eutrophic lakes, cyanophytes dominate the phytoplankton assemblage. Furthermore, in lakes in Finland the quantity of cyanophytes seems not to have increased in the 1990s.

6 Yhteenveto

Eri tyyppisissä vesissä on niille ominainen kasviplanktonyhteisö. Pienikokoiset, nopeasti lisääntyvät kasviplanktonsolut heijastavat herkästi ympäristössään, kuten veden laadussa tapahtuvia muutoksia. Kasviplanktonin koostumukseen vaikuttavista tekijöistä tarkastellaan etenkin ravinnesuhteita, veden väriä ja happamuutta. Myös veden virtaus- ja kerrostuneisuusolosuhteet, valaistusolosuhteet, valuma-alueen ominaisuudet ja altaan morfologia vaikuttavat kasviplanktonin koostumukseen. Tässä työssä tarkastellaan kasviplanktonyhteisöjen lajikoostumusta ja määrää erityyppisten järvien ekologisen tilan ilmentäjinä. Jär-

Taulukko. Erityyppisten järvien keskimääräisen (kesä–heinäkuu) kasviplanktonbiomassan (mg L⁻¹) ja *a*-klorofyllin pitoisuuksien (µg L⁻¹) vaihtelu kokonaisfosforin (µg L⁻¹) ja veden väriluvun (mg L⁻¹ Pt) muuttuessa. SD % kuvaa standardipoikkeaman prosentuaalista vaihtelua.

Järvityyppi	Kok. P µg L⁻¹	Veden väri mg L⁻¹ Pt	Biomassa mg L⁻¹	SD %	*a*-klorofylli µg L⁻¹	SD %
Oligotrofinen	6	20	0.3	67	2.7	44
Dystrofinen	14	70	0.9	78	6.2	48
Mesotrofinen	18	30	2.3	87	8.7	55
Eutrofinen	57	90	7.6	100	36.9	82
Hyper-eutrofinen	65	75	13.2	94	52.4	84
Lokan tekoallas	36	80	3.0	80	12.3	59
Porttipahdan tekoallas	19	70	1.0	90	6.7	79

vien luokittelussa on ensisijaisesti käytetty kokonaisfosforin keskimääräisiä pitoisuuksia. Kun veden värilukua käytetään luokittelevana tekijänä, valtalajit ja niiden runsausjärjestys muuttuvat, vaikka ravinnepitoisuudet eivät juurikaan muutu.

Vähäravinteisten, oligotrofisten, pääosin kirkasvetisten järvien ryhmässä kasviplanktonbiomassa on alhainen ja sen vaihtelu vähäistä. Pienikokoiset kultalevät, joista osa on miksotrofisia, nielulevät, panssarisiimalevät, piilevät mutta myös pienisoluiset sinileväyhdyskunnat muodostavat pääosan kasviplanktonista. Tummavetisissä, eli dystrofisissa järvissä ja molemmissa tutkituissa tekoaltaissa kasviplanktonin määrä on suurempi kuin oligotrofisissa vesissä ja lajisto koostuu lähinnä piilevistä, poikkeuksena kuitenkin tummavetiset pienet metsäjärvet, ja nielulevistä. Miksotrofisia lajeja on runsaasti. Tyypillisiä lajeja ovat *Mallomonas crassisquoma* (Chrysophyceae), *Rhizosolenia longiseta* (Diatomophyceae) ja *Gonyostomum semen* (Raphidophyceae).

Mesotrofisista, lievästi rehevöityneistä järvistä osa on suhteellisen kirkasvetisiä ja osa melko ruskeavetisiä. Piilevät ovat vallitsevina ja nielulevät muodostavat merkittävän osan näiden järvien kasviplanktonista. Sinilevien osuus on keskimäärin 10 % kesän kasviplanktonbiomassasta, mutta niiden osuus saattaa kasvaa loppukesällä ja suotuisissa olosuhteissa saattaa muodostua massaesiintymiä. Pääosa sinilevistä on typensitojia, joista yleisimpiä ovat *Anabaena flos-aquae* ja *Aphanizomenon* spp. Reheviksi, eli eutrofisiksi luokitelluissa vesissä sinilevien osuus biomassasta on keskimäärin 20 %, mutta saattaa heinäkuussa nousta liki 50 %:iin. Typensitojasuvut *Anabaena* ja *Aphanizomenon* ovat valtalajeina, mutta *Microcystis* -sukuun kuuluvia lajeja on myös runsaasti. Sentristen piilevien ja viherlevien osuus biomassasta on suurimmillaan eutrofisissa järvissä. Erittäin rehevissä, eli hyper-eutrofisissa järvissä sinilevien osuus on keskimäärin 60 % biomassasta ja ne runsastuvat jo toukokuusta lähtien toisin kuin muissa järviryhmissä. Hyper-eutrofisissa järvissä *Microcystis* -suvun lajien osuus kesän sinileväbiomassasta on suurin mutta runsaimmin tavattu yksittäinen taksoni on *Aphanizomenon* spp.

Mitä rehevimmistä vesistä on kyse sitä suurempi on yksittäisten lajien (taksonien) ja leväryhmien merkitys biomassasta, mikä alentaa lajidiversiteettiä. Yksittäisen leväryhmän biomassa ei välttämättä muutu ravinnesuhteiden (lähinnä N:P-suhteen) muuttuessa, mutta ryhmän sisällä

lajikoostumus saattaa muuttua merkittävästi. Kasviplanktonlajit ovat yleensä ympäristövaatimuksiltaan joustavia, ja niitä tavataan kaikissa tarkastelluissa järviryhmissä. Kasviplanktonlajien keskinäinen kilpailu ja niihin kohdistuva saalistus rajoittavat kuitenkin niiden esiintymistä suhteessa toisiinsa, ja niiden määrä saattaa olla alhainen epäsuotuisissa olosuhteissa. On kuitenkin poikkeuksia, kuten *Microcystis viridis* ja muutamat silmälevät, kuten *Euglena oxyuris*, joita tavataan pelkästään rehevissä vesissä.

Tehokkaiden vesiensuojelutoimenpiteiden ansiosta järvet näyttäisivät karuuntuneet viimeisten parin vuosikymmenen aikana. Kasviplanktonyhteisö reagoi jätevesipäästöjen loppumiseen ja alentuneisiin ravinnepitoisuuksiin sekä välittömästi että pitkän ajan kuluessa. Typpiyhdisteiden vähenemisen takia *Planktothrix* -suku ei kykene kilpailemaan ravinteista typpeäsitovien sinilevien kanssa. Sinileväyhteisö saattaa jopa romahtaa täydellisesti muutaman vuoden kuluttua jätevesipäästöjen lopettamisesta. Sisäinen kuormitus tuottaa veteen edelleen typensidontaa varten riittävästi fosforiyhdisteitä ja typensitojat *Anabaena* ja *Aphanizomenon* vuorottelevat ei-typpeä sitovan *Microcystis* -suvun kanssa, joka puolestaan kilpailee tehokkaasti ravinteista. Ajan myötä vähäravinteisemmille vesille tyypilliset piilevät kuten *Rhizosolenia* ja *Tabellaria*, sekä *Dinobryon*-kultalevät yleistyvät, samalla kuin lajisto monipuolistuu ja muuttuu pienikokoisemmaksi ja biomassa laskee.

Rakentaminen, vedenpinnan säännöstely ja ikääntyminen ovat nähtävissä Lokan ja Porttipahdan tekoaltaiden veden laadussa ja kasviplanktonyhteisöissä. Nuorissa tekoaltaissa vallitsi ns. jokiplankton, jossa pienisoluiset sinileväyhdyskunnat, ja esimerkiksi *Monoraphidium contortum* -viherlevä sekä siimalliset ja heterotrofiset lajit olivat runsaina. Voimakas säännöstelyjakso lisäsi ravinteiden ja silikaattipiin pitoisuuksia vedessä, ja runsas orgaaninen aine tummensi vettä entisestään. Vaikka vesi oli sameaa, runsas silikaattipii edesauttoi piilevien kasvua. *Aulacoseira italica* muodosti pääosan kasviplanktonista.

Altaiden ikääntyessä veden ravinnepitoisuus ja orgaanisen aineen määrä laskivat. Lokan tekoaltaassa kokonaisfosforia on kuitenkin edelleen keskimäärin kaksinkertainen määrä mesotrofisiin järviin verrattuna, liki eutrofisten järvien tasolla. Vedessä oleva runsas humus sitoo osan fosforista, eikä se ole kasviplanktonin käytettävissä. Ehkä sen vuoksi Lokan kasviplanktonbiomassa vastaa-

kin mesotrofisen järven keskimääräistä biomas-saa. Porttipahdan tekoaltaassa ravinteiden pitoi-suudet ovat alhaisempia, mesotrofisille vesille tyypillisiä, mutta kasviplanktonin biomassa on alle puolet mesotrofisten järvien keskimääräisestä biomassasta. *Aulacoseira italica* on edelleen tyy-pillinen molemmille tekoaltaille mutta Porttipah-dan lajistolle tyypillinen on *Rhizosolenia lon-giseta*. Poikkeuksellisen lämmin kesä saattaa yhä edesauttaa sinilevien massaesiintymien muodos-tumista Lokan tekoaltaassa.

Biologisen tuotannon lisääntyminen järvien vähitellen rehevöityessä ilmenee haitallisina levä-esiintyminä. Alkavan rehevöitymisen myötä ke-väiset kultalevien ja piilevien maksimit runsastu-vat ja aiheuttavat haju-ja makuhaittoja, jotka ovat kiusallisia etenkin raakavesilähteenä käytetyissä pintavesissä. Sinilevät runsastuvat loppukesällä mesotrofisissa järvissä mutta erittäin rehevissä järvissä jo alkukesällä. Pahimmillaan leväesiinty-mät ovat myrkyllisten *Microcystis*-lajien muo-dostamia. *Gonyostomum semen*-limalevä runsas-tuu loppukesällä jo lievästi rehevöityneissä jär-vissä. Tummavetisten järvien lievä rehevöitymi-nen ei lisää merkittävästi sinilevien määrää.

Suomalaisten järvien tila kasviplanktonseu-rannan tulosten perusteella arvioituna näyttäisi 1990-luvulla kohentuneen, vaikka ilmoitukset si-nileväesiintymistä ovatkin lisääntyneet. Ainoas-taan mesotrofisissa järvissä kasviplanktonin mää-rä on 1990-luvulla kasvanut, lähinnä piilevien li-sääntymisen takia. Kyseessä saattaa olla hidas re-hevöityminen eli ns. "nuhraantuminen". Erittäin rehevissä järvissä kasviplanktonin kokonaisbio-massa samoin kuin sinilevien ja piilevien määrä on selvästi laskenut 1990-luvulla. Noin 50 % sini-levistä on niitä, jotka harvemmin muodostavat myrkyllisiä kantoja. Erittäin rehevän Tuusulan-järven tila on selvästi parantunut tehokkaiden kunnostustoimenpiteiden ansiosta.

Kasviplanktonin määrän mittaaminen *a*-kloro-fyllin pitoisuuksina on menetelmänä nopea ja te-hokas mutta ei rutiinimenetelmänä kerro kas-viplanktonin koostumusta. Sinilevien esiintymis-tä pintavettä käyttävän vesilaitoksen raakavedes-sä seurataan yhä useammin mikroskopoimalla, jopa kvalitatiivisesti, jolloin veden laadusta saa-daan aina lisätietoa. Syynä normaalista poikkea-vaan *a* klorofyllipitoisuuteen saattaa esimerkiksi olla runsaasti kloroplasteja sisältävä *Gonyosto-mum semen.*

Kasviplanktonbiomassa korreloi *a*-klorofyllin pitoisuuden kanssa sekä karuissa että tummaveti-sissä järvissä, koska niissä on pienikokoisia nielu-ja muita leviä, joiden *a*-klorofyllin pitoisuus on suuri. Rehevissä järvissä sen sijaan dominoivat suurikokoiset sinilevät ja piilevät, joiden *a*-kloro-fyllin pitoisuus on suhteellisen alhainen, jolloin kasviplanktonbiomassa on suhteellisesti suurem-pi. Biomassa-arvoja saattaa lisäksi nostaa etenkin suurten sinileväyhdyskuntien tilavuuden arvioin-tivirheet, samoin kuin muut mikroskooppisen analysoinnin virheet.

Pitkäaikaisessa seurannassa kasviplanktonin kasvukauden aikainen ja vuosittainen vaihtelu, lä-hinnä sääolosuhteista johtuen, saattaa olla huo-mattava. Vaihtelu on sitä suurempaa, mitä rehe-vämmistä vesistä on kysymys. Luonnollisen vaih-telun erottaminen rehevöitymisen aiheuttamasta vaihtelusta on seurannan perushaaste. Kasvi-planktonyhteisön "uudet lajit" saattavat jo var-hain ennustaa järven ekologisen tilan muutoksia, mutta "uusien" lajien ilmaantuminen tai joidenkin lajien häviäminen pitkän seurannan aikana johtuu myös taksonomisista muutoksista. Mahdollisuuk-sien mukaan tulisi kasviplanktonanalyysien teki-jöiden ja tutkimusmenetelmien olla samoja mah-dollisimman pitkään. Myös säännöllisesti toiste-tut interkalibroinnit takaavat vertailukelpoiset tu-lokset. Pahimmillaan kasviplanktonyhteisössä havaitut muutokset eivät kuvasta muutoksia ym-päristössä, vaan pelkästään tutkijan vaihtumista.

Yhteenvetona voidaan todeta, että tulokset osoittavat kasviplanktonin kuvastavan järvien ekologista tilaa ja reagoivan sekä määrällisesti että laadullisesti niiden tilassa tapahtuviin muu-toksiin. Kasviplanktonin keskimääräinen biomas-sa ja sen vaihtelu kasvavat rehevöitymisen myötä. Vaihtelu on suurinta rehevissä järvissä mutta las-kee jonkin verran erittäin rehevissä järvissä. Vä-häravinteisissa järvissä eri leväryhmien osuus on biomassana lähes yhtä suuri mutta solumäärältään kultalevät ovat merkittävin ryhmä. Tummavetisil-le järville on tyypillistä piilevien ja nielulevien suuri määrä, mutta pienissä erittäin tummavetisis-sä järvissä piileviä on vähän. Myös lievästi rehe-vöityneissä järvissä piilevät dominoivat ja sinile-vien määrä on verraten alhainen lisääntyen loppu-kesällä. Sinileväyhteisö koostuu pääasiassa typ-peäsitovista sinilevistä. Rehevissä ja erittäin rehe-vissä vesissä sinilevät ovat vallitsevina, ja niitä on usein runsaasti jo alkukesällä. Lopuksi voidaan todeta, että pääosassa tutkituista järvistä piilevät ovat merkittävin ryhmä, nieluleviä on jonkin ver-

ran vähemmän, ja vain rehevissä järvissä sinilevät dominoivat kasviplanktonyhteisöä. Tutkimuksen perusteella sinilevien määrä ei näyttäisi lisääntyneen Suomen järvissä 1990-luvulla.

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Appendix 1. Some valid names and their synonyms of the species in the studied material (≠, not synonym).

Valid names	Synonyms
Aphanocapsa planctonica (G.M. Smith) Kom. & Anagnostidis	Aphanocapsa elachista f. planctonica G.M. Smith
Aphanocapsa reinboldii (Forti) Kom. & Anagnostidis	Microcystis reinboldii (Richter) Forti
	(In fertilized fish ponds, less common in lakes)
Merismopedia tenuissima Lemmermann	≠Merismopedia minima Beck
Merismopedia warmingiana Lagerheim	
Snowella lacustris (Chod.) Kom. & Hindák	Gomphosphaeria lacustris Chodat
Woronichinia naegeliana (Unger) Elenkin	Coelosphaerium naegelianum Unger
	Gomphosphaeria naegeliana (Unger) Lemmermann
Anabaena flos-aquae Brébisson	≠Anabaena circinalis Kützing
Aphanizomenon yezoense Watanabe	≠Aphanizomenon flos-aquae (L.) Ralfs
Leptolyngbya mucicola (Lemm.) Kom. & Anagnostidis	Lyngbya mucicola Lemmermann
Limnothrix planctonica (Wolosz.) Meffert	Oscillatoria planctonica Woloszynska
Phormidium tenue (Ag. ex Gom.) Anagn. & Komárek	Oscillatoria tenuis Ag. ex Gomont
Planktolyngbya limnetica (W.West) Anagn. & Komárek	Lyngbya subtilis W.West, Lyngbya limnetica Lemmermann
Planktothrix agardhii (Gom.) Anagn. & Komárek	Oscillatoria agardhii Gomont
Pseudanabaena limnetica (Lemm.) Anagn. & Komárek	Oscillatoria limnetica Lemmermann
Pseudanabaena mucicola (Naum. & Hub.-Pest.) Anagn. & Komárek	Phormidium mucicola Naum. & Hub.-Pestalozzi
Pseudanabaena sp. (Cyanodictyon sp.)	"Phormidium dictyothallum" Skuja
Trichodesmium lacustre (Klebahn) Anagn. & Komárek	Oscillatoria lacustris (Klebahn) Geitler
Ceratium spp.	Ceratium hirundinella (O.F. Müller) Schrank
Ceratium furcoides (Lev.) Langhaus	≠ "-"
Peridinium umbonatum Stein	Peridinium inconspicuum Lemmermann
Bicosoeca lacustris J. Clark	Bicoeca lacustris J. Clark
Bicosoeca planctonica v. multiannulata (Skuja) Bourrelly	Bicoeca multiannulata Skuja
Mallomonas punctifera Korshikov	Mallomonas reginae Teiling
Ochromonadales	mainly Uroglena cells, Flagellata cetera
Uroglena spp.	Uroglena americana Calcins
"-"	Uroglena volvox Ehrenberg
Synura spp.	Synura uvella Stein em. Korshikov
Acanthoceras zachariasii (Brun) Simonsen	Attheya zachariasii Brun
Cyclotella radiosa (Grun.) Lemmermann	Cyclotella comta (Ehrenb.) Kützing
Aulacoseira alpigena (Grun.) Simonsen	Melosira distans v. alpigena Grunow

Aulacoseira ambigua (Grun.) Simonsen
Aulacoseira italica (Ehrenb.) Simonsen
Aulacoseira distans (Ehrenb.) Simonsen
Aulacoseira granulata (Ehrenb.) Simonsen
Aulacoseira granulata v. angustissima (O. Müll.) Simonsen
Aulacoseira lirata (Ehrenb.) R. Ross
Aulacoseira islandica (O. Müll.) Simonsen
Diatoma tenuis Agardh
Fragilaria berolinensis (Lemm.) Lange-Bertalot
Fragilaria nanana Lange-Bertalot
Fragilaria ulna (Nitzsch) Lange-Bertalot
Fragilaria ulna (Nitzsch) Lange-Bertalot
Tabellaria flocculosa (Roth) Kützing
Bacillariales

Goniochloris fallax Fott
Istmochloron trispinatum (W.&G.S.West) Skuja
Pseudostaurastrum enorme (Ralfs) Chodat
Pseudostaurastrum planctonicum (G. M. Sm.) Chodat

Chlamydocapsa ampla (Kütz.) Fott
Nephrocytium limneticum (G. M. Smith) G. M. Smith
Pseudosphaerocystis lacustris (Lemm.) Nováková
Pseudosphaerocystis neglecta (Teil.) Bourrelly
Sphaerocystis planctonica (Korš.) Bourrelly
Sphaerocystis schroeteri Chodat

Thorakochloris cf. nygardii Komárek
Ankistrodesmus fusiformis Corda
Koliella spiculiformis (Visk.) Hindák
Monoraphidium mirabile (W. & G. S. West) Pankow
Chlorolobion ?;
Chlorolobion braunii (Näg.) Komárek
Koliella setiformis (Nyg.) Nygaard
Monoraphidium contortum (Thuret) Kom.-Legnerová
Closteriopsis longissima v. longissima Lemmermann
Keratococcus suecicus Hindák
Botryococcus spp.

Melosira ambigua (Grun.) O. Müller
Melosira crenulata (Ehrenb.) Kütz., M. italica (Ehrenb.) Kützing
Melosira distans (Ehrenb.) Kützing
Melosira granulata (Ehrenb.) Ralfs
Melosira g. v. angustissima O. Müller
Melosira distans v. lirata (Ehrenb.) Hustedt
Melosira islandica O. Müller
Diatoma elongatum (Lyngb.) Agardh
Synedra berolinensis Lemmermann
Synedra nana Meister
Synedra acus Kütz, S. acus var. angustissima (Grun.) van Heurck
Synedra ulna (Nitzsch) Ehrenberg
Tabellaria fenestrata (Lyng.) Kützing
Diatomaceae cetera

Tetraedron trigonum Auctor
Tetraedron trispinatum (W.&G.S.West) Hub.-Pestalozzi
Tetraedron enorme (Reinsch) Hansgirg
Tetraedron planctonicum G. M. Smith

Gloeocystis gigas (Kütz.) Lag. sensu Bachmann
Gloeocystopsis limnetica G. M. Smith
Gemellicystis neglecta Teiling em. Skuja
Gemellicystis neglecta Teiling em. Skuja
Gloeococcus schroeteri (Chod.) Lemm. sensu Skuja
Gloeococcus schroeteri (Chod.) Lemm., Eutetramorus fottii (Hind.) Komárek
Gloeocystis planctonica (W. et G.S.West) Lemm. sensu Bourrelly
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus mirabilis (W. & G. S. West) Lemmermann
Ankistrodesmus falcatus v. mirabile sensu Hortobogay
Monoraphidium braunii (Näg.) Kom.-Legnerová
Ankistrodesmus falcatus v. setiforme Nygaard
Ankistrodesmus falcatus v. spirilliformis G.S. West
Ankistrodesmus longissimus (Lemm.) Wille
Ankistrodesmus setigerus (Schröder) G. S. West sensu Skuja
Botryococcus braunii Kützing

Botryococcus neglectus Komárek & Marvan
Botryococcus terribilis Komárek & Marvan
Korschikoviella limnetica (Lemm.) Silva
Crucigeniella rectangularis (Näg.) Komárek
Crucigeniella truncata (G. M. Sm.) Komárek
Crucigenia lauterbornii (Schm.) Schmidle
Fusola viridis Snow
Kirchneriella contorta v. elongata (G. M. Smith) Komárek
Nephrochlamus willeana (Printz) Korshikov
Pediastrum angulosum (Ehr.) ex Meneghini
Pediastrum duplex v. gracillimum W. & G. S. West
Pediastrum duplex Meyen
Pediastrum tetras (Ehr.) Ralfs
Teilingia granulata (Roy & Biss.) Bourrelly
Scenedesmus subspicatus Chodat
Scenedesmus obtusus f. alternans (Reinsch) Compère
Didymocystis bicellularis (Chod.) Komárek
Didymocystis fina Komárek
Scenedesmus ecornis (Ehr.) Chodat
Scenedesmus linearis Komárek.
"
Scenedesmus denticulatus Lagerheim
Scenedesmus quadricauda (Turp.) Bréb. sensu Chodat

Staurodesmus convergens (Ehr.) Teiling
Staurodesmus dejectus (Br.) Teiling

Anagnostidis & Komárek 1988
Ettl & Gärtner 1988
Haworth 1988
Komárek & Fott 1983
Komárek & Marvan 1992
Komárek & Anagnostidis 1999
Koppen 1975
Tikkanen & Willén 1992
Williams et al. 1988

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Characium limneticum Lemmermann
Crucigenia rectangularis (Näg.) Gay
Crucigenia truncata G. M. Smith
Hofmania lauterbornii (Schmidle) Wille
Elakatothrix viridis Printz
Kirchneriella elongata G. M. Smith
Nephrocytium willeana Printz
Pediastrum araneosum (Racib.) Raciborski
Pediastrum gracile A. Br., P. gracillimum Thunmark
Pediastrum limneticum Thunmark
Pediastrum tetras v. tetraodon (Corda) Hansgirg
Sphaerozosma granulatum Roy & Bisset
Scenedesmus abundans (Kirchn.) Chod. sensu G.M. Smith
Scenedesmus alternans Reinsch
Scenedesmus bicellularis Chodat
Scenedesmus bicellularis Chodat
Scenedesmus bicellularis Chod. sensu Uherkovich
Scenedesmus bijugatus (Turbin) Kütz. (sensu auct. post)
Scenedesmus bijuga sensu auct. post Fott & Komárek
Scenedesmus fenestratus (Teil.) Uherkovich
Scenedesmus longus Meyen

Arthrodesmus convergens Ehrenberg
Staurastrum dejectum Brébisson