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Yhteenveto: Kasviplanktonin kehitys vuosina 1968—1990 subarktisessa Lokan tekoaltaassa

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PHYTOPLANKTON SUCCESSION FROM 1968 TO 1990 IN THE SUBARCTIC LOKKA RESERVOIR

Liisa Lepistö

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The phytoplankton community in the Lokka reservoir, constructed in 1967 in the Finnish Lapland, has been monitored from 1968 to 1990.

The biomass, cell density and the number of taxa were low during the first year reflecting oligotrophic conditions, but increased rapidly during the period from 1968 to 1971. Maximum values were observed at the beginning of the 1980s at which time the biomass values already reflected eutrophy. At the end of the decade biomasses and cell densities, but not the number of taxa, decreased once again. Chlorophyll *a* concentrations have been showing an increasing trend throughout the study period.

I Initially the dominant algal groups were small colony-forming blue-greens, mixotrophic cryptomonads as well as heterotrophic craspedomonads. At this time centric diatoms were rare but only 10 years later they dominated the biomass. In the summer of 1988, 20 years after reservoir construction, the blue-green algae *Planktothrix* and *Aphanizomenon* developed a biomass maximum which was also visible as a water bloom. This successional change in phytoplankton composition over the study period is reflected in the increased cell size of the algae.

The first development stage typical for a reservoir was observed, the second erosion phase is still processing. Today the colour of the water and the nutrient concentrations have decreased, although they can still be considered high. According both to water quality variables, and to phytoplankton quantity and composition, the water continues to be meso-eutrophic. No clear signs of the last stage in the history of a reservoir, the oligotrophication, is yet observable. However should the uniform water level manipulations continue, this will ultimately lead to stabilization of the biological system.

Keywords: phytoplankton, phytoplankton succession, subarctic reservoir, monitoring

1 INTRODUCTION

Man-made lakes can be considered systems intermediate between rivers and lakes. They are much younger than lakes and their ageing process very much depends upon watershed inputs (Tundisi 1993). As in lakes, the water quality of man-made lakes is primarily based on the soil types within their catchment area. Immediately after damming, nutrients are supplied by decomposition processes with material in the inundated land area functioning as substrate. This may cause high nutrient levels and dark water colour, especially in areas with large peatlands (Vogt 1978, Kinnunen 1982). The often strong water level variations disturb the macrophyte covered shoreline resulting in erosion, an effect also brought about by ice erosion during winter. Consequently, phytoplankton, not having to compete with macrophytes, are of great importance as primary producers in these ecosystems (Garnier 1992).

The biological systems in artificial lakes have been found to be constantly changing. These changes can be classified in successive stages, yet with a tendency towards oligotrophication (Garnier 1992). According to Vogt (1978) the primary production of phytoplankton is at its highest during the early phase at which time an artificial lake can be characterized as potentially eutrophic. With time the biota in the water as well as the nutrient status changes (Kinnunen 1985, Krzyzanek et al. 1986, Trifonova 1989, Garnier 1992). During a period of 28 years Krzyzanek et al. (1986) described five different stages in the establishment of biota in a Polish reservoir. The changes during the first months were rapidly succeeded by a brief oligotrophica-tion period. The following five years were characterized by a lack of chemical or biological stability and by large numbers of algae. After another oligotrophication period of ten years, with the ensuing formation of stable communities, the trophic status of the reservoir increased once again. This was exemplified by the intense development of animals and plants, especially phytoplankton with resultant blooms of Microcystis (Krzyzanek et al. 1986).

According to Vogt (1978), the intensive early phase, lasting approximately five years, gives way to an erosion phase, when there is still plenty of organic matter available but which is more resistant to decomposition. In addition, during the erosion phase, primary production decreases and

stable communities develop (Krzyzanek et al. 1986). This stage continues for as long as there is a constant supply of organic matter from either the reservoir shores or from the peat bottom. In Finland this stage continues for tens, perhaps even for hundreds of years (Vogt 1978).

Environmental conditions remain balanced in the reservoir if there are no dramatic changes in water level fluctuations (Kinnunen 1985). When reservoirs reach some stage of stabilization their community composition and water quality corresponds to the characteristics of lakes whose water level has been regulated for a long period of time (Vogt 1978).

In Finland there are 32 reservoirs whose size exceed 1 km². It may seem strange that a country so rich in lakes needs to construct reservoirs, however, these man-made lakes are situated in lake-poor areas along the western coast of Finland and in the inland north, where natural lake coverage is only three percent of the land area (Vogt 1978). Most man-made lakes in Finland are built by damming a river in the upper regions of its watercourse, areas which are rich in marshy soils. These reservoirs are primarily constructed for hydroelectric power generation, as in the case of the Lokka reservoir (Kinnunen 1982), but also to prevent floods (Vogt 1978).

The aim of this study was to investigate the development of phytoplankton composition, abundance and biomass in the Lokka reservoir during a period of 23 years. Special emphasis was placed on the long-term succession as well as on the seasonal succession of the communities. This was done by following the development of the riverine planktonic algae, observed in the earlier stages, into the typical lake planktonic algae of the later stages. Algal succession two years after damming and ca. twenty years after damming is discussed. The physico-chemical properties of reservoir water such as colour, pH, alkalinity, conductivity, oxygen, silica, phosphorus, nitrogen and iron were investigated as background data. Chlorophyll a concentrations are compared with the biomass values.

2 THE STUDY AREA

The Lokka reservoir is situated in the Finnish Lapland (Fig. 1). It is the biggest man-made lake area-wise in western Europe (Vogt 1978). Its damming was initiated in July 1967 after a clearance

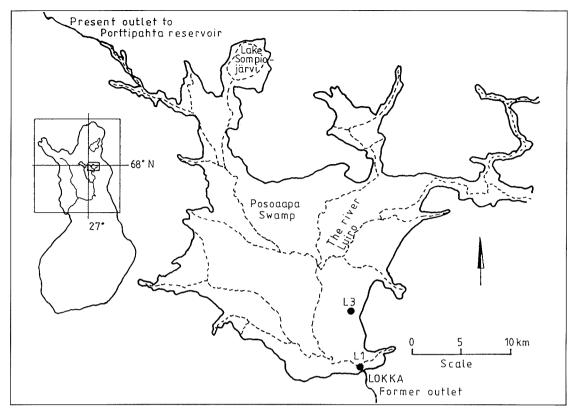


Fig. 1. The Lokka reservoir. Submerged rivers (- - - -) and sampling sites L1 and L3.

of only minor areas from trees and bushes. The area covered by water in the reservoir consisted of 80 % marsh grounds, the rest were fields and meadows. The Posoaapa swamp (Fig. 1), one of the most magnificent swamps in Europe with an area of more than 100 km², was subsequently drowned. Several rivers e.g. the Luiro river and Lake Sompiojärvi, with an area of 9 km², were submerged (Fig. 1). Drifting floats of peat formed dense mats in the summers of 1970 and 1971 (Nenonen and Nenonen 1972). Ice and waves contributed to the dispersal of the peatfloats, but in sheltered areas they remained intact for considerable periods of time (Ruuhijärvi et al. 1976).

The flat bottomed Lokka reservoir is subarctic (Ahti et al. 1964) and part of the Kemijoki watercourse. Morphological details are given below (Nenonen and Nenonen 1972):

Catchment area 2 380 km²
Maximum depth 12 m
Mean depth 4.3 m

Due to its northern location the reservoir has a thick ice cover from the end of October to the end of May (National Board of Waters and the Environment 1987). The reservoir is filled during autumn as well as by floods during spring and lies at minimum holding in winter due to water level regulation (Kinnunen 1982). The retention time is thus relatively short. Water level manipulation does not necessarily mean only allowing the level to fluctuate between its established maximum and minimum levels, but very much depends on the requirements for hydroelectric power. The established maximum and minimum water levels are 245 m and 240 m above sea level. The resulting reservoir areas and volumes are given below (Nenonen and Nenonen 1972):

Maximum area 417 km²
Minimum area 216 km²
Volume at the highest water level 2 063 · 106 m³
Volume at the lowest water level 500 · 106 m³

In 1968 the water level was raised to 242 metres above sea level. Withdrawal of water started in 1971-1972 and was continued throughout the winter by keeping the water running through a dam to the river Luiro. Since 1981 the water was running through a channel to another reservoir, Porttipahta, built in the vicinity of the Lokka

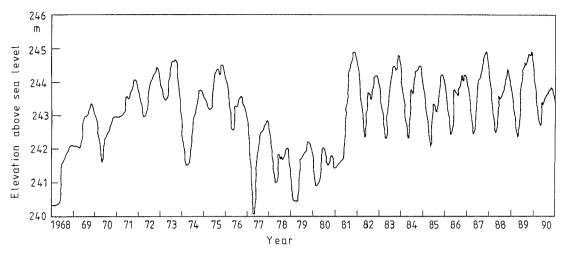


Fig. 2. Regulation of the water level in the Lokka reservoir in 1968 to 1990.

reservoir (Fig. 1). In 1977 the water level was dramatically lowered, almost to its established minimum level and remained at low level until spring 1981 (Fig. 2). During that period the minimum water volume of the reservoir fluctuated between 572 and 946 million m³.

Since 1981 the minimum water level has been above 242 metres and thus the minimum water volume has exceeded 1100 million m³. At present, the water level fluctuation normally varies within three metres (Fig. 2). The minimum and maximum water levels from the hydrological data bank of the National Board of Waters (NBW) - since 1986 the National Board of Waters and the Environment (NBWE) - are given in Appendix 1. The corresponding water volumes and areas are also shown.

3 MATERIAL AND METHODS

In the autumn of 1965 some water quality data was collected from the river Luiro before the reservoir was constructed (Oy Vesitekniikka Ab 1967). After filling, it was unclear whether the water authorities or the users of the reservoir were responsible for its monitoring (Kinnunen 1985). Consequently the data concerning water quality, phytoplankton and zooplankton is temporally and spatially scattered (Lepistö and Kerminen 1970, Heinonen and Airaksinen 1974, Sundbäck 1976, Arvola 1980, Lepistö et al. 1981, Jones and Ilmavirta 1983 and Puro 1989).

The water quality data for sampling site L1 is taken from the water quality data bank of the

NBWE. The sampling site, with a total depth of 12 metres, is close to the dam itself (Fig. 1). According to Kinnunen (1985), water quality data at this site is representative for the main part of the reservoir. Samples from the surface to a depth of two metres were chosen to represent the water quality in water layers from which phytoplankton samples were taken. Only silica results were from a depth of five metres. The samples were analysed according to the standard methods of the laboratories of the NBW (National Board of Waters 1981, 1984).

In the spring of 1968 a phytoplankton study with monthly sampling intervals was started and lasted until January 1970. Otherwise phytoplankton samples were collected during the period from June to September (Table 1). The samples were collected from the whole epilimnion, which was determined by the temperature distribution using a Ruttner-type sampler, and preserved with buffered formaldehyde.

In 1977, the sampling depth was changed to 0-2 metres for all monitoring samples of phyto plankton. Since 1982 the samples have been preserved with acid Lugol's solution. Buffered formaldehyde has been added afterwards in the laboratory (National Board of Waters 1984).

Phytoplankton counts were performed by phase-contrast illumination under an inverted microscope according to Utermöhl (1958). The algae were identified and counted, always from a 50 ml sample and from a constant area of the chamber with the magnifications x800 and x200. The counting units were cells, colonies and trichomes

Table 1. Phytoplankton sampling dates in the Lokka reservoir in 1968-1990. * = one sample.

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Year												
1968					*	*	*	*	*	*	*	
1969	*	*	*		*	*	*	*	*	*	*	*
1970	*											
1971						*		*	*			
1972												
1973												
1974												
1975												
1976												
1977						**	*		*			
1978						*		*				
1979						*			*			
1980								*				
1981							*		*			
1982						*	*	**				
1983						*		*				
1984												
1985						*						
1986						*	*	*	*			
1987												
1988					*	***	****	****	*	*		
1989												
1990							**	*				

with a length of 100 μ m. The identification of Au-lacoseira species was confirmed by making diatom slides.

Cell counts were converted to volumes using the database of the NBWE with cell volumes of phytoplankton. The biomasses are given as fresh weight (mg l⁻¹ fw). Results have been added to the biological data bank of the NBWE.

In the summer of 1988, phytoplankton was sampled monthly or even weekly, as part of a zooplankton study by Puro (1989), from sampling site L3 which is found in the same main basin as sampling site L1 (Fig. 1). There were no marked differences in water quality between these two points according to the results of Puro (1989). In the present study the total number of samples was 62, 49 of them representing the growth period from June to September (Table 1).

In the phytoplankton investigation the period of observations was divided into two parts. The

period 1968-1971 was used to represent the early stage in the development of the reservoir. The period 1977-1990 was used to represent the erosion stage of the reservoir as defined by Vogt (1978) and Krzyzanek et al. (1986). The data from these periods were treated separately so as to identify the long term successional trend. Also the different months were treated separately to identify the different periods of growing season from June to September.

Those species which comprised more than 10 % of either total number or total biomass were regarded as abundant. The small species, although numerous, do not generally dominate the biomass. Thus in this paper the abundance of different taxa is also treated on the basis of their cell density. Those species which occurred almost every year, or periodically during several years are also considered. The share of small (nanoplankton), flagellated and heterotrophic species of the

total cell number and total biomass is also treated. Determining of heterotrophic species is based on literature.

In order to classify the species into different indicator groups the indices of Järnefelt (1952, 1956) and Järnefelt et al. (1963) and Heinonen (1980) were applied to the material.

Systematics used in this work is based on the classification of Christensen (1980). In general the literature used for identification is the same as that presented in Tikkanen (1986) and Tikkanen and Willén (1992). The list of species with author name is given in Appendix 2.

4 RESULTS

4.1 Water quality

The annual average values of physico-chemical water quality variables from three periods, namely: 1968-1971, 1972-1981 and 1982-1990 (Table 2) were used together with phytoplankton results. The first period represents the early stage of the reservoir before regulation was initiated, the second the erosion stage when water level fluctuations were large, including the period of strong regulation in 1977-1981, and the third represents the period with a more uniform regulation.

When water level regulation started it caused a massive transport of organic matter into the reservoir. This increased load of organic compounds into the recently filled reservoir was reflected by changes - which were reversed once water quality improved - in water colour, oxygen and nutrient concentrations as well as by changes in other water quality variables.

Secchi depth is low in the Lokka reservoir (Fig. 3), on average only 1.3 metres. The original water colour in the Luiro river was 60 mg l⁻¹ Pt (Oy Vesitekniikka Ab 1967), which is slightly higher than what is typical for northern lakes (40 mg l⁻¹ Pt; Kortelainen 1993). During the first year water colour increased to an annual mean of 175 mg l⁻¹ Pt. Although water colour has decreased almost steadily since 1968 to 75 mg l⁻¹ Pt in 1990 (Fig. 4a), no clear change in Secchi depth has been found. A water colour maximum of 280 mg l⁻¹ Pt was measured during oxygen depletion in April 1979.

Water colour is primarily caused by the content of organic matter, measured as COD (chemical oxygen demand) (Fig. 4b). This showed the same decreasing tendency over time as water colour. During the first years COD was on average 14 mg l¹O₂, but once water level manipulations started organic matter was effectively eroded from the surrounding shores and the amounts increased, especially so when water level fluctuations were large since 1974. There has been a gradual decrease during the 1980s to the present 9 mg l¹O₂.

Table 2. Water quality of the Lokka reservoir in the early stage, 1968-1971, during 1972-1981, when water level fluctuations were large including the strong regulation in 1977-1981 and during 1982-1990 when fluctuations had stabilized, as mean values. The sampling depth was 0-2 metres (*5 metres). N = number of observations.

Water quality variable	[Year	s 1968-1971]	[Year	s 1972-1981]	[Years 1982-1990]		
variable	N	mean	N	mean	N	mean	
pH	27	6.5	91	6.4	57	6.5	
Colour, mg l ⁻¹ Pt	26	156	92	133	55	94	
Conductivity, mSm ⁻¹	27	2.6	91	2.3	57	2.1	
Total P, µg l ⁻¹	11	67	90	62	67	41	
Total N, µg l-1	11	1060	89	835	66	574	
COD _{Mn} , mg l ⁻¹ , O ₂	26	14	90	14	56	11	
Total Fe, mg l ⁻¹	9	1.2	82	1.0	58	0.7	
SiO ₂ , mg l ⁻¹ *	-	-	8	4.7	6	3.1	
Chlorophyll a,µg l ⁻¹	-	-	12	14.2	27	10.3	
Oxygen, sat.%	23	62	94	70	54	80	
Alkalinity, mmol l ⁻¹	6	0.11	77	0.11	57	0.09	

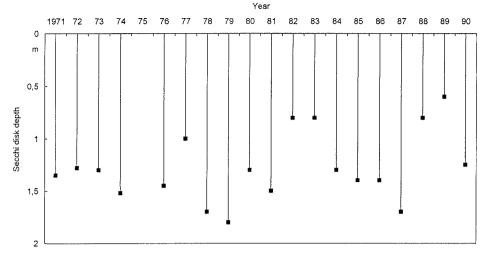


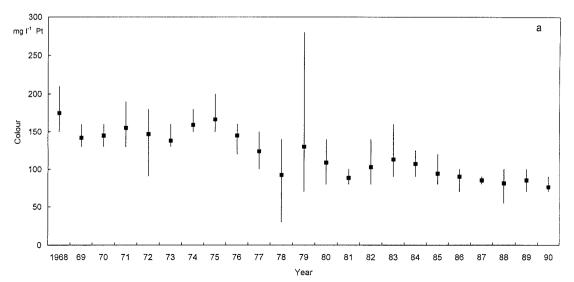
Fig. 3. The Secchi depth as annual mean in the Lokka reservoir in 1971 to 1990.

In addition to organic matter, iron affects water colour particularly during oxygen depletion when it is dissolved from the near-bottom layers (Fig. 4c). Synchronously with water colour the concentration of total iron has gradually decreased from an average of 1.1 mg l⁻¹ during the first years to 0.5 mg l⁻¹ in 1990. A maximum value was caused by oxygen depletion in April 1979.

Oxygen comsumption was enormous during the first years and the minimum oxygen saturation values were close to 20 % (Fig. 4d). Two complete oxygen depletions were observed, one in April 1974 and one in March 1979, both during ice-covered periods. At the same time maxima of conductivity, total phosphorus, total nitrogen and iron were found. Also the amounts of organic

matter were high during these anoxic periods. Once water level fluctuations diminished, together with the amount of decomposing organic matter, oxygen conditions improved. This can be seen by the increase in the annual mean saturation percentage to 85 in 1990, with no signs of oxygen depletion since 1979 in the epilimnion. In the hypolimnion the oxygen depletions are still observed every winter.

In the epilimnion, during the first ten years, the average total phosphorus concentration was close to 60 μ g l¹ (Fig. 5a). The maximum value of 510 μ g l¹ was measured during the spring oxygen depletion in 1979. Nevertheless, phosphorus concentrations have decreased gradually, and in 1990 the annual average concentration of total phos-



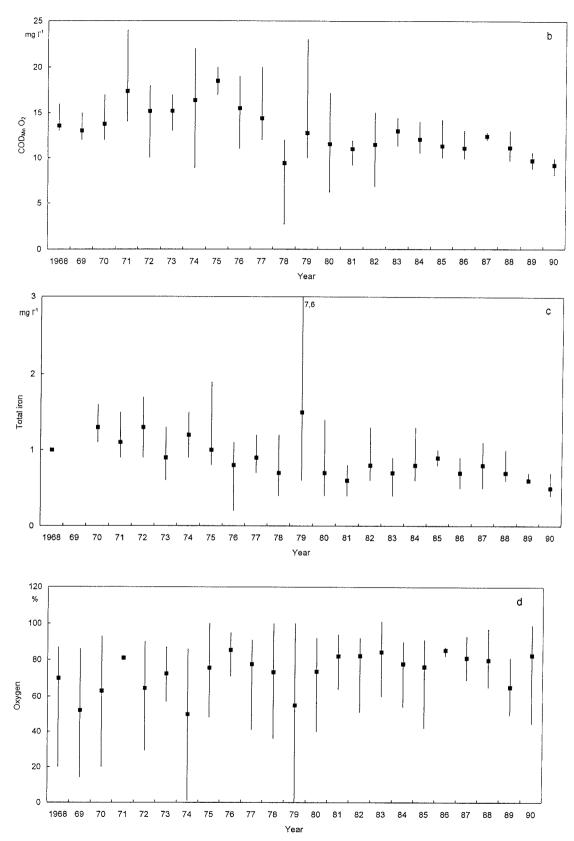


Fig. 4. The average annual values of colour (a), chemical oxygen demand (b), total iron (c) and oxygen (d) in the Lokka reservoir in 1968 to 1990. Beside the annual mean the maximum and minimum values from the epilimnion are given.

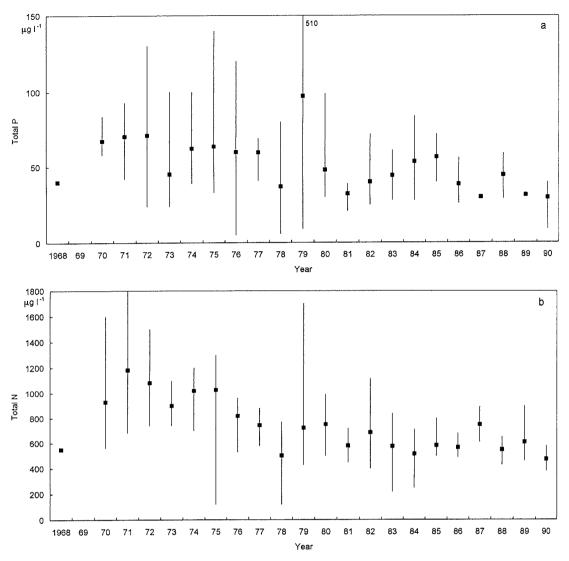


Fig. 5. The average annual values of total phosphorus (a) and total nitrogen (b) in the Lokka reservoir in 1968 to 1990. Beside the annual mean the maximum and minimum values from the epilimnion are given.

phorus was ca. 30 μ g l⁻¹. The phosphorus concentration in Finnish lakes as median is clearly lower, ca. 18 μ g l⁻¹ (Pietiläinen and Kauppi 1993).

Average concentrations of total nitrogen (Fig. 5b) increased during the first years. Since 1974 nitrogen has markedly decreased to the mean annual concentration of 470 μ g l⁻¹ in 1990. In 1971 the maximum concentration of total nitrogen was 1 800 μ g l⁻¹ at the same time as the amount of organic material in the water, expressed as oxygen consumption, also was high. The same phenomenon occurred in 1979 during the second oxygen depletion. The present nitrogen concentrations in

the Lokka reservoir are comparable with median nitrogen level in Finnish lakes as given by Pietiläinen and Kauppi 1993.

Silica (Fig. 6) a key nutrient especially for diatoms, has been determined since 1974 but only during the spring overturn. The silica concentrations were markedly elevated during the period in 1977-1982 when water level fluctuations were large. At this time the maximum concentration of 7.1 mg l⁻¹ was measured which has since then decreased to a level of 2.7 mg l⁻¹ in 1990.

Only minor changes were observed in the other variables measured. Immediately after damming

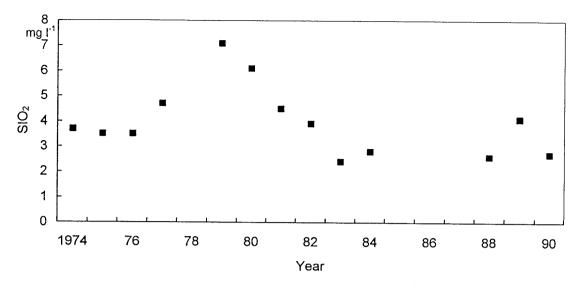


Fig. 6. The silica sampled from a depth of 5 metres in the Lokka reservoir in 1974 to 1990 during spring overturn.

pH was low, ca. 5.6 (Fig. 7a), another minimum was measured in March 1972, but otherwise pH values have varied only slightly. Similarly, the buffering capacity (Fig. 7b) has shown unregular fluctuations during the whole study period. Usually the values have varied between 0.08-0.13 mmol l⁻¹. Whereas, the total amount of inorganic

ions (Fig. 7c), determined as conductivity, decreased slightly throughout the study period.

The mean water temperature from depth of one meter in summer (Fig. 7d) has fluctuated partly due to different summersand the different timing of the measurements during the summer.

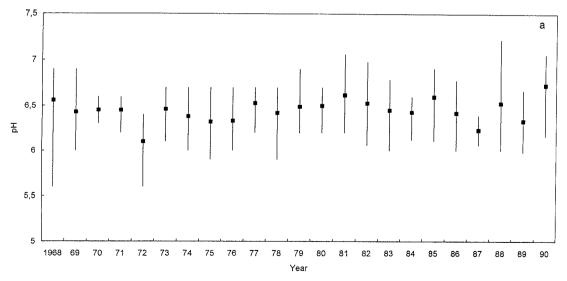
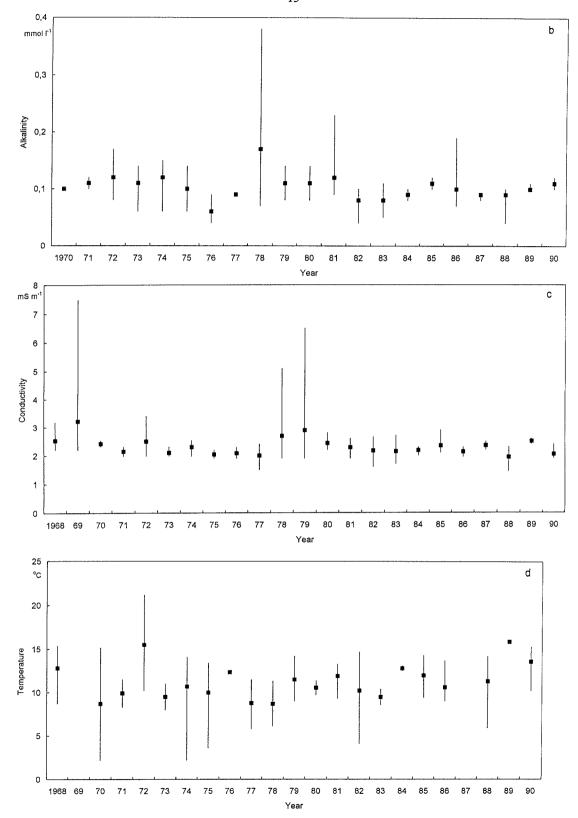


Fig. 7. The average annual values of pH (a), alkalinity (b) and conductivity (c) in the Lokka reservoir in 1968 to 1990. Beside the annual mean the maximum and minimum values from the epilimnion are given. The mean water temperature (d) in June-September is determined from a depth of 1 metre. The maximum and minimum values are also given.



4.2 Phytoplankton succession: biomass and species composition

The annual average biomass (Fig. 8) increased rapidly in the early stage from 0.3 mg I⁻¹ to 1.4 mg I⁻¹. The almost steady increase continued well into the erosion stage until 1981, when the biomasses significantly increased. At the end of the 1980s the biomass decreased once again to its former level. The number of species indicating eutrophy was in the first years generally low but increased markedly during the strong regulation with exception of July observations. Since 1982 there has been a decreasing tendency in general. The number of species indicating oligotrophy has been low.

Chlorophyll a concentrations (Fig. 9) varied seasonally as well as annually within a wide range. The maximum value of 24.6 μ g l¹ was obtained in late July in 1977 and another high value of 22.6 μ g l¹ was found at the end of August in 1990. The temporal differences between chlorophyll concentrations and phytoplankton biomass were at times large.

The dominant phytoplankton species were typical of moderately mesotrophic waters (Table 3). In the early stage of the reservoir blue-green algae were rare, only 16 taxa were observed. *Aphanocapsa delicatissima* was present almost every year, but only once in high densities. Species such as *Aphanocapsa biformis and Eucapsis minuta* were

occasionally abundant. *Merismopedia warmingiana* was recorded only twice during the study period. Arvola (1980) and Jones and Ilmavirta (1983) did not observe this species in their material from the Lokka reservoir.

During the erosion stage a maximum biomass was developed at the end of July 1988 and again in July 1990 by the non-nitrogen fixing *Planktothrix mougeotii*. In this material the species was earlier identified as *P. agardhii*. In August 1988, *Planktothrix* was replaced by the nitrogen-fixing *Aphanizomenon flos-aquae*. *Anabaena flos-aquae*, including "A. circinalis" with small rounded cells, was present in low densities in general as was *A. lemmermannii*.

In the first years cryptomonads of the genus *Cryptomonas* generally dominated. Arvola (1980) and Jones and Ilmavirta (1983) found this group to be very important in the Lokka reservoir in 1974 and 1976. The other important cryptomonad, *Rhodomonas lacustris*, has been identified since 1977. *Katablepharis ovalis* was until 1977 included among the flagellated chrysophyceans. Its numbers appear to be quite stable; only in 1980 and 1983 did its density increase markedly. The dinoflagellate *Peridinium umbonatum (P. inconspicuum)* was recorded in moderately low cell densities from 1977 onwards.

In addition to cryptomonads, chrysophyceans were dominant during the first years but their species diversity decreased during the period in 1977

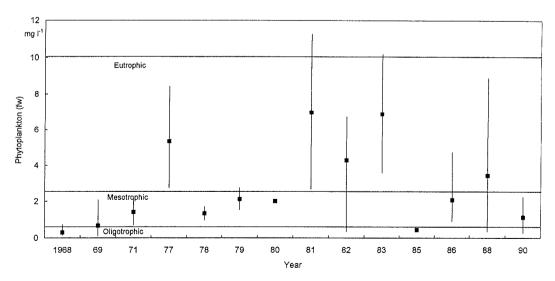


Fig. 8. The annual mean biomasses (mg l^{-1} fw) from the Lokka reservoir in 1968 to 1990. Total biomasses indicating oligotrophy (<0.50 mg l^{-1} fw), mesotrophy (<2.50 mg l^{-1} fw) and eutrophy (<10.00 mg l^{-1} fw) as given by Heinonen (1980), are shown by lines. Please, note the uneven scale of the x-axis.

Table 3. The abundance of certain phytoplankton species in the Lokka reservoir with reference to their occurrence in specific habitats. Species (taxa) regularly observed are shown (*).

Species	Abundance	Trophicity	Habitat	Tot.P µg l ⁻¹	pН	Reference
CYANOPHYCEAE						
phanocapsa delicatissima *	abundant	oligotrophic	brownish waters			1
phanocapsa elachista	±rare	eutrophic		>100	8-9	2
phanothece chlatrata (Rhabdoglea chlathrata)	±rare	mesotrophic	slow-moving	25-50	8-9	2
ucapsis minutata ferismopedia warmingiana (M. tenuissima)	occasionally rare	ultraoligotrophic	cold waters brownish waters	2-10	5-7	3 1, 2, 4
nowella lacustris (Gomposphaeria lacustris)	±rare	eutrophic	common in all waters	<2, >100	7-9	2, 3
nabaena flos-aquae, (A. circinalis)	common	mesoeutrophic	very common	10-25, >50	8-9	2, 3
lemmermannii	occasionally	moderately eutrophic	common in all waters			2, 3
hanizomenon flos-aquae	u	eutrophic	low temperature,	25-50	8-9	2, 8
	none	hunorouteanhia	low light	50 100	7.10	2565
anktothrix agardhii (Oscillatoria agardhii)	none	hypereutrophic	deep maxima, low temperature,	50-100	7-10	2, 5, 6, 7
mougeotii (O. mougeotii, agardhii v. isothrix)	occasionally	mesotrophic	low light			4, 5
RYPTOPHYCEAE						
yptomonas spp. *	abundant	oligotrophic-eutrophic	mixotrophy	10-100	4-9	2, 4, 10
stablepharis ovalis	"	ultraoligot,-mesotrophic	. ,	2-50	6-9	2, 4, 10
odomonas lacustris *	P	ultraoligotmesotrophic	humic waters	2-100	6-8	2, 9, 10
NOPHYCEAE ridinium umbonatum (P. inconspicuum)	common	oligomesotrophic		<2	4-5	2, 4
		0		~~		
IRYSOPHYCEAE richia chodatii (Diceras chodatii)	oligotrophic rare	oligotrophic	± wide	2-10	4-7	4 2
nobryon bavaricum	common	oligomesotrophic	humic waters	10-25	4-7 5-6	2, 11
borgei	rare	oligotrophic	clear/humic	2-10	5-0 6-7	2, 11
suecicum	rare	oligotrophic	humic	2-10	6-7	2
allomonas akrokomos	occasionally	oligotrophic	brown-water	2-50	6-7	2, 3, 12
allomonas caudata	common	oligotrophic		10-50	5-6	2
iniferomonas spp.	rare	oligotrophic		2-10	6-7	2
nura spp.	common	mesotrophic	cold, humic waters	10-50	7-8	1, 2, 4
oglena americana	common	oligomesotrophic		5-25	6-8	2
атоморнусеае						
lacoseira ambigua (Melosira ambigua)	abundant	mesotrophic		10-50	7-8	4, 2
lacoseira distans (M. distans)	rare	oligotrophic		5-10	6-7	2
lacoseira islandica (M. islandica)	±rare	eutrophic	doub motor-	25 100	7.0	3
italica v. tenuissima (M. italica v. tenuissima)	abundant	eutrophic	dark waters	25-100	7-9	1, 2
clotella comta	none	oligomesotrophic		5-10	8-9 6-8	2
izosolenia longiseta *	rare abundant	oligomesotrophic oligomeseutrophic		2-25 10-100	7-8	2, 4
terioneiia jormosa	common	ongomes,-canopine		10-100	1-0	۷, ۳
agilaria crotonensis bellaria flocculosa *	abundant	oligotrophic		5-25	6-7	1, 2, 3
арні дорнус еа є						
nyostomum semen	rare	mesoeutrophic	humic waters	5-25	7-8	2, 4
JGLENOPHYCEAE		eutrophic	acid swamps	£0.400	7.0	2, 13
glena viridis	±rare	eutrophic	org, and inorg, nutrients	50-100	7-8	11
achelomonas volvocina	±rare	mesotrophic	humic	28-100	7-8	2, 4, 11
achelomonas volvocinopsis	common	eutrophic				12
ILOROPHYCEAE	obundo-+	aligatrophic	cold waters	10.25	16	2 2
lamydomonas spp.	abundant common	oligotrophic	cold waters cold waters	10-25	4-6	2, 3 3
lorogonium spp. kistrodesmus falcatus	abundant	mesotrophic	colu waters	50-100	8-10	2
kistroaesmus faicatus ucigenia quadrata	common	eutrophic		10-25	5-8	2, 3
ucigenia quaaraia ciyosphaerium pulchellum *	abundant	mesoeutrophic		25-50	7-9	2, 4
subsolitarium (D. simplex)	occasionally		common in all waters	2-5	6-7	2, 3
moraphidium contortum	abundant					•
-chneriella obesa	occasionally	eutrophic				3
ikistrodesmus falcatus v. spirilliformis)	,	oligotrophic, eutrophic	"pioner"	5-10,50-100	6-8	2, 12, 14
onoraphidium komarkovae (M. setiforme)	common	oligotrophic		7-9	6-7	2
enedesmus armatus	common	eutrophic		50-100	8-9	2
rastrum staurogeniaforme	occasionally	eutrophic				3
liella spiculiformis	abundant	ultraoligotrophic		2-10	5-7	2
osterium aciculare	±rare	eutrophic				12
pronum	±rare	eutrophic				12
urastrum spp.	±rare	eutrophic				4
urodesmus spp.	rare	oligotrophic	clear water	24		4
COSOECOPHYCEAE, CRASPEDOPHYCEAE,						
COSOECOPHYCEAE, CRASPEDOPHYCEAE, DOFLAGELLATES						
cosoeca lacustris (Bicoeca lacustris)	common					
planctonica	occasionally	ultraoligotrophic		2-25	4-7	2
planctonica v. multiannulata	common	eutrophic			6	3
smarella moniliformis	occasionally	eutrophic	inpure waters, sulfite mill effluents			3, 15
			same mm cinacins			
romitus cordiformis	abundant	(ultra)oligotrophic		10-25	6-9	2

¹⁼ Ilmavirta 1980, 2= Brettum 1989, 3= Tikkanen and Willén 1992, 4= Rosén 1981, 5= Skolberg and Skolberg 1985, 6= Niemi 1971, 7= Lindholm 1992, 8= Steinberg and Hartman 1988, 9= Ilmavirta 1983, 10= Smolander and Arvola 1988, 11= Järnefelt 1952, 1956, Järnefelt et al. 1963, 12= Heinonen 1980, 13= Prescott 1962, 14= Arvola 1980, 15= Järnefelt 1961

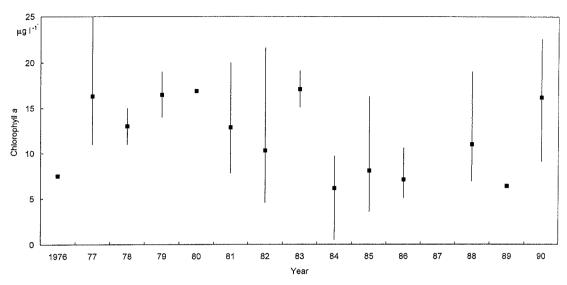


Fig. 9. The average annual values of chlorophyll a concentrations in the Lokka reservoir in 1974 to 1990.

to 1980 when the water level was extremely low. Ochromonadales, mostly cells of *Dinobryon* and *Uroglena*, were usually present every year and present in high densities especially during the 1970s. Common, although in moderately low densities were *Dinobryon bavaricum*, *Mallomonas caudata*, *Synura* spp. and *Uroglena americana*.

The diatoms Asterionella formosa and Tabellaria flocculosa were abundant at the beginning almost every year, whereas centric diatoms were almost absent during the first years. Aulacoseira distans was only occasionally observed in low densities. In 1977 Aulacoseira ambigua and A. italica v. tenuissima became dominant. In July 1988 the cells of Aulacoseira appeared to suffer from silica depletion: the frustules were very thin and therefore looked atypical (Turkia and Lepistö 1991). In Lake Ontario Aulacoseira islandica, including the morphotype A. islandica ssp. helvetica (O.Müll.) Simonsen, formed thin walls during a silica depletion (Stoermer et al. 1985) and Kling (1993) reported that thinly silicified valves of diatoms were bent and distorted when silica concentrations were low. In fact, minimum silica concentrations in the Lokka reservoir were measured in March 1988. As samples were studied within a few months of sampling dissolution due to a long storage time can be ruled out.

The discoid *Cyclotella stelligera*, very commonly identified from lakes, was recorded only twice but there were no records of *Cyclotella comta*. *Cy*-

clotella species were thus quite rare but some unidentified Eupodiscales, perhaps Stephanodiscus spp. were observed, even in moderately high densities. The fragile Rhizosolenia longiseta was very rare in the whole material.

The flagellated and large sized *Gonyostomum semen* (Raphidophyceae) was rare in the Lokka reservoir, in fact, there are only a few observations of this species from the northern parts of Finland (Lepistö et al. 1994). *Vacuolaria* spp. was observed in this material, but also its occurrence was sparse.

In all 13 Euglenophyceae taxa were identified. They occurred only occasionally and then in low densities. During the first years the most common euglenids were *Euglena* and *Menoidium* species. *Trachelomonas* species, which live enclosed in a firm gelatinous shell, were more abundant in later years. The most common euglenids in the whole material were *Euglena viridis* and *Trachelomonas volvocinopsis*. *Phacus curvicauda* and *Trachelomonas volvocina* were also observed but sporadically.

Green algae were numerous, altogether 106 Chlorophyceae taxa were identified. The most abundant green algae were *Chlamydomonas* spp.. *Chlamydomonas* is an important green algal genus in the Lokka reservoir (Arvola 1980), *Chlorogonium* was less common. Since 1969, *Dictyosphaerium pulchellum* has been abundant every year. Several *Monopraphidium* and *Scenedesmus* species as well as some other green algae were ob-

served, especially during the strong regulation in 1977-1981 in moderately high cell densities (Appendix 2). *Monoraphidium contortum (Ankist rodesmus falcatus v. spirilliformis)*, a very important species in the Lokka reservoir, according to Arvola (1980) and Jones and Ilmavirta (1983), was recorded for the first time in August 1971, and in very high densities. Another peak occurrence was in June and July 1977. Since 1982 its cell density decreased clearly and after 1988 there are no records of the species. At this time the water level fluctuations diminished markedly.

Before 1980 Koliella spiculiformis was identified as Ankistrodesmus falcatus. The morphology of these two species differ only slightly: Koliella has the typical transverse cell division of Ulotrichales. The possibility of erroneous identification was pointed out by Tikkanen and Willén (1992) among others. However, their ecology differs clearly (Table 3). Occasionally K. spiculiformis was present in high cell densities. In all Ulotrichales, generally filamentous species, increased clearly during the 1980s.

Desmids such as *Closterium aciculare* and *C. pronum* were present in 1977 in high densities. This may have been partly caused by flushing from the littoral zone when the water level fluctuated strongly. Several species of *Cosmarium, Staurastrum* and *Staurodesmus* were observed occasionally in low cell numbers in 1988 and 1990.

During the first years colourless *Bicosoeca* lacustris and *B. planctonica* were abundant. Bacterial amounts must have been enormous during the first years because of the decomposing matter. Colourless craspedomonads were particularly abundant in the early years, *Desmarella* moniliformis developed rather high cell densities. The zooflagellate *Gyromitus* cordiformis was present every year, generally in July-August with only a few exceptions.

4.2.1 The early stage: 1968-1971

In the early stage, the highest number of taxa found in June was 24 including three eutrophy indicating species (Table 4). Average biomass was 0.87 mg l^{-1} (s=1.1 and n=3). During the first years chrysophyceans, like *Syncrypta* spp. and cryptomonads were alternatively dominant (Table 5). These flagellated algae were generally small (Table 6). In 1971 the blue-green alga *Eu*-

capsis minuta and the flagellated green alga Chlamydomonas spp. were prevalent causing a higher biomass (Fig. 10). Only Aphanocapsa delicatissima, Desmarella moniliformis and unidentified Bacillariales were recorded in all three years. No Eupodiscales (centric diatoms) were observed.

The species composition in July varied between the years 1968 and 1969 (Fig. 11) and the biomasses were low, 0.18 mg l⁻¹ and 0.11 mg l⁻¹ respectively (Table 4). The number of taxa was low, including, at the most, only four eutrophy indicators. Flagellated, generally small (Table 6) chrysophyceans and also cryptomonads were dominant. *Monoraphidium komarkovae* and Tabel laria flocculosa were observed in both years (Table 7). Euglenid *Menoidium* spp. occurred in higher density in 1969.

In August the species composition also varied between the years 1968, 1969 and 1971 although the cell density was generally higher than in July. The mean biomass was 1.11 mg l^{\perp} (s=0.9, n=3) (Fig. 12). A maximum of 34 taxa was identified with no more than three eutrophy indicators (Table 4). *Cryptomonas* spp. were dominant with high cell numbers in all three years. In 1971 green algae almost dominated the biomass. Green alga *Monoraphidium contortum* accounted for 61 % of the total cell density, although the biomass remained low because of their small size (Table 8). Also flagellated species were important (Table 6).

In September 1965 before the damming of the river Luiro was initiated the phytoplankton biomass in the river Luiro was 0.03 mg l⁻¹ and the number of species was high, altogether 55. The cell density was low, with unidentified Bacillariales as the dominant species. Eupodiscales were rare. A total of 12 eutrophy indicators were recorded and the number of oligotrophy indicators was three (Oy Vesitekniikka Ab 1967).

In September 1968-1971 the mean biomass in the reservoir was 0.54 mg l⁻¹ (s=0.7, n=3). The number of taxa was at its highest 44, altogether with six eutrophy-indicating species (Table 4). Aphanocapsa delicatissima, Cryptomonas spp. and Mallomonas akrokomos were observed in all samples. More than one half of the biomass and cell density was due to Asterionella formosa in 1971 (Fig. 13, Table 9), when Monoraphidium contortum accounted for 15 % of the total cell density. Flagellated small species were still important (Table 6).

Table 4. Biomasses (mg l^{-1} fw) of total phytoplankton, the total number of counting units l^{-1} (cells, trichomes and colonies), the total number of taxa and the number of species indicating eutrophy and oligotrophy in the Lokka reservoir in June-September in 1964-1971.

Date	Total phyto- plankton biomass	Total number of counting units (x10 ⁶)	Total number of taxa	Number of species indicating eutrophy	Number of species indicating oligotrophy
June					
180668	0.13	0.05	14	2	1
090669	0.31	1.55	24	3	0
170671	2.18	2.29	24	3	2
July					
040768	0.18	0.15	11	1	0
060769	0.11	0.19	25	4	2
August					
150868	0.74	0.33	12	2	0
050869	2.09	2.71	20	2	1
050871	0.69	2.86	31	3	1
September					
110964	0.03	0.04	55	12	3
120968	0.14	0.16	13	1	0
150969	0.15	0.28	29	6	0
090971	1.35	2.42	44	6	1

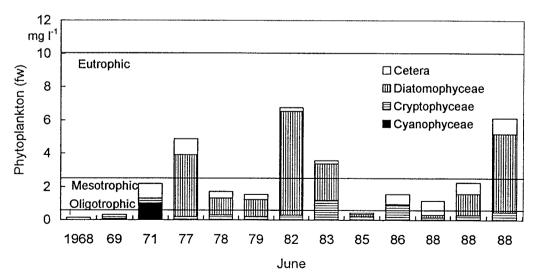


Fig. 10. Total biomasses (mg l^{-1} fw) from the Lokka reservoir in June 1968 to 1988. Sampling dates for the years are given in Table 10. Total biomasses indicating oligotrophy (<0.50 mg l^{-1} fw), mesotrophy (<2.50 mg l^{-1} fw) and eutrophy (<10.00 mg l^{-1} fw) as given by Heinonen (1980) are shown by lines. Please, note the uneven scale of the x-axis.

Table 5. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in June 1968-1971. (C = cells %, B = biomass %).

Phytoplankton	[1968]	[1969]		[1971]		
species	C	В	$\overline{\mathbf{C}}$	В	\overline{C}	В	
Aphanocapsa biformis	•	•	68	17			
Eucapsis minuta	•			•	27	28	
Microcystis firma				•	5	18	
Cryptomonas spp.	•		3	32	5	13	
Kephyrion ovale	13	0.5		•	•		
Ochromonadales		•	19	10	50	21	
Syncrypta spp.	11	86		•	•		
Synura spp.		•	0.1	12	•		
Chlamydomonas spp.		•		•	7	12	
Monoraphidium komarkovae	11	1	•				
Desmarella moniliformis	52	6	8	12			

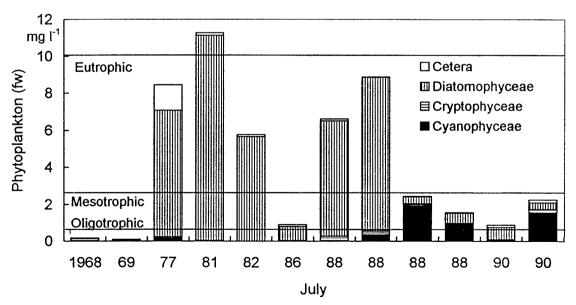


Fig. 11. Total biomasses (mg l-1 fw) from the Lokka reservoir in July 1968 to 1990. Sampling dates for the years are given in Table 10. Total biomasses indicating oligotrophy (<0.50 mg l-1 fw), mesotrophy (<2.50 mg l-1 fw) and eutrophy (<10.00 mg l-1 fw) as given by Heinonen (1980) are shown by lines. Please, note the uneven scale of the x-axis.

4.2.2 The erosion stage: 1977-1990

In June the highest number of taxa was 68 and the number of eutrophy indicators varied between 2 and 13 (Table 10). The mean biomass was 3.0 mg 1^{-1} and the highest 6.7 mg 1^{-1} (s=2.2, n=10). The maximum biomass in 1982 was composed almost entirely of *Aulacoseira ambigua*. The second biomass maximum in 1988, however, was made up of the species *Aulacoseira islandica* and *A. italica v. tenuissima* (Fig. 10). On occasion *Cryptomonas* spp., *Rhodomonas lacustris* and unidentified Ochromonadales dominated.

Five taxa occurred in every year studied: Cryptomonas spp., especially in 1982 and 1988, Aulacoseira italica v. tenuissima, A. ambigua and A. islandica, Asterionella formosa and at a lower cell density Tabellaria flocculosa. Chlamydomonas spp. were abundant every year and Dictyosphaerium pulchellum and Scenedesmus armatus almost every year, as were Katablepharis ovalis and Rhodomonas lacustris.

Monoraphidium contortum dominated the total cell number in 1977 but decreased already in 1978 to only about 3 % of the cell density (Table 11). Since 1985 there are no records of this species. Generally every identified species was observed several times during the study. Aphanocapsa delicatissima was not found after 1979 although it was abundant during 1968 to 1979 in June. Flagellated small cells were still abundant, but heterotrophic species were very rare (Table 6).

In July the mean biomass was 4.9 mg 1⁻¹ (s=3.8, n/10). The highest number of taxa was 70 and the number of eutrophy indicators was close to ten (Table 10). Exceptionally high biomasses were composed of the diatoms *Aulacoseira italica v. tenuissima*, *A. ambigua* and *A. islandica*, with the exception of July 19, 1988 and July 31, 1990 when *Planktothrix mougeotii* dominated (Fig. 11).

Asterionella formosa, Aulacoseira italica v. tenuissima and A. ambigua were abundant every year. Dictyosphaerium pulchellum was also present. Cryptomonas spp. usually occurred in July but in lower cell densities than in June. Katablepharis ovalis, Rhodomonas lacustris and Tabellaria flocculosa were common in almost every sample studied (Table 12). Monoraphidium contortum contributed 6 % to the cell density in 1977 and only 1 % in 1981. Thereafter its share diminished and in 1988 and 1990 the species was not recorded at all. Small flagellated species were succeeded by non-motile larger species (Table 6).

In August the mean biomass was 2.89 mg l⁻¹ (s=2.8, n=12). The highest number of taxa was 53 but the number of eutrophy indicators was lower than in July (Table 10). The species composition was quite stable. *Cryptomonas* spp. and *Rhodomonas lacustris* occurred in rather high densities during the first years. Populations of *Aulacoseira italica v. tenuissima* and *A. ambigua* increased in 1980, with a maximum in 1983 but decreased again in 1986. *Aulacoseira*-species were succeeded by *Planktothrix mougeotii* in Au-

Table 6. The percentage (%) of flagellated, small (nanoplankton, $<20 \mu m$) and heterotrophic species as mean of the total cell number and biomass from June to September in 1968-1971 and 1977-1990. (C = cells %, B = biomass %).

		Flagellated species		Small	Small species		otrophic species
		C	В	C	В	C	В
June	1968-1971	60	63	89	54	21	3
	1977-1988	47	41	54	32	4	1
July	1968-1969	70	67	66	24	29	16
-	1977-1990	20	8	25	7	1	0.3
August	1968-1971	68	81	54	23	3	0.7
Ü	1978-1990	29	16	37	16	6	1
September	1968-1971	43	48	48	22	19	17
•	1978-1988	29	23	52	22	11	4

Table 7. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in July 1968 and 1969. (C = cells %, B = biomass %)

Phytoplankton	[1968	.]	[1969]		
species	\overline{C}	В	C	В	
Cryptomonas spp.	40	78	4	14	
Bicosoeca lacustris	28	17			
Ochromonadales	•	•	26	5	
Tabellaria flocculosa			6	22	
Tribonema spp.			3	10	
Menoidium spp.	•		21	9	
Monoraphidium komarkovae	14	4			
M. mirabile	12	1	·		

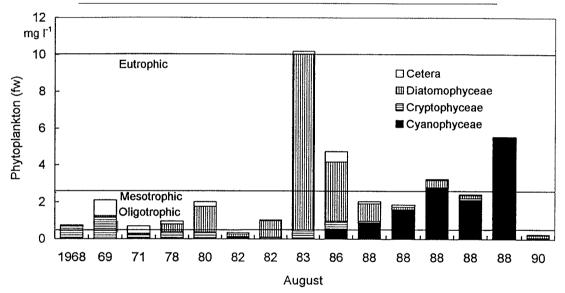


Fig. 12. Total biomasses (mg l¹ fw) from the Lokka reservoir in August 1968 to 1990. Sampling dates for the years are given in Table 10. Total biomasses indicating oligotrophy (<0.50 mg l¹ fw), mesotrophy (<2.50 mg l¹ fw), eutrophy (<10.00 mg l¹ fw) and hypereutrophy (>10.00 mg l¹ fw) as given by Heinonen (1980) are shown by lines. Please, note the uneven scale of the x-axis.

gust 1988, but at the end of August Planktothrix was in turn replaced by Aphanizomenon flosaquae. In 1990 P. mougeotii dominated once again (Fig. 12, Table 13). The cell numbers of Monoraphidium contortum decreased clearly after 1982 and there are no observations of this species in August since 1986. The average proportion of small flagellated species decreased but was higher compared to June values (Table 6).

The mean biomass of September was 1.92 mg l^{-1} (s=1.1, n=5), but the biomass at the end of

September 1988 was very low (Table 10, Fig. 13). The number of taxa was rather high, varying between 31 and 52 and the maximum number of eutrophy indicators was fifteen.

Altogether six taxa were present in the erosion stage in all samples studied: Asterionella formosa, Cryptomonas spp., Dictyosphaerium pulchellum, Rhodomonas lacustris, Aulacoseira italica v. tenuissima and A. ambigua. Aulacoseira species dominated almost every September (Table 14). Monoraphidium contortum dominated the

cell density in 1977 and 1979 but decreased sharply in 1981. Small species were still abundant but they were generally not mobile. Heterotrophic

species were important. The percentages were almost equal to those observed in the early phase (Table 6).

Table 8. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in August 1968-1971. (C = cells %, B = biomass %).

Phytoplankton	[1968]	[1969]	[1971]		
species	C	В	C	В	C	В	
Cryptomonas spp.	89	91	19	57	2	23	
Ochromonadales			52	7	14	24	
Chlamydomonas spp.			16	31			
Koliella spiculiformis					17	13	
Monoraphidium contortum				•	61	13	

Table 9. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in September 1968-1971. (C = cells %, B = biomass %).

Phytoplankton	[1968]	[1969]	[1971]		
species	C	В	C	В	C	В	
Cryptomonas spp.	9	24	10	42	•	•	
Bicosoeca lacustris	36	28					
Mallomonas akrokomos	18	18	•			-	
Ochromonadales		•	30	5	15	11	
Asterionella formosa			39	31	59	60	
Aulacoseira ambigua			•	•	2	13	
Monoraphidium contortum		•	•		15	1	
Gyromitus cordiformis	16	19					

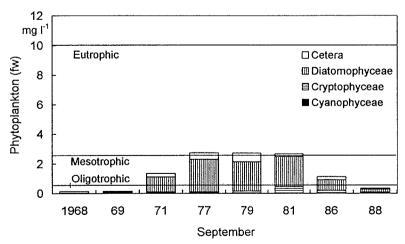


Fig. 13. Total biomasses (mg l⁻¹ fw) from the Lokka reservoir in September 1968 to 1988. Sampling dates for the years are given in Table 10. Total biomasses indicating oligotrophy (<0.50 mg l⁻¹ fw), mesotrophy (<2.50 mg l⁻¹ fw) and eutrophy (<10.00 mg l⁻¹ fw) as given by Heinonen (1980) are shown by lines. Please, note the uneven scale of the x-axis.

Table 10. Biomasses (mg Γ^1 fw) of total phytoplankton, the total number of counting units Γ^1 (cells, trichomes and colonies), the total number of taxa and the number of species indicating eutrophy and oligotrophy in the Lokka reservoir in June-September in 1977-1990.

Date	Total phyto- plankton biomass	Total number of counting units (x10 ⁶)	Total number of taxa	Number of species indicating eutrophy	Number of species indicating oligotrophy
June					
280677	4.87	6.37	46	13	1
120678	1.72	2.11	37	9	2
180679	1.54	1.64	43	12	1
140682	6.75	3.06	17	2	1
080683	3.57	9.80	40	2	0
270685	0.44	0.71	38	2	1
090686	1.56	3.28	38	2	2
130688	1.16	0.93	41	3	0
220688	2.25	2.32	60	7	3
280688	6.13	6.44	68	9	3
July					
190777	8.45	12.45	30	3	1
230781	11.27	17.46	42	5	0
150782	5.76	2.96	22	2	0
090786	0.90	1.21	42	6	2
050788	6.61	7.50	49	10	2
120788	8.89	6.47	34	6	0
190788	2.44	1.06	34	7	1
260788	1.56	0.89	48	10	1
100790	0.88	1.02	56	10	2
310790	2.25	1.57	70	15	2
August					
230878	0.96	2.06	44	11	1
250880	2.01	2.76	53	10	1
020882	0.34	0.75	19	1	1
250882	1.03	0.79	32	1	0
260883	10.18	15.65	31	3	0
070886	4.74	6.59	28	3	0
020888	2.04	1.33	40	7	1
090888	1.86	0.88	47	9	2
150888	3.25	1.41	47	7	1
230888	2.42	1.44	32	4	1
300888	5.55	2.24	16	3	0
200890	0.27	0.29	31	5	1
September					
060977	2.74	2.49	46	10	1
040979	2.71	7.73	52	15	1
100981	2.67	4.09	37	7	Õ
030986	1.13	2.04	44	8	0
260988	0.35	0.61	31	5	1

Table 11. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in June 1977-1988. (C = cells %, B = biomass %).

Phytoplankton species	[1977]		[1978]		[1979]		[1982]		[1983]	
species	C	В	C	В	c	В	C	В	C	В
Cryptomonas spp.			22	16	16	12	13	4	8	18
Rhodomonas lacustris									45	15
Ochromonadales			14	2	11	1				
Aulacoseira ambigua	12	50	9	37	13	43	63	92		
A. islandica										
A. italica v. tenuissima	29	25	27	22	31	21			33	58
Chlamydomonas spp.			8	15						
Lobomonas ampla										
Sphaerellopsis spp.										
Monoraphidium contortum	39	3								

Table 11. Continued.

Phytoplankton	[1985]		[1986]		[1988]		[1988]		[1988]	
species	C	В	c	В	c	В	c	В	C	В
Cryptomonas spp.	24	47	31	59	29	13	10	12		
Rhodomonas lacustris					•				10	1
Ochromonadales			45	17						
Aulacoseira ambigua							14	9	13	8
4. islandica				9	28	13	41			
4. italica v. tenuissima	16	17			15	8	29	19	38	26
Chlamydomonas spp.										
Lobomonas ampla					7	18				
Sphaerellopsis spp.				•			2	12		
Monoraphidium contortum	•									

Table 12. The percentage of dominant species accounting for more than 10% of the total phytoplankton cell density or biomass in July 1977-1990. (C = cells \%, B = biomass %).

Phytoplankton	[1977]		[1981]		[1982]		[1986]		[1988]	
species	C	В	C	В	C	В	C	В	C	В
Cryptomonas spp.					•					
Planktothrix mougeotii										
Rhodomonas lacustris									10	1
Ochromonadales	41	10	,							
Aulacoseira ambigua	10	45		•	52	86	40	41	31	17
A. islandica									13	45
A. italica v. tenuissima	33	31	97	98	34	11			40	29
Asterionella formosa							23	20		
Tabellaria flocculosa							7	20		
Dictyosphaerium pulchellum				,						
Cryptomonas spp.									12	6
Planktothrix mougeotii		-	48	78	27	59			34	67
Rhodomonas lacustris			22	1	12	1			17	1
Ochromonadales										
Aulacoseira ambigua	35	14			17	5	16	16		
A. islandica	31	68	10	12	13	23	6	20		
A. italica v. tenuissima	20	9			14	5	31	23		
Asterionella formosa										
Tabellaria flocculosa							5	13		
Dictyosphaerium pulchellum							10	5		

Table 13. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in August 1978-1990. (C = cells %, B = biomass %).

Phytoplankton	[1978]		[1980]		[1982]		[1982]		[1983]		[1986]	
species	С	В	C	В	C	В	c	В	c	В	C	В
Aphanocapsa delicatissima			•		21	21						
Aphanizomenon flos-aquae												
Planktothrix mougeotii												
Cryptomonas spp.	17	35	14	15			11	7				
Rhodomonas lacustris					28	7	14	1				
Ochromonadales	10	2			18	2						
Aulacoseira ambigua	4	28	5	21	5	33	34	79			11	8
1. islandica												
l. italica v. tenuissima	11	15	51	46			11	5	83	83	53	48
abellaria flocculosa							,					
Dictyosphaerium pulchellum					10	9						
Monoraphidium contortum	31	3										

Table 13, Continued.

Phytoplankton	[1988]		[1988]		[1988]		[1988]		[1988]		[1990]	
species	C	В	C	В	C	В	C	В	C	В	C	В
Aphanocapsa delicatissima							,					
Aphanizomenon flos-aquae									68	66		
Planktothrix mougeotii	18	44	47	84	52	85	39	87	21	32	7	23
Cryptomonas spp.												
Rhodomonas lacustris	10	1	14	1			27	2			12	2
Ochromonadales							13	1				
Aulacoseira ambigua	12	4			12	3						
A. islandica	16	31						,				
A. italica v. tenuissima	22	10	10	3	12	3	•					
Tabellaria flocculosa											21	15
Dictyosphaerium pulchellum											10	22
Monoraphidium contortum											16	7

Table 14. The percentage of dominant species accounting for more than 10 % of the total phytoplankton cell density or biomass in September 1977-1988. (C = cells %, B = biomass %)

Phytoplankton	[1977]		[1979]		[1981]		[1986]		[1988]	
species	C	В	C	В	C	В	C	В	C	В
Cryptomonas spp.					6	15	6	11	6	12
Rhodomonas lacustris							12	3		
Ochromonadales	16	1							32	6
Aulacoseira ambigua	26	77	2	18			28	25		
4. islandica									6	32
A. italica v. tenuissima			28	52	67	67	27	32	17	20
Monoraphidium contortum	37	2	38	5			•			

4.3 Phytoplankton succession in three different summers

The phytoplankton successions of summers 1968 and 1969 were fairly similar but in 1988 the differences were quite obvious. The biomass of phytoplankton in the very first sample in May from the recently filled Lokka reservoir was extremely low, only 0.03 mg l-1 (Fig. 14). It was equal to the biomass measured in the river Luiro in autumn 1965 (Oy Vesitekniikka Ab 1967). Cryptomonas spp., Aphanocapsa delicatissima, Bicosoeca ainikkiae and Mallomonas caudata were abundant. Planktothrix mougeotii was also observed as a few trichomes in May. Later chrysophyceans and Desmarella moniliformis were dominant. The biomass increased gradually, so that in August there was a maximum biomass of 0.74 mg 1⁻¹, caused almost solely by Cryptomonas spp. A major part of the species were small, flagellated and also heterotrophic, particularly in June (Fig. 15).

A low biomass, 0.02 mg l¹, was again recorded the following May (Fig. 16), consisting mainly of heterotrophic species. The maximum in August was dominated by *Cryptomonas* spp. and *Chlamydomonas* spp. was subdominant. Small, flagellated algae were still abundant during the growing season (Fig. 15). During the first two years the annual succession had only one maximum in August. The cell numbers remained low in both years.

In May 1988 the biomass was 0.47 mg l⁻¹ (Fig. 17), ca. twenty times higher than in 1968. In June, *Cryptomonas* spp. and *Chlamydomonas* spp. dominated the biomass. The biomass increased gradually until the middle of July, with a maximum value of 8.89 mg l⁻¹ caused almost solely by *Aulacoseira italica v. tenuissima, A. ambigua* and *A. islandica*. The proportion of small, flagellated species decreased sharply from May to July (Fig. 18).

In the second half of July the biomasses suddenly decreased. Diatoms were succeeded by *Planktothrix mougeotii*, which dominated throughout August and reached a maximum of 87 % of the total biomass. *Planktothrix mougeotii* was subsequently succeeded by *Aphanizomenon flos-aquae*, which formed a second biomass maximum at the end of August (Fig. 17).

At this time there was an observation of a mass occurrence of blue-green algae determined as *Planktothrix mougeotii*, which clogged the nets. In September and October the biomasses decreased to the vernal level with dominance of *Aulacoseira* species. From late August the amounts of flagellated and small cells again increased (Fig. 18).

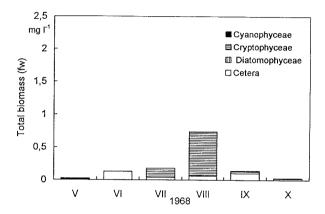


Fig. 14. The succession of phytoplankton as biomass (mg l⁻¹ fw) from May to October 1968 in the Lokka reservoir.

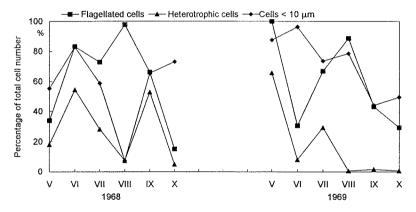


Fig. 15. The proportion of flagellated and heterotrophic cells and nanoplankton ($< 20 \mu m$) of the total cell number in the Lokka reservoir in 1968 to 1969.

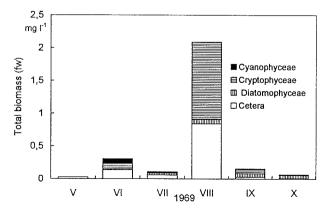


Fig. 16. The succession of phytoplankton as biomass (mg l^{-1} fw) from May to October 1969 in the Lokka reservoir.

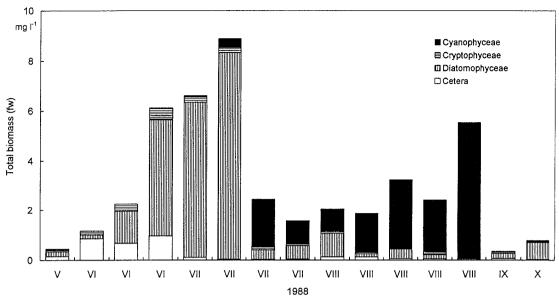


Fig. 17. The succession of phytoplankton as biomass (mg I-1 fw) from May to October 1988 in the Lokka reservoir.

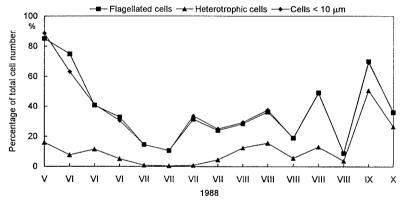


Fig. 18. The proportion of flagellated and heterotrophic cells and nanoplankton ($< 20 \mu m$) of total cell numbers in the Lokka reservoir in 1988.

5 DISCUSSION

5.1 Water quality

Man-made lakes receive their initial nutrient input immediately after filling from dissolution of matter originating in the inundated land area. Reservoirs situated in subarctic regions are further characterized by a feature which continually supplies new nutrients to the system. This is the "pumping" of fine-grained organic matter and pellicular water into the reservoir due to ice erosion (Kinnunen 1982). In the Lokka reservoir this is coupled with peat land erosion due to extreme

water level manipulations. In fact, severe oxygen depletions were the result of regulating the water volume to its minimum level. By decomposing the fine-grained, soluble organic matter the bacteria deplete the oxygen supplies during the long ice-covered period, which usually lasts seven months. Moreover, oxygen also strongly controls the solubility of inorganic nutrients. Humic compounds still abound in the Lokka reservoir making the water brown, slightly acidic and with a low Secchi depth. A dark water colour has the effect of decreasing and "flattening out" the photic productive-layer. This slows down the

trophication process and Ilmavirta (1983) has found evidence of naturally dark lakes also often being oligotrophic.

The water quality of the reservoir has improved during the past 23 years, which is indicated by the decrease in values of some important water quality variables. Water colour has decreased by more than a half to the present annual mean of 75 mg l⁻¹ Pt. The amount of particulate organic matter has also decreased as well as the amount of iron.

Within a period of only two decades the concentrations of total phosphorus have decreased by ca. 70 % and total nitrogen by 40 %. On the basis of the present annual average phosphorus concentration, 30 μ g l¹, the Lokka reservoir is still eutrophic (Wetzel 1983, Brettum 1989, Willén 1992) whereas the nitrogen concentration of 470 μ g l¹ reflects a meso-eutrophic status (Wetzel 1983). These nutrient concentrations reflect a rather eutrophic water environment in Lapland as noted earlier by Kinnunen (1985).

Because of the acidic nature of the Finnish bedrock and soil the alkalinity of lakes and reservoirs is rather low and the waters have a low pH. The Lokka reservoir is no exception to this rule. Only minor changes - decreases - were observed in these variables. The water is still poor in electrolytes and has a low pH, confirming the observations of Heinonen and Airaksinen (1974).

The increase in the oxygen saturation level reflects the improved oxygen condition in the reservoir.

5.2 Phytoplankton

5.2.1 Algal response to environmental changes

Light

In the Lokka reservoir it is the autotrophic phytoplankton that are the responsible primary producers due to the lack of higher littoral plants. Phytoplankton communities are known to react rapidly to changes in the environment (Willén 1987, Garnier 1992, Jacobsen and Simonsen 1993). In Finnish lakes, whether manmade or natural, environmental conditions change rapidly because of the short growing season. These changes are quickly responded to by phytoplankton emerging as either morphological or physiological adaptations, or both. Changes in pigment concentrations of individual algae is good example (Ilmavirta 1982). Total phytoplankton biomass in the Lokka reservoir, determined as chlorophyll, reflected eutrophy using the limits set by e.g. Trifonova (1989), but there was no clear correlation between chlorophyll and biomass. The high chlorophyll content could be partly explained by light limitation, which would lead to increased cellular chlorophyll levels (e.g. Ahlgren 1970, Vörös and Padisák 1991). In brown-water lakes the colour of the water and the depth of the trophogenic layer are more important factors than nutrient concentrations in determining the composition of phytoplankton as noted by Ilmavirta (1980).

Diatoms are favoured by low light, low temperature and a moderately nutrient-rich environment during turbulence or the onset of stratification (Lund 1971, Willén 1991). A reservoir thus offers an excellent environment for diatoms because of the water level manipulations which cause both turbulence and recirculation of nutrients, especially of silica. For instance Aulacoseira italica v. tenuissima which is characteristic of extremely dark waters due to its low light demands (Talling 1957) is very abundant in the Lokka reservoir. On the other hand bluegreen alga Planktothrix forms deep biomass maxima because of its low light requirements (e.g. Lindholm 1992), which will be missed if only samples from the upper water layer are used (Harris 1986). Also Aphanizomenon is typical of waters with low temperatures and low light levels (Steinberg and Hartmann 1988).

Life forms

Algal response to environmental change is often reflected by changes in life forms. For instance the presence of flagella have been found important for the survival of phytoplankton during long winters (Rott 1988). In lakes flagellated species compose more than 50 % of the biomass when the water colour is more than 50 mg l-1 Pt (Ilmavirta 1983). In the early stage of the Lokka reservoir flagellated species contributed, on average, more than 60 % to the total cell density and to the biomass. The proportion of flagellated species decreased below 50 % in the subsequent erosion stage. For the flagellated cells, such as Cryptomonas spp., Uroglena spp. and Chlamydomonas spp. which are very common in the Lokka reservoir, mobility is of great advantage and can be considered an adaptation to the ambient humic waters (Ilmavirta 1983, Salonen et

al. 1984, Eloranta 1988, Smolander and Arvola 1988, Arvola et al. 1990). With their flagella e.g. cryptomonads are able to migrate through the thermocline to take up additional nutrients from the hypolimnion (Salonen et al. 1984, Arvola et al. 1990).

Cell size

In the early stage, in the chemically and biologically unstable environment, the majority of the species were small, which is also typical for oligotrophic waters (Pavoni 1963, ref. Harris 1986, Harris 1994), despite the high nutrient concentrations at that time. Algae with a small cell size are very efficient users of nutrients and are capable of rapid growth in unstable environments and may outcompete larger algae, e.g. blue-green algae (Reynolds and Walsby 1975, Harris 1984, Padisák et al. 1988, Steinberg and Hartmann 1988). In the Lokka reservoir the stabilization of the environment through decreased regulation. decreased colour and decreased, but stillavailable nutrients may explain the increase of the larger species like blue-greens towards the end of the study period.

In this material the small sized species Monoraphidium contortum was observed as early as in 1971 and for the last time in 1986. It was also very abundant in the material of Arvola (1980) and Jones and Ilmavirta (1983). According to Arvola (1980) this species is probably a pioneer species, able to survive in a new labile ecosystem. Monoraphidium contortum seems to have a wide ecological habitat encompassing both oligotrophic and polyeutrophic conditions (Komárková-Legnerová 1969, Brettum 1989). Brettum assumes that the oligotrophy indicating species M. irregulare is often included in M. contortum, which indicates eutrophy. The correct identification is therefore very important. Reynolds (1988) has classified M. contortum as a true river phyto plankton, which tolerates highfrequency hydraulic disturbances. I found M. contortum to be almost the only species present in the strongly regulated River Nurmonjoki with turbid water. No strong correlation between either the cell density or the biomass of Monoraphidium with the studied variables was found. Water colour and organic matter content gave weak positive correlations whereas with conductivity a negative correlation was found. Ilmavirta (1982) observed that in humic waters

correlations are never strong not even between biomass and chlorophyll.

Nutrional requirements

Though phytoplankton in general are autotrophs, there are species which depend on organic substrates and are subsequently heterotrophic. The craspedomonad Desmarella moniliformis for instance, prefers waters in which organic compounds are present in moderately high concent rations and where bacteria are abundant. According to Tikkanen and Willén (1992), Desmarella occurs in eutrophic and impure waters. Järnefelt (1961) has concluded that the species indicates the presence of effluents from sulfite mills. There are also algae suspected of mixotrophy like Cryptomonas (Haffner et al. 1980) which is an indicator of waters rich in nutrients and organic material (Rosén 1981) and Rhodomonas (Haffner et al. 1980) which tolerates waters with mud and clay particles (Brettum well 1989) as as Dinobryon bavaricum (Straškrabová and Šimek 1993). Euglenids are also typical of waters with organic nutrients (Prescott 1962). The abundancy of colourless species was high during the first spring and autumn in 1968 and still so during the spring of 1969 when decomposition was efficient. Obligate autotrophy is difficult to demonstrate.

5.2.2 Long term and seasonal successions

The development of phytoplankton communities can be investigated as an indicator of the productivity of the lakes by measuring the total biomass (Heinonen 1980, Trifonova 1986). Year-to-year variations in the quantitative values are possible. even when the biomasses are studied monthly. The different abundances of the various algal species, especially colony forming species, cause this variation as noted among others by Trifonova (1986) and Eloranta (1988). Also several ecological factors e.g. grazing pressure of zooplankton as well as weather conditions affect phytoplankton (Porter 1973, Brettum 1989, Jacobsen and Simonsen 1993, Reynolds et al. 1993). In the Lokka reservoir the year to year variations were large though the results were treated as annual means or separatelly in different months. This may be explained partly by different water regulation practice in the different years.

Long term succession

The long term succession of phytoplankton communities during the ageing process of lakes from oligotrophy to eutrophy is associated with the evolution of the lakes and with the availability of nutrients, generally phosphorus (e.g. Rosén 1981, Trifonova 1988, 1989). The biomass of the river Luiro before it was submerged was comparable with the reservoir biomass values of the early stage, which were relatively low. The measured seasonal averages indicated oligotrophy and oligo-mesotrophy, according to Heinonen (1980), Brettum (1989) and Trifonova (1989). Biomass increased rapidly during the first years. Partly, this may be caused by different sampling depths in the beginning of the monitoring programme. Diatoms caused maximum biomasses at the beginning of strong regulation and again when the regulation decreased. Depending on whose classification system one uses the biomass either reflected mesotrophy, meso-eutrophy or eutrophy (Heinonen 1980, Brettum 1989, Trifonova 1989) during the different years of the erosion stage. Although the biomass has decreased toward the 1990s, there is still no indication of oligotrophy.

When plankton development progresses from oligotrophic plankton via mesotrophic to eutrophic plankton the species composition changes reflecting the trophic status of a water body (e.g. Trifonova 1986, 1989, Willén 1987, Brettum 1989, Tikkanen and Willén 1992). Looking at the development in the Lokka reservoir over a longer time perspective significant changes in the plankton community can be observed. During the first years the dominant groups of phytoplankton were typical for oligotrophic conditions, including e.g. small colony forming bluegreen algae, chrysophyceans (partly mixotrophic), craspedophyceans, small green algae and pennate diatoms. The species composition was more or less similar to the species composition of the river Luiro. On the other hand abundant cryptomonads reflected the influence of a dark water colour (Ilmavirta 1983, Eloranta 1988, Smolander and Arvola 1988). Cold water dinophyceans were rare, although they are typical in oligotrophic waters (Willén 1987, Trifonova 1988, Tikkanen and Willén 1992). Centric diatoms, mainly Aulacoseira species, dominated during the erosion stage, for all in the period just after the strong regulation. These diatoms are typical of more eutrophic waters. At the end of the 1980s large blue-green algae increased, with mass occurrences as noted before. Large desmids, typical in different water bodies in Lapland (Järnefelt 1962), were also observed more often. The increase of filamentous Ulotrichales may be explained by the creation of new niches for these periphytic species once water level fluctuations had stabilized. Nevertheless, there are always "background" species, as noted by Padisák (1992), that remain in the system irrespective of the environmental changes. In the Lokka reservoir eight such "background" taxa were observed throughout the studied years.

Different trophic status may be determined by counting indicator species. The value of individual species as indicators of trophic state must be evaluated with some caution (Järnefelt 1952, 1956, Järnefelt et al. 1963, Heinonen 1980, Rosén 1981, Brettum 1989). Planktothrix agardhii for instance, is not included as an indicator of eutrophy by either Järnefelt (1952, 1956), Järnefelt et al. (1963) or Heinonen (1980). On the other hand Niemi (1971) found it to be a good indicator of eutrophication in brackish waters. According to Skolberg and Skolberg (1985) and Brettum (1989), P. agardhii indicates very eutrophic conditions whereas P. mougeotii prefers mesotrophy. Consequently the correct species identification is of great importance. In this material the proportion of species indicating eutrophy was generally low, but during the strong regulation the number of eutrophy indicating species increased. In July the tendency was opposite, anyhow. The number of oligotrophy indicating species was always very low.

Seasonal succession

The seasonal succession is caused by periodic dominance of successive algal populations in the annual cycle (Trifonova 1986). According to Heinonen (1982), whose observations of annual variations in phytoplankton are based on the results only from southern and central Finland, a biomass maximum occurs in oligotrophic and mesotrophic lakes in June. After a decrease of biomass in July a weaker second maximum appears in August. In oligo-mesotrophic lakes of the Carelian isthmus studied by Trifonova (1986, 1989) the spring maxima rapidly decreased in June. In July a slight increase was observed which perhaps could be considered the weaker

second maximum. In mesotrophic lakes three maxima were observed; one in May, one in July-August and one in September. The same phenomenon is illustrated by cell density values from Lake Erie in 1927, when the lake was still mesotrophic (Davis 1964).

In the Lokka reservoir in 1968 and 1969 the phytoplankton successions had features both of oligotrophic and mesotrophic lakes; the June maximum was weak with oligotrophy indicating biomass, but the maximum in August in both years (Figs. 14, 16) was clear and more mesotrophic according to biomass values. Approximately twenty years later in June-July 1988 a long-lasting maximum was produced by diatoms. There was even a slight depression of biomass at the end of July. The second maximum in August was caused by blue-greens (Fig. 17). This mass occurrence was persistent for a long time and can be considered as evidence for eutrophication (Willén 1987).

5.3 The Lokka reservoir today

The biotic development in reservoirs occur via several different stages (Vogt 1978, Kinnunen 1982, Krzyzanek et al. 1986). After damming the changes are very rapid lasting only a few months. As sampling in the Lokka reservoir was not started until ten months after damming, this initial period of rapid change has not been monitored. The low biomass of the first years illustrated the first oligotrophic phase. The dark water colour seems to have reduced the development of phytoplankton, although the nutrient concentration was very high. Besides this, the species composition observed reflected the availability of organic nutrients favouring mixotrophic cryptomonads, chrysophyceans and euglenids and heterotrophic craspedophyceans like Desmarella.

The erosion stage may last tens or even hundreds of years and ends in a stabilization stage (Vogt 1978). The erosion stage began in the mid-1970s. At this time, water level fluctuations, due to manipulation, were large and the water volume at its minimum. Moreover, the number of taxa was high as were the biomasses and cell densities, indicating eutrophy untill the mid-1980s. This period was a time of change when the oligotrophic (mixotrophic) chrysophycean-group decreased and was replaced by large, more eutrophic, centric diatoms. Partly, this may have

been caused by the efficient recycling of silica and other nutrients due to the large water level fluctuations. The mixing of the water column in mid summer may cause blooms of *Melosira (Aulacoseira)* as noted by Lund (1971).

In the 30 year old Rybinsk reservoir the diatoms Aulacoseira italica and Asterionella formosa were dominant in spring, whereas later in summer blue-green algae such as Aphanizomenon flos- aquae and Microcystis aeruginosa dominated (Sorokin 1972). In the Lokka reservoir bluegreen algae have increased in addition to diatoms. However, only one record of *Microcvstis* aeruginosa colonies has been made. This was in 1986. According to Sorokin (1972) and Porter (1973) the filtering zooplankton are not able to use the larger blue-green algae, dinoflagellates or desmids directly, only via a bacterial link. Thus the primary food chain is lengthened, with serious losses as a consequence. The proportion of nanoplankton has decreased during the history of the Lokka reservoir. The small fast-growing pioneer species are replaced by larger colonies or trichom-forming species in July and August. At this time the productivity of filtering zooplankton is high. If zooplankton are not able to utilize phytoplankton directly, this may have an influence on the nutrient chain culminating in fish (Puro 1989).

During the last ten years water level fluctuations in the Lokka reservoir have been stabilized (Fig. 2). The colour values have decreased and the water quality has improved. Stocking of the reservoir with whitefish since the 1970s (Salonen and Mutenia 1992) may have caused an imbalance in the phytoplankton community. The erosion phase still continues, primarily due to the high nutrient concentrations, consequently, the reservoir can still be considered meso-eutrophic with eutrophic features such as blooms of bluegreens. As yet there are no signs of the assumed oligotrophication which is the last phase in the generalized reservoir development.

6 CONCLUSIONS

1. The normal development of reservoirs with an unstable oligotrophic period after damming was observed. The biomasses and the number of species were low and like the species composition, in accordance with the samples taken prior to filling.

- 2. The river plankton consisted of chrysophyceans, cryptomonads and colonies of small bluegreens. It was replaced by centric diatoms, desmids and blue-greens of larger size, which indicate biological stabilization in the Lokka reservoir. Only eight taxa were observed during all the years studied.
- 3. It is difficult to evaluate the present state of the Lokka reservoir solely on the basis of phyto plankton variables. Not only the ageing of the reservoir, but also water level regulation, the continued high nutrient concentrations, the dark water colour, short water retention time, predation, fish stocking and several other factors will affect the composition as well as the quantity of phytoplankton.
- 4. The erosion phase is still in progress with no signs of the assumed oligotrophy, the last stage in the history of a reservoir. The reservoir could still be characterized as meso-eutrophic on the basis of phytoplankton and physico-chemical results. Although an evaluation based on only the physico-chemical data indicates a tendency towards oligotrophication.
- 5. This study of the Lokka phytoplankton is part of the Finnish lake monitoring programme. Sampling was performed at ca. five-year intervals. The biomasses fluctuate for many reasons but show a general trend in the trophic status from oligotrophy to meso-eutrophy and the changes in main species composition are obvious
- 6. In addition to the monitoring programme, monthly samplings were performed during three different years. These results provide information on the changes in seasonal succession. This more intensive sampling, even if performed only once in a decade, or even less frequently, could provide useful additional information on monitored lakes.

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YHTEENVETO

Vuonna 1967 rakennetun Lokan tekoaltaan kasviplanktonin koostumusta ja määrää on tutkittu vuodesta 1968 vuoteen 1990 osana seurantatutkimusta.

Biomassa, yksilötiheys ja taksonien lukumäärä olivat alhaisia ensimmäisenä vuotena ilmentäen vähäravinteisuutta, mutta kasvoivat nopeasti vuodesta 1968 vuoteen 1971. Suurimmat runsasravinteisuutta ilmentävät biomassa-arvot todettiin 1980-luvun alussa. Vuosikymmenen lopussa biomassat ja yksilötiheydet laskivat, mutta ei taksonien määrä. Sen sijaan *a*-klorofyllin määrät ovat koko tutkimusajan lievästi kohonneet.

Ensimmäisinä vuosina, alkuvaiheen aikana, vallitsevia leväryhmiä olivat pienet sinileväyhdyskunnat, miksotrofiset nielulevät ja kultalevät sekä heterotrofiset kaulusflagellaatit. Sentrisiä piileviä oli vähän, mutta niistä tuli vallitseva ryhmä kymmenen vuotta altaan rakentamisen jälkeen. Kesällä 1988, noin kaksikymmentä vuotta altaan rakentamisesta, sinilevät *Planktothrix* ja *Aphanizomenon* muodostivat massaesiintymiä. Leväyhteisön lajisto oli muuttunut suurikokoisemmaksi.

Tekoaltaille ominainen ensimmäinen kehitysvaihe oli todettavissa ja toinen ns. eroosiovaihe on yhä meneillään. Tänä päivänä veden väriarvot ja ravinnepitoisuudet ovat laskeneet, joskin ne vieläkin ovat korkeat. Mitään selviä merkkejä tekoaltaan kehityksen viimeisestä köyhtymisvaiheesta ei ole nähtävillä. Mikäli säännöstelykäytäntöä ei voimakkaasti muuteta, eliöyhteisön tasapainoinen kehitys jatkuu.

Sekä vedenlaatumuuttujien että kasviplanktonin määrän ja koostumuksen perusteella vesi on edelleen meso-eutrofista.

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Appendix 1. The annual minimum and maximum water stages of the Lokka reservoir and the corresponding areas and volumes at two dates; m = 15th of May and o = 15th of October. Data of the years 1970-1984 according to Kinnunen (1985).

Year		Height	Volume	Area
		$N_{43}+ (m)$	(10^6 m^3)	(10^6 m^2)
1968	m	240.42	616.0	281.5
	О	242.05	1049.6	293.8
1969	m	242.17	1079.4	298.6
	О	243.29	1468.2	346.8
1970	m	241.80	974.1	286.0
	О	242.88	1 318.2	328.3
1971	m	243.18	1 428.2	339.8
	О	244.03	1 729.3	371.0
1972	m	243.07	1 394.2	335.9
	О	244.37	1 843.3	389.4
1973	m	243.58	1 564.2	355.4
	0	244.03	1 729.3	371.0
1974	m	241.56	904.1	277.0
	0	243.78	1 632.2	363.2
1975	m	243.71	1 598.2	359.3
-,,,	0	244.42	1 862.3	389.4
1976	m	242.86	1 302.2	328.3
1770	0	243.50	1 530.2	351.5
1977	m	240.28	572.1	226.2
1711	0	242.69	1 254.2	320.9
1978		240.98	750.1	250.0
1970	m	241.96	1 016.2	295.0
1070	0	240.94	728.1	246.6
1979	m	242.19	1 094.2	302.4
1000	0	242.19	778.1	254.5
1980	m		960.1	281.5
1001	0	241.73		281.5
1981	m	241.72	946.1	
4000	О	244.93	2 052.3	412.4
1982	m	242.98	1 360.2	332.0
4000	0	244.20	1 786.3	380.2
1983	m	243.36	1 479.2	347.6
4004	0	244.60	1 938.3	398.6
1984	m	243.00	1 360.2	332.0
	0	244.38	1 862.3	389.4
1985	m	242.25	1 116.7	302.5
	0	244.05	1 719.9	372.0
1986	m	242.90	1 323.3	328.5
	О	244.05	1 719.9	372.0
1987	m	242.54	1 256.6	313.0
	O	244.84	2 023.3	406.5
1988	m	242.93	1 330.0	328.7
	0	244.23	1 766.7	380.6
1989	m	243.64	1 566.7	357.5
	О	244.85	2 023.3	406.9
1990	m	243.39	1 486.6	346.8
	o	243.76	1 616.7	362.3

Appendix 2. The average number of observed phytoplankton cells (counting units) in 100 ml of water sample in Lokka in June-September 1968-1990.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
СУАПОРНУСЕЛЕ								~~~~						
Chroococcales														
Aphanocapsa biformis A. Braun		1053												
A. elachista W.& G.S.West		112	1568	420	726									
A. delicatissima W.& G.S.West	336	411	1719	6417	2745	1008	336	60	9345	400		4295	283	60
Aphanothece clathrata W.& G.S.West		224	336		112									30
Chroococcus dispersus (Keissl.) Lemmermann													140	
Eucapsis minuta F.E. Fritsch			61400											
Gomphosphaeria aponina Kützing			224											
Merismopedia warmingiana (Lemm.) Lagerheim		448											280	
Microcystis aeruginosa (Kütz.) Kützing												4		
M. firma (Kütz.) Schmidle		224	11000											
Snowella lacustris (Chod.) Komárek & Hindák			504		224	560		1210		165			4	
Synechococcus linearis (Näg.) Komárek				2240										
Woronichinia naegeliana (Unger) Elenkin	16									,			90	16
Oscillatoriales														
Limnothrix planetonica (Wolosz.) Meffert						6380	4930							
L. redekei (van Goor) Meffert			20							400				140
Planctolyngbya contorta (Lemm.) Anagnostidis& Kom.								120						
Planktothrix mougeotii (Bory ex Gom.)1)Anag.& Kom.												3127	27249	1877
Pseudanabaena limnetica (Lemm.) Komárek		448		112			784							
P. mucicola (HubPestal. & Nauw.) Bourrelly	•	448									•			
Nostocales														
Anabaena flos-aquae (Lyngb.) Brébisson ²⁾	240	16		144			336		296	1260		8000	121	148
A. lemmermannii P.Richter				3920				240					60	240
Anabaena spp.	8			560		12						6		
Aphanizomenon flos-aquae (L.) Ralfs		40			•			60		540		1985	51060	421
СКУРТОРНУСЕЛЕ														
Cryptomonas spp.	12203	14783	7200	5537	20665	9985	19625	4297	11014	18453	5710	13349	3105	3990
Cyathomonas truncata (Fres.) Fisch								400					210	
Katablepharis ovalis Skuja				7817	3695	2410	11300	3400	2830	10600	4400	2635	5357	280
Rhodomonas lacustris Pasch.& Ruttner				1830	2635	1343	13100	12400	16000	227800	3600	12025	26522	11220

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
DINOPHYCEAE									·					
Glenodinium spp.		4											60	
Gymnodinium spp.									1456	400		400	260	400
Peridinium umbonatum Stein		•		1542	170	727	112	1215	112	2490	840	1335	4228	2
BICOSOECOPHYCEAE														
Bicosoeca ainikkiae Järnefelt											400		700	
B. conica Lemmerman												1200	153	
B. cylindrica (Lack.) Bourrelly								400		600	90	400	2800	140
B. lacustris James-Clark	3511	894						2000	112			420	420	
B. planctonica Kisselev			2020						448			400	1954	
B. planctonica v. multiannulata (Skuja) Bourrelly	391	224		280			•	1200	224		400	400	1176	340
PRYMNESIOPHYCEAE														
Chrysochromulina spp.						•	•	800	2350	400	800	3750	1517	413
CHRYSOPHYCEAE														
Bitrichia chodatii (Rev.) Chodat		112												
Chrysidiastrum catenatum Lauterborn											400		140	420
Chrysococcus biporus Skuja			448						168	1200		400	3845	
C. cordiformis Naumann												400	330	
C. furcatus (Dolg.) Nicholls		112											140	
C. minutus (Fritsch) Nygaard		3920	336										190	
Chrysosphaera melosirae (K. Meyer) Bourt.													8330	
Chrysosphaerella longispina Lauterborn												115		30
Chrysostephanosphaera globulifera Scherffel								30					3080	16
Dinobryon acuminatum Ruttner									112				420	
D. bavaricum Imhof		224		635	224	3305	72		64		120	30	6213	1260
D. borgei Lemmermann		112											760	
D. cylindricum Imhof		1340	96										355	
O. divergens Imhof					76							140	140	3027
O. sociale Ehrenberg				1736									140	
D. suecicum Lemmermann				112										
Dinobryon spp.		112	4	423	168					270		2	280	30
Kephyrion inconstans (Schmid) Bourrelly													420	
Covale (Lack.) HubPestalozzi	672												280	
K. rubri-claustri Conrad			112											

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
Kephyrion spp.					112			•				800	280	
Kephyrion spirale (Lack.) Conrad			112									800	140	
Mallomonas akrokomos Ruttner	2800	392	504										610	140
M. caudata Iwan.Em.Krieger		52	192				224	120	40	90	30	170	62	30
M. crassisquama (Asm.) Fott								400		600	400		230	140
M. punctifera Korshikov			6										3216	
M. tonsurata Teil. em. Krieger								. '					380	
Mallomonas spp.							112		112				235	
Monochrysis spp.								400		31000	4000	6000	280	
Paraphysomonas spp.													350	
Pseudopedinella spp.								400		3200	2400	280	601	
Ochromonadales	560	45580	63900	114632	25050	10019	16500		7531		600	39260	3232	997
Ochromonas spp.									3760			800	157	
Spiniferomonas spp.													380	
Syncrypia spp.	56000													
Synura spp.	112	104		4200			112		16			800	1291	
Stichogloea olivaceae Chodat			1230											
Uroglena umericana Calkins	6400	800	800	1600			800				•		165	
DIATOMOPHYCEAE														
Eupodiscales														
Cyclosella stelligera (Cleve&Grun.) Van Heurck				112						400				
Cyclotella spp.							448		112					
Eupodiscales							784	13200		1000			140	420
Aulacoseira ambigua (Grun.) Simonsen			3505	87433	14250	18750	13200	5200	117533	36243	390	36416	27281	3486
A. distans (Ehr.) Simonsen		224	112					1230					142	
A. granulata (Ehr.) Simonsen												1200		
A. granulata v. angustissima (O.Müll.) Simonsen										,				910
A. islandica (O.Müll.) Simonsen												60	35345	4280
A. islandica (O. Müll.) Simonsen ⁴⁾													19092	
A. italica (Ehr.) Simonsen									27100	,				420
A. italica v. tenuissima (Grun.) Simonsen				202400	39750	134200	141000	982000	55200	810000	11600	103465	76578	13993
Melosira varians G.A. Agardh													411	
Rhizosolenia longiseta Zacharias	•	112			•		448						424	280
Bacillariales														
Asterionella formosa Hassal		11731	48192	22236	414	1475	1620	6110	2801	46590	5220	9517	1233	2760
Bacillariales	58	2463	345	290		168	224		1744			30		

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
Cocconeis spp.		,										4000		
Cymbella spp.														140
Eunotia spp.	112											12000	4	
Fragilaria capucina Desmaziere				164	178	400	112							
F. construens (Ehr.) Grunow			16							660				
F. crotonensis Kitton	12	672	224	667	112	787	20						159	820
pinnata Ehrenberg				142	448	180	224							
Meridion circulare (Grev.) C.A.Agardh							8							
lavicula spp.	16									30		200		
Rhoicosphenia abbreviata (C.A.Ag.) Lange												12000		
ynedra acus Kützing		4								300			60	
berolinensis Lemmermann	271			840	336	672		420		150			190	140
S. nana Meister						144	224							
S. ulna (Nitzsch) Ehrenberg	5	4												
abellaria flocculosa (Roth) Kützing	14	1455	430	52	64	348	412	180	173	240	150	9060	380	463
АРНІДОРНУСЕЛЕ														
Sonyostomum semen (Ehr.) Diesing													2	
'acuolaria spp.				2800				120					2	280
**														
RIBOPHYCEAE														
Centritractus belonophorus Lemmermann						336							280	
stmochloron trispinatum (W.& G.S. West) Skuja													165	
ribonema spp.		672		-					-					1230
CUGLENOPHYCEAE														
Suglena acus Ehrenberg			12											
. gracilis Klebs						10	8						4	
. proxima Dangeard		20						400					7	4
. viridis (O.F.Müll.) Ehrenberg			4		10	6	32	12					Ċ	52
epocinclis ovum (Ehr.) Lemmermann						·						•	2	-
. steinii Lemmermann			4	112									-	•
fenoidium spp.		4030	4											•
hacus curvicauda Svirenko		4										200	•	
succicus Lemmermann			8											•
rachelomonas aculeata Dolgoff		24		:			•		•			•		•
hispida (Perty) Stein												•	17	30
. mspida (1 erry) siem . volvocina Ehrenberg		118	8		•	•	•	:	•	•	,	200	186	
volvocinopsis Swirenko	4		36	•				30	8	•	120	107	124	180

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
PRASINOPHYCEAE														
Scourfieldia spp.		٠	•		•					400	400		•	
CHLOROPHYCEAE														
Volvocales														
Chlamydocapsa ampla (Kütz.) Fott					120	114						400	140	
C. planctonica (W.& G.S.West) Fott					112							8	104	
Chlamydomonas spp.		14647	6296	3660	10005	8315	3020	1400	5456	3000	2000	4000	1395	345
Chlorogonium spp.	136		114		444	40			64		60	350	1767	
Eudorina elegans Ehrenberg						20	896	270		210		1389	37	100
Gonium pectorale O.F.Müller		8												
Gonium sociale (Duj.) Warming									112					
Hemitoma maeandrocystis Skuja										180		180	140	
obomonas ampla Pascher										400	400	3600	1318	
Monomastix spp.		,						400		1200	2400		476	
Pandorina morum (O.F.Müll.) Bory							112					75	420	30
aulschulzia pseudovolvox (Schutz) Skuja					,		,		8				238	
Planktosphaeria gelatinosa G.M.Smith		4												
Polytoma spp.								400		800	800	1000	393	420
Pseudosphaerocystis lacustris (Lemm.) Novakova		8					448	400	568			2630	1917	120
Pteromonas spp.			760										280	140
Sphaerellopsis spp.													2680	
dinanian dia														
Chlorococcales														
Ankistrodesmus falcatus (Corda) Ralfs ⁵⁾		336	26105	1008	1006	10124	1010							
Ankyra judayi (G.M.Sm.) Fott			2130	224	432	673		400	1340			800	281	
4. lanceolata (Korsh.) Fott								1600				705		
Botryococcus braunii Kützing								30		30	30	87		30
Chlorococcales			3420	2240									600	
Closteriopsis longissima (Lemm.) Lemmermann								210		90		45	150	
Coelastrum microporum Nägeli												400	2	
Crucigenia fenestrata (Sch.) Schmidle								90	896	180		840	140	
C. quadrata Morren			112	1737	1623	1913	112			800			140	840
C. tetrapedia (Kirchn.) W.&G.S. West					112			400	703	,		1300		
Dictyosphaerium ehrenbergianum Nägeli					28	1680	896	570	40				49	32
D. elegans Bachmann		132	16	20	32									
D. pulchellum Wood		224	190	3908	616	6440	2910	7600	6291	120	300	1410	359	6113
D. subsolitarium Van Goor				2130	616	27405								

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
Didymocystis inconspicua Korshikov						•		400	448	800	400	4600	150	1190
D. bicellularis (Chod.) Komárek				280	3040	784	448		,			1120		
Dimorphococcus lunatus A.Braun														120
Franceia ovalis (France) Lemmermann							336							140
Fusola viridis Snow		16												
Kirchneriella contorta (Schmidle) Bohlin			16	2520					2900					
K. lunaris (Kirchn.) Möbius					1790									
K. obesa (W.West) Schmidle			112	156	2967	1792		400				60	32	270
Lagerheimia chodatii Bernard					1230	504								
L. ciliata (Lagerh.) Chodat						112								140
L. genevensis Chodat													190	
Micractinium pusillum Fresenius				1215	168	1340		30		8000		400	450	140
Monoraphidium contortum (Thur.) KomLegnerova			104800	138933	35110	152315	15100	22000	2633	2600		540		
M. griffithii (Berk.) KomLegnerova					112				,					
M. komarkovae Nygaard	1009	822	532	1400	10295	897	8		1541				700	
M. minutum (Näg.) KomLegnerova	,		224	5600									150	140
M. mirabile (W.&G.S.West) Pankow	1790	897	448	5665	7662	9036	448		112					
M. tortile (W.&G.S.West) Kom.									728					
Docystis borgei Snow			72	16										
O. parva W.& G.S.West			464					1200						
D. submarina Lagerheim			896			448								280
Pediastrum boryanum (Turp.) Meneghini			2										2	30
duplex Meyen													2	2
Scenedesmus armatus Chodat				2940				30	112		400	487	61	
S. bicaudatus Dadus									112					
S. granulatus W.& G.S.West								400				400		
S. lefevrii Deflandre												400		247
S. quadricauda (Turp.) Brébisson				3052	168	336	336				30	30		
S. serratus (Corda) Bohlin												140		420
Scenedesmus spp.				1400	1460	448	224							. 1
Schroederia setigera (Schröd.) Lemmermann	507	7906		112		336								
Selenastrum gracile Reinsch		16												
Sphaerocystis schroeteri Chodat		8	116	284	52	8						150	55	
Tetraedron minimum (A.Br.) Hansgirg													190	
Tetrastrum staurogeniaeforme (Schröd.) Lemmermann					280	895	3697	112	1600					
T. triacanthum Korshikov				280										
Westella botryoides (W.West) Wildeman								1605		180		120		144

Appendix 2. Continued.

Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
Ulotrichales														
Elakatothrix gelatinosa Wille		16					20					700	4	60
E. genevensis Hindák												60	420	1400
Gloeotila fennica Järnefelt											2000	13400	420	5423
G. pelagica (Nyg.) Skuja				1680						400		14000		170
G. spiralis Chodat						61000								
Koliella longiseta Hindák								1600		6400	400	2600	1718	420
K. spiculiformis (Vischer) Hindák		336	26105	1008	1006	10124	1010			12800			600	
Microspora spp.												36000		88
Mougeotia spp.	12	16					92					175	51	77
Oedogonium spp.		52										25600		
Spirogyra spp.						36						200		
Ulothrix spp.	120		4			2812			64				86	
Zygnematales														
Closterium acerosum (Schrank) Ehrenberg						8								
C. aciculare T.West				945				30		90				150
C. acutum Brébisson	6							30		30			2	24
C. gracile Brébisson						38			40			4		
C. parvulum Nägeli			4											
C. pronum Brébisson				976	24		92		8			8		
Cosmarium abbreviatum Raciborski													2	
C. contractum Kirchner													2	
C. humile (Gay) Nordstedt	112													
C. phaseolus Brébisson		Ţ.	·	4				Ċ						71
C. pygmaeum Archer	•	•	,	4	4				·	•	•	•	:	
Spondylosium planum (Wolle) W.&G.S.West				Ċ					64				22	44
Staurastrum anatinum Cooke & Wills	•	•		•	Ċ		· ·	•	• •	•	•		2	• • •
S. anatinum f. vestitum (Ralfs) Brook	•	•	•	•	•		•	•		•	•		-	12
S. arachne Ralfs	•	•	•	•					•		•		•	4
S. avicula Brébisson	•	4	•		•	•		•	•	•	•	•	•	•
S. cingulum v. obesum G.M.Smith		-	•	•	•	•	•	•	•	•	•	•	•	4
S. inconspicuum Nordstedt	•	•	•					•	•	•				60
S. paradoxum v. parvum W. West			•		•	•	•		•	•	•	•	2	-
S. pseudopelagicum W.&G.S.West	•	•			•	•						•	9	2
		•	•	•		•	•				•	•	2	-
Staurastrum spp.			•	•		•	•	30	•	•		•	-	43
Staurodesmus dejectus (Bréb.) Teiling			•	•		•	•	30				•	•	2
S. incus (Bréb.) Teiling	•	•		•				•						8
S. incus v. ralfsii (W.&G.S.Weest) Teiling			•	•	•	•	•							0

Appendix	2.	Continued.
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Species	1968	-69	-71	-77	-78	-79	-80	-81	-82	-83	-85	-86	-88	-90
. mamillatus (Nordst.) Teiling													6	30
. mamillatus v. maximus (W. West) Teiling													4	
eilingia granulata (Roy&Biss.) Bourrelly	•					84		•		•			•	
CRASPEDOPHYCEAE														
ulomonas purdyi Lackey								400	168		400	270	868	
Desmarella brachycalyx Skuja		100		,								٠.		
), moniliformis Kent	2015	6820	2690											
Aonosiga spp.								800		2000	2000	400	280	
Calpingoeca frequentissima (Zach.) Lemmermann			1515	3920	84		2910					900	1657	
telexomonas dichotoma Lackey		•	•	112		٠			336		•	•		
COOFLAGELLATES														
Syromitus cordiformis Skuja	2580	116	224	1064	1010	224	24	1815	448			280	707	14

 ¹⁾ Earlier identified as *Planktothrix agardhii* (Gomont) Anagnostidis & Komárck
 ²⁾ Includes cf. *Anabaena circinalis* Kützing, (small cells)
 ³⁾ Possibly *Aphanizomenon yezoense* Watanabe
 ³⁾ The morphotype with thin walls (A. islandica ssp. helvetica (O.Müll.) Simonsen
 ⁵⁾ Includes *Koliella spiculiformis* (Vischer) Hindák