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PLANKTON CHANGES IN ESTONIAN SMALL LAKES in 1951–93

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Abstract. Changes of phyto- and zooplankton in 205 and bacterioplankton in 304 Estonian lakes in 1951–93 are discussed. In eutrophic lakes the average values of the total count of bacteria in bacterioplankton were lower in the 1990s than in the 1970s. The deterioration of the regime in lakes is characterized by changes in the structure of bacterial communities in the bottom water layers and increasing total count of bacteria. Relatively extensive changes occurred in phyto- and zooplankton species composition, specifically replacement of species with larger dimensions by smaller ones. The concentration of nutrients and the amount of plankton were on the highest level in the 1970s. Subsequently these values, as well as the trend of precipitation, fell. It means that there existed the effect of dilution. The values of the parameters of the ecological state were the highest in the 1980s. The response of biota to the influence of eutrophic factors was shifted in time. The recent improvement demonstrates the self-purification capability of Estonian lakes.

Key words: bacterio-, phyto- and zooplankton; plankton species composition; long-term changes.

1. INTRODUCTION

In the 1950s and 1960s, of the total of 1200 lakes in Estonia 8% were oligotrophic, 5.8% semidystrophic, 9% dystrophic, 36.4% eutrophic, 36.6% mixotrophic (dyseutrophic), 2.6% alkalitrophic, 1.4% halotrophic, and 0.2% siderotrophic (Mäemets, 1974, 1976, 1977). At present, the situation is essentially different. Typical oligotrophic lakes, as well as part of the dystrophic lakes, have disappeared, whereas soft-water eutrophic and hypertrophic lakes have appeared, etc. The present paper deals with the changes that have been taking place in plankton during the last 40 years. Their possible reasons and peculiarities in all material and lake types are discussed. In the literature, long-term changes are usually treated on the basis of single lakes with a dense dataset (Bailey-Watts et al., 1990; Morling & Willen, 1990; Reynolds & Bellinger, 1992; Talling, 1993). The present study, however, is based on data gathered from a great number of lakes.

2. MATERIAL AND METHODS

The lakes discussed include several different types (Table 1). The typology of Estonian lakes that was created by A. Mäemets (Mäemets, 1976) is based principally on their natural accumulation type and it differs from the other classifications that are based on the trophic state in the strict sense. Beside nutrient conditions, the classification created by A. Mäemets takes into account water hardness, organic substances, natural stratification, etc. Estonian inland waters are rich in humic compounds and their influence is essential. Every type and subtype is characterized by a certain complex of water quality parameters and a certain level of flow of substances, energy, and information, together with the corresponding biota and parameters of biological production.

The samples for **microbiological analysis** in 304 lakes were taken in 1973–93. Unfortunately, for the 1960s only some data on a few lakes were available for

Table 1

Distribution of lake types

Type or subtype (abbreviation)	No. of lakes in material of phyto- and zooplankton	No. of lakes in material of bacterioplankton
Alkalitrophic (A)	4	16
Dystrophic (D)	5	17
Eutrophic (E)	54	97
Halotrophic (HA)	1	0
Hypertrophic (HY)	29	32
Macrophytic (MF)	17	18
Mesotrophic (EM)	12	20
Mixotrophic, hard-water (DEK)	24	41
Mixotrophic, soft-water (DEP)	25	24
Oligotrophic (O)	17	20
Semidystrophic (SD)	17	19

comparison (Mäemets, 1966; Mäemets & Mäemets, 1976). The bacterial total count (TC), indicating the trophic level of lakes, the number of saprophytic bacteria (plate count, PC), and total Coliforms, since 1988 also biochemical oxygen demand (BOD_5), were determined. Samples for microbiological studies were taken during the vegetation period (15 May–15 Sept., with 72% taken in July) into sterile bottles from the subsurface (0.5 m) and the near-bottom layer (0.5–1.0 m from the bottom). In order to assess the results of the analyses, the classification of microbiological parameters in different lake types based on the data from 160 Estonian lakes was used (Lokk, 1982).

The samples of **phytoplankton** were collected during the vegetation period starting from 1951. Investigations were performed mainly during the summer stagnation period. During the period 1951–72, sampling was done mainly by Maia Pork and Viive Kõvask, later by the authors of this report. The following characteristics were studied: phytoplankton biomass (data begin from 1973, sporadically from earlier years); abundance on a six-step scale (0–5); a compound index, which is an improved version of the well-known Thunmark index (Ott, 1987); partial abundance of species, that is the ratio of the sum of abundances of all species in the sample and the number of species (Ott, 1987). The methods of sampling and treating have changed over more than 40 years; the results are also affected by the difference in researchers. Qualitative data, however, should be more or less comparable as most earlier samples have been studied repeatedly by the authors of this paper. Qualitative samples were taken with a plankton net (25–85 μm of mesh size), samples for counting with the Ruttner sampler in the deepest part of the lake, 0.5 l from two to seven layers, depending on the depth. Starting from 1987, the samples were collected on the surface layer (at 0.3–0.5 m), above the oxycline, and 1 m above the bottom. Samples were preserved with formalin (R. Laugaste) or Lugols solution (I. Ott), concentrated by precipitation (R. Laugaste) or filtration (I. Ott), counted in lined ground slice (R. Laugaste) or Goryaev and Fuchs-Rosenthal chamber (I. Ott), using light-field microscopes MBI-3 and Ergaval (magnification 70–400 times).

Altogether 926 samples of **zooplankton** were collected from the investigated 205 lakes in 1951–93. Sampling was repeated on the average 4.5 times for each lake. All the material was treated by A. Mäemets. The samples were taken with an Apstein net (N 49-59), trawling it vertically through the water column from the near-bottom layer up to the surface. In shallow lakes (below 1 m in depth) 100 l of water was filtered through the same net in most cases. Samples were preserved with a formalin solution. The species composition, number of individuals for each species, the total amount and biomass of zooplankton, and the index of eutrophy (ZE; Mäemets, 1991) were determined. The counting method was identical during the entire investigation period (a certain volume of the sample in Bogorov's chamber). Abundance is given in a 5-step scale.

3. RESULTS

3.1. Changes in bacterioplankton

The total count of bacteria of different lake types, as based on the data collected during 1973–93 from 304 lakes, is presented. The ecological classification of Estonian lakes by Mäemets (1974, 1976) was used in the ascending order of the trophic level (Table 2).

In alkalitrophic lakes, the bacterial abundance in the near-bottom layer was lower than in the subsurface layer of water. In the other types of lakes, the total amount of bacteria was higher in the bottom water layer. The higher bacterial abundance in the bottom layer in comparison with that in the subsurface layer is a characteristic trend of eutrophication. Macrophyte lakes (mixotrophic and eutrophic but covered with high vegetation) are usually shallow water bodies. Therefore, the difference in the density of bacteria between the surface and bottom layers of water was not essential in lakes of this type.

Table 2

The total count of bacteria (10^6 cells ml^{-1}) in lakes of different type in Estonia 1973–93*

Lake type, layer	Number of lakes	Total count		
		min.	max.	Mean ± SE
A, surface	16	0.1	5.1	1.62 ± 0.19
A, bottom	16	0.2	3.6	1.26 ± 0.33
O, surface	20	0.5	4.0	1.86 ± 0.12
O, bottom	20	0.8	8.0	2.56 ± 0.10
EM, surface	20	0.5	5.9	2.13 ± 0.13
EM, bottom	20	0.6	9.2	2.77 ± 0.25
SD, surface	19	1.2	4.6	2.15 ± 0.11
SD, bottom	19	1.4	7.6	3.09 ± 0.24
D, surface	17	0.8	6.5	2.80 ± 0.27
D, bottom	17	1.1	8.7	3.48 ± 0.32
DEK+DEP, surface	65	0.9	11.7	4.25 ± 0.18
DEK+DEP, bottom	65	1.0	17.4	5.80 ± 0.35
E, surface	97	0.9	14.5	4.13 ± 0.15
E, bottom	97	1.1	41.0	5.84 ± 0.20
MF, surface	14	1.4	10.2	4.05 ± 0.26
MF, bottom	14	1.4	9.2	4.31 ± 0.25
HY, surface	36	2.9	23.6	8.56 ± 0.56
HY, bottom	36	3.7	95.4	13.21 ± 1.82

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* EM, mesotrophic lakes; for other abbreviations see Table 1.

The difference in comparison with the results from the 1970s (Lokk, 1982) arises from the choice of lakes as well as from the trend of the decreasing trophic level in the 1990s. In the 1990s the average values of TC in eutrophic lakes were lower ($p < 0.001$); in alkalitrophic, mesotrophic, and hypertrophic lakes the trend of decreasing was not so remarkable ($p > 0.10$). However, the state of some hypertrophic lakes became worse, their TC increased. The average values of dystrophic lakes remained on the same level.

Values of **BOD_5** rise and their fluctuation increases according to the rising order of the trophic level in lake types. BOD_5 was significantly higher in macrophytic and hypertrophic lakes (average 4.2 and 8.3 mg O l^{-1}, respectively). Like TC, BOD_5 was associated with the type of lake. The correlations between BOD_5 and TC ($r = 0.59$, $p < 0.001$), TC and destruction ($r = 0.60$, $p < 0.001$), TC and total P ($r = 0.67$, $p < 0.01$) were determined by Ojaveer et al. (1993). The correlation coefficient between TC and BOD_5 was the highest ($r = 0.91$, $p < 0.001$) in the near-surface water of eutrophic and hypertrophic lakes.

The values of **PC** in the surface layer in different lakes were nearly on the same level (except for hypertrophic lakes). The averages ranged from 290 to 405 cells ml^{-1}.

In the near-bottom water layer the averages of PC increased with the increasing trophic state: in alkali-, oligo-, and mesotrophic, semidystrophic, and dystrophic lakes the averages were 400–630 cells ml^{-1}; in mixotrophic, eutrophic, and macrophytic lakes 660–800 cells ml^{-1}. A comparative study of different lake types indicated the highest PC and TC in hypertrophic lakes. The PC on 135 samples of hypertrophic lake water ranged from 54 to 13600 with an average of 813 cells ml^{-1} in the surface layer and 1090 cells ml^{-1} in the near-bottom layer. The development of saprophytic bacteria is on the minimum level in our lakes in summer. Therefore, the average values of the PC were relatively similar – in different lake types the maximum values were obviously dependent on the higher trophic level.

The number of **total Coliforms** indicated a good sanitary state of the lakes on the basis of 56.8% of the samples (coli-index < 250), 37.9% of the samples gave satisfactory results (index 250–5000), and in 5.3% of the analyses the number of total Coliforms was higher than the permitted value for water bodies of recreation areas (> 5000). The sanitary state of oligo- and mesotrophic lakes was better in comparison with macrophyte and hypertrophic lakes, where respectively 7 and 16.7% of the samples did not meet the sanitary requirements. In oligo- and alkalitrophic, semidystrophic, and dystrophic lakes the coli-index was not higher than the permitted sanitary limit value.

Changes in the microbiological parameters, first of all in the near-bottom water layer, were revealed. In unstratified lakes, changes were observed in **bacterial communities** above the bottom or the density of bacteria increased in the whole water column. In stratified lakes, signs of deterioration (appearance of H_2S, decreasing concentration of oxygen) were revealed by presence of organisms preferring microaerophilous and anaerobic conditions for their development. Iron bacteria like *Siderocapsa = Arthrobacter*, *Ochrobium*, *Procaryotes T2*, and *T4* and green photosynthetic bacteria *Chloronema* appeared in microaerophilic conditions; green bacteria *Ancalochloris, Chlorobium, Chlorochromatium,* and *Pelochromatium* and purple sulphur bacteria *Amoebobacter* and *Thiopedia,* and colourless sulphur bacteria *Peloploca* were found in strictly anaerobic conditions. In moderately eutrophied lakes iron bacteria *Planctomyces* and in the near-bottom water layer *Metallogenium* were determined. Very numerous are iron bacteria in the lakes of the Haanja Heights: *Leptothrix*, *Spirothrix*, *Hyalosoris*, *Siderocapsa = Arthrobacter*, *Metallogenium*, and *Ochrobium* were found. Eutrophication involves a change in the abundance and species composition of bacteria. The vertical distribution and composition of bacteria in stratified Estonian lakes were studied earlier (Gorlenko & Lokk, 1979).

3.2. Changes in phytoplankton

Species composition. Algal bloom, caused by cyanophyte genera *Anabaena* and *Microcystis,* was noticed in Estonian lakes already at the beginning of this century. In the 1950s, during our earlier investigation period, the same genera were widely distributed in the plankton of meso- and eutrophic lakes and algal bloom was very common in summer. Since the 1970s some filamentous blue-green species (*Oscillatoria limnetica* Lemm., *Planktothrix agardhii* (Gom.) Anagnostidis & Komárek, *Limnothrix redekei* (van Goor) Meffert) have expanded their abundance and distribution considerably. Simultaneously a reduction of great *Microcystis* colonies and some species of *Anabaena* (*A. flos-aquae* Bréb., *A. hassalii* (Kütz.) Wittr., *A. lemmermannii* P. Richt.) has been noticed. Beside *Aphanizomenon flos-aquae* (L.) Ralfs, which was a very common species in the 1950s, some species of the genus with narrower filaments, like *A. gracile* Lemm. and others, appeared. The total abundance of blue-green algae increased somewhat during 30–40 years, but the change is not statistically confident. The biomass of blue-green algae has decreased since the 1970s owing to the replacement of the colonial species by remarkably smaller filamental species. On the other hand, some species like *Planktothrix agardhii* and *Anabaena spiroides*, have quite large dimensions, forming the greatest biomasses of phytoplankton in Estonian lakes (over 700 g m^{-3} in summer 1985 and 1986; the former in L. Verevi, the latter in L. Rummu). The proportion of macroscopic colonies of *Gloeotrichcia echinulata* (J. E. Smith) Richter diminished drastically during the period under study. This alga was found earlier in 14 small lakes, in 3 as a dominant one. At present it exists only in our greatest Lake Peipsi. The dominant cyanophyte complex of species transformed radically in 60 lakes; of these 10 have a low, 23 a medium, and 27 a high trophic state at present.

Green algae were the group with the greatest number of species in all lake types, from 2–3 filament forms in the plankton of dystrophic to 30–40 mostly chlorococcal species in highly eutrophic lakes. The number of green algae species increased remarkably during the period under study. Such an increase is one of the most reliable features among biological parameters (Table 3). The abundance of green algae in plankton also increased to a considerable extent. The biomass increased less, as the relatively large forms of *Pediastrum, Dictyosphaerium*, etc. were replaced in many lakes by smaller forms of the same genera and also by very tiny algae from the genera *Ankistrodesmus, Monoraphidium*, *Scenedesmus*, *Oocystis*, etc.

Although belonging to green algae, desmids have generally opposite demands to the environmental conditions. In the 1950s oligotrophic, semidystrophic, and soft-water mixotrophic lakes were quite rich in desmids. The average number of

Table 3

Statistically reliable changes (others not presented) of some phytoplankton parameters by lake types in 1951–91 (values in 1970–91 are divided with values in 1951–69)*

Parameter	Lake type									
	O	SD	DEK	DEP	EK	TE	HY	D_{1+2}	D_{3+4}	DEPR
FLA			0.65			0.65		1.5	2.1	1.4
FKI	1.8	2.5				1.7	1.6	2.6	4.6	2.4
FO		1.1	1.2				1.2			
FR	2			1.8	1.7		1.9	1.4	2	2.2
FDesm	0.3	0.2	0.2	0.2	0.3	0.2	0.4			0.4
FEu					2.5		4	12	9	2.6
Cy species number					0.7			2.3	4	
Cy amount	1.3	1.3					1.2	1.5		2.2
Anabaena spp.	0.8	1.3				0.9	0.8			
Microcystis spp.	1.4	1.2					0.9			
Aphanizomenon, wide					0.6	0.7	0.5			
Aphanizomenon, narrow				1.5	2.2	1.6	2.4			
Planktothrix agardhii			1.5	1.6	1.2		2.4			
Limnothrix redekei			1.2	1.4	1.2		1.8			

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* FLA, number of phytoplankton species; FKI, compound index; FO, partial abundance; FR, number of chlorophyte species; FDesm, number of desmid species; FEu, number of euglenophytes; Cy, cyanophyte; D_{1+2}, dystrophic on mineral landscape; D_{3+4}, lakes in mires; DEPR, eutrophied dystrophic lakes; TE, typical eutrophic; EK, hard-water eutrophic; for other abbreviations see Table 1.

desmid species diminished in all our material 3.4 times, in different lake types from 2.5 to 5 times (Table 3); all changes are statistically confident.

Euglenophytes also underwent remarkable changes. The number of species increased 2.6 times in the whole material, 1.9 in the hard-water and 3.1 in the soft-water lakes. Drastic increases occurred in hypertrophic (4 times) and dystrophic lakes (about 10 times). Irrespective of such a notable increase, the number of species in dystrophic lakes was not big.

An abrupt increase in the abundance and distribution of the raphidophyte alga *Gonyostomum semen* (Ehrenberg) Diesing was registered in the 1980s and particularly in the 1990s. This alga was not registered in the earlier investigation period (may be it was overlooked). The species was quite numerous in some forest and bog dystrophic lakes at the beginning of the 1980s, forming a great biomass. At the beginning of the 1990s it was very abundant in dystrophic lakes. It was a dominant also in some semidystrophic, soft-water mixotrophic, and in two formerly oligotrophic lakes. Up to now *G. semen* has been found in 60 lakes, most of them belonging to bog and forest dystrophic or mixotrophic lakes. Figure 1 shows the connection of its distribution and biomass with tot-N and tot-P and their ratio. The biomass increases with the diminishing of the N : P ratio.

A considerable increase took place in the abundance and distribution of cryptomonads in all lake types. For example, the number of species increased 5.2 times and the abundance 4.2 times in the forest dystrophic lakes, and 8 and 4.2, respectively, in the bog dystrophic lakes (Table 3).

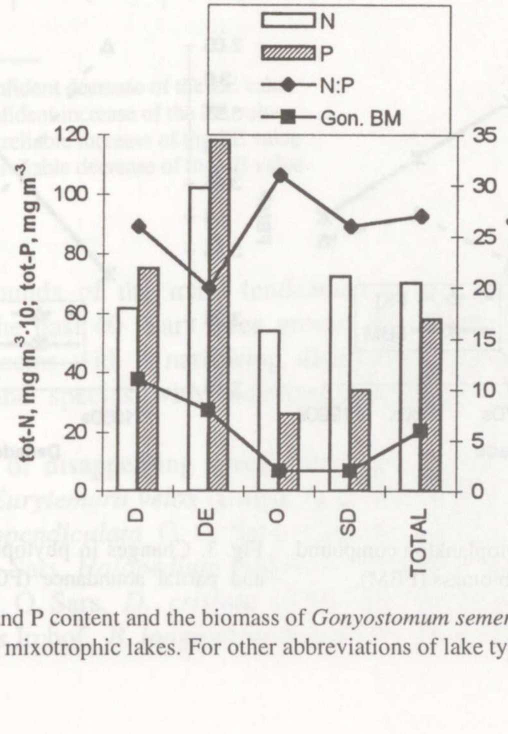

Fig. 1. Average N and P content and the biomass of *Gonyostomum semen* (Gon. BM) in different lake types. DE, mixotrophic lakes. For other abbreviations of lake types refer to Table 1.

The total number of phytoplankton species showed a downward trend almost in all lake types during the investigation period; however, the changes are reliable only in hard-water mixotrophic and typical eutrophic lakes. Nygaard's phytoplankton compound index (FKI), modified by Laugaste & Ott (1988), which indicates the ecological status, rose 1.9-fold in the total material; changes took place in almost all lake types. The rise is statistically confident in the whole material also by decades during the entire investigation period (Fig. 2).

The total abundance of phytoplankton (FBMP) had also a tendency to decrease in the 1980s (Fig. 3). However, considerable changes were revealed only in hard-water eutrophic lakes (0.91 times).

The partial abundance (FO) increased simultaneously with the fall of the total abundance of phytoplankton (Fig. 3). In spite of quite a strict range of fluctuations (1.2–3.5, most values 1.2–2.0 in our material), a considerable rise became evident in the total material, in the hard-water assembled group, hard-water mixotrophic, semidystrophic, and hypertrophic lakes (Table 3).

Data on **phytoplankton biomass** (Fig. 2) were available for the last 30 years only (in most cases 20 years). Both the average for decades and individual biomass values show a decreasing tendency, with the exception of some hypertrophic lakes, where *Planktothrix agardhii* or *Anabaena spiroides* prevailed. In the 1990s biomass increased also in the lakes where *Gonyostomum semen* predominated.

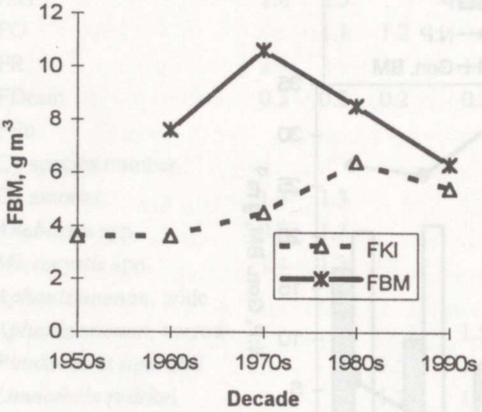

Fig. 2. Changes in phytoplankton compound index (FKI) and biomass (FBM).

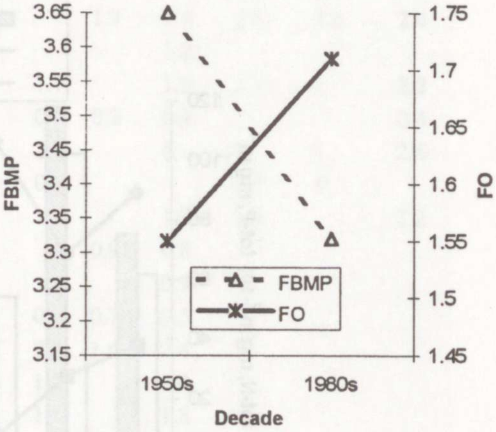

Fig. 3. Changes in phytoplankton total (FBMP) and partial abundance (FO) in hard-water lakes.

3.3. Zooplankton

Species composition. Although all the found zooplankton taxa were included into the quantitative calculations, only the dynamics of 33 pelagial crustacean taxa and the occurrence of the larvae of *Dreissena* and *Chaoborus* were studied thoroughly. According to the zooplankton eutrophy index (ZE), the ecological state of the lakes rose continuously from the 1950s up to the 1980s (Table 4) and dropped at the beginning of the 1990s. Impoverishment of the crustacean fauna, particularly a fall in the number of the species of cladocerans, was noticeable during the period under study.

Table 4

Dynamics of zooplankton eutrophy index by decades according to the statistical model (A. Mäemets, T. Möls & H. Starast, unpublished data)*

Decade	1950s	1960s	1970s	1980s	1990s
1960s	↓				
1970s	↑	↑			
1980s	↑	↑	↑		
1990s	+	↑	+	–	
2000s	↓	↓	↓	↓	↓

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* ↓ statistically confident decrease of the ZE value
↑ statistically confident increase of the ZE value
+ statistically nonreliable increase of the ZE value
– statistically nonreliable decrease of the ZE value

On the grounds of the main tendencies in the dynamics of zooplankton species over the past 40 years three groups can be distinguished: disappearing species (or species with a narrowing distribution), species with an expanding distribution, and species with indistinct changes in distribution (indifferent species).

The group of disappearing species includes 22 taxa: *Eudiaptomus gracilis* (G. O. Sars), *Eurytemora velox* (Lillj.), *E. lacustris* (Poppe), *Heterocope saliens* (Lillj.), *H. appendiculata* G. O. Sars, *Cyclops scutifer* G. O. Sars, *Limnosida frontosa* G. O. Sars, *Holopedium gibberum* Zaddach, *Daphnia hyalina* (Leydig), *D. galeata* G. O. Sars, *D. cristata* G. O. Sars, *Bosmina longispina* (Leydig), *B. berolinensis* Imhof, *B. longicornis* Schoedler, *B. insignis* Lillj., *B. lilljeborgi*

G. O. Sars, *B. gibbera* Schoedler, *B. thersites* Poppe, *B. crassicornis* Lillj., *Bythotrephes longimanus* Leydig, *B. cederstroemi* Lillj., and *Ophryoxus gracilis* G. O. Sars. The most expressive one is the oligo-mesotrophic species *Heterocope appendiculata* (Fig. 4) with the maximum abundance and frequency of occurrence in the 1950s (in 37% of the investigated lakes). The amount of this species revealed a positive correlation with water transparency ($r = 0.25$). *Holopedium gibberum* disappeared from numerous lakes where it had occurred in the 1950s–60s (Fig. 4), and its abundance decreased in many others. It is surprising that this species reappeared in some lakes during the last decade (Viitna Pikkjärv and others). Its occurrence is obviously related to the pH value of the water (Tauson, 1932; Mäemets, 1961), and the upper limit of its survival is about pH 7.4–7.6.

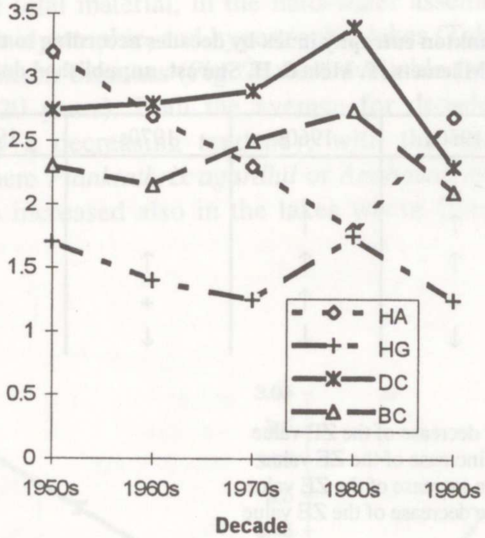

Fig. 4. Changes in the abundance of *Heterocope appendiculata* (HA), *Holopedium gibberum* (HG), *Daphnia cucullata* (DC), and *Bosmina coregoni* (BC).

Eight taxa expanded their distribution: *Cyclops vicinus* Uljanin, *Mesocyclops crassus* (Fischer), *Daphnia cucullata* G. O. Sars (Fig. 4), *Bosmina longirostris* (O. F. Müller), partially also *B. coregoni* (Baird) (Fig. 4), *Leptodora kindti* (Focke), the larvae of *Chaoborus* and *Dreissena*.

Five species were more or less indifferent: *Cyclops kolensis* Lillj., *Mesocyclops oithonoides* (G. O. Sars), *Diaphanosoma brachyurum* (Lieven), *Daphnia longispina* (O. F. Müller), and partially even *Chydorus sphaericus* (O. F. Müller). The last species prefers lakes that are rich in detritus and phytoplankton and belongs thus to the eutrophic group (ME species, Mäemets, 1991).

The character of zooplankton **communities** and the direction of changes in lakes are determined by the trends in the occurrence of different species. The introduction experiments made in 1969–71 on eight lakes with about ten zooplankton species showed that the composition of the communities is not occasional but determined by several factors: a positive result was obtained only in one coastal lake with unsaturated fauna – in mixotrophic Veskijärv, where *Daphnia cucullata* was introduced successfully (Mäemets, 1969). Zooplankton communities of Estonian lakes have been discussed in some other publications (Mäemets, 1958, 1971). The communities have been denominated according to the leading species with a certain trophic inclination. The communities with *Holopedium gibberum, Cyclops scutifer*, and *Heterocope appendiculata* and other oligo-mesotrophic species dominating are disappearing in Estonian lakes, despite the usual stability of species composition of summer zooplankton.

The **number of individuals** (ZA) and **biomass** (ZB) fluctuated within a very large range during the vegetation period. In some lakes the amount of zooplankton was negligible, for example in alkalitrophic L. Äntu Sinijärv (ZA 0.35×10^3 ind. m^{-3}, ZB 0.0006 g m^{-3} in May 1992). However, the polluted mixotrophic karst L. Savalduma (ZA 1330×10^3 ind. m^{-3}, ZB 67.4 g m^{-3} in July 1988) was quite the opposite.

During the period under study the dynamics of zooplankton showed the maximum number of individuals and biomass in the 1970s (Fig. 5). The highest ratio between ZA and ZB was observed in the 1970s, which means that the average size of zooplankton was the smallest in that decade. Some changes were noticed in the proportion of copepods, cladocerans, rotifers, and *Chaoborus* larvae in ZA. The share of copepods was the greatest in the 1950s and the 1980s, cladocerans in the 1950s and the 1990s, rotifers in the 1960s, and larvae of *Chaoborus* in the 1990s.

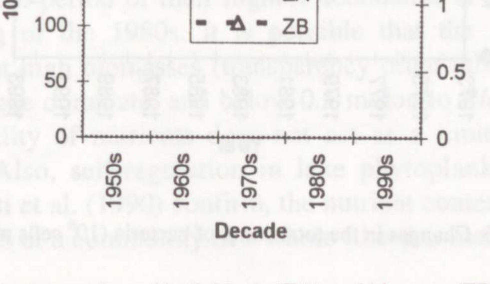

Fig. 5. Changes in the number of individuals (ZA) and biomass (ZB) of zooplankton.

4. DISCUSSION

4.1. Bacterioplankton

Investigation of long-time dynamics of TC and PC in the surface and bottom layers of water revealed that the abundance of bacteria had been significantly higher in the 1970s than in the 1990s (Fig. 6). The average values of TC in the surface layer of water had negative correlations with the amount of summer precipitation (Spearman's $r = -0.44$, $p < 0.05$). However, saprophytic bacteria did not reveal statistical correlations with climatic factors (precipitation, temperature). The average PC had a correlation with the total amount of fertilizers applied the year before.

TC of bacteria decreased in 1973–93. This might be connected with long-term changes in the climate – in the Tartu region the average air temperature rose by 0.65 °C in 1955–89, in summer the increase was even 2.5 °C, and the amount of precipitation increased as well (Ross, 1990; Ross & Russak, 1991). When the weather becomes warmer, species that prefer hypertrophic conditions (including blue-green algae) will dominate among phytoplankton. Such species can emit bactericidal substances and compete in using nutrient elements. On the other hand, in comparison with the other part of plankton, blue-green algae excrete into water significantly less extracellular substances, which are a suitable substrate for pelagic bacteria (Bell & Tranvik, 1993). When cyanobacteria dominate in phytoplankton, a simultaneous decrease of TC is noticed. The

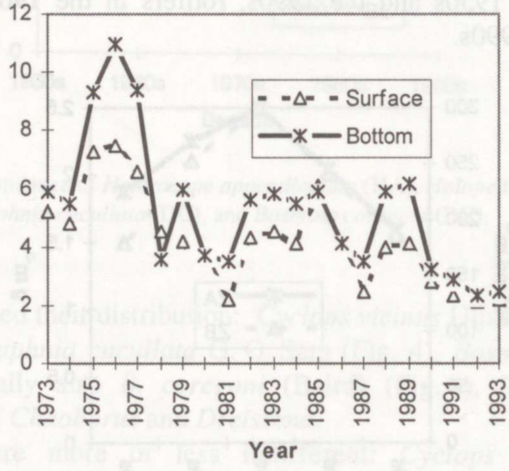

Fig. 6. Changes in the total count of bacteria (10^6 cells ml^{-1}).

abundance and dynamics of bacterioplankton might be influenced by these factors or there might exist the dilution effect due to the increasing of precipitation (see below).

4.2. Phytoplankton

A trend towards the eutrophication of lakes was evident, but problems concerning its course and ways need further investigation. Changes proceeded in different ways in different lake types. The resistance of lakes to human impact depends upon the morphometrical features and the character of the buffering system, that is, the content and ratio of mineral and organic substances in the water. An interesting problem is the alternation of algal groups and their dependence on lake type. A most widespread and classical succession line – desmids–chrysophytes–diatoms–cyanophytes – is common in large, well-mixed lakes, which have been the main long-time object of research in all countries. Such lakes have a balanced, well-buffered ecosystem and quite a slow process of eutrophication. Small lakes and ponds lose more easily their balance, and many of them had reached the hypertrophic level with a very high amount of nutrients; succession of phytoplankton communities may be quite different, depending on the buffering system and the type of pollution.

The increasing role of green algae, and even their prevalence in the hypertrophic stage, were referred to by Heinonen (1980) and Mikheeva (1984). According to Shapiro (1984), green algae thrive if pH decreases and the amount of CO_2 increases. Numerous studies confirm the importance of the N and P ratio. Schindler (1977) notes that the bloom of cyanophytes takes place at N : P below 5. Different findings about the optimum N : P for different algal groups have been published. However, all the authors confirm that green algae demand more N than most others. Mantere and Heinonen (1982) connect the dominance of the group of *Protococcales* with a high abundance of available forms of N. According to our material, the prevalence of green algae is evidently not associated with a particularly high N content. The dominant blue-green species seem to demand more N than green algae. Unfortunately, we do not have sufficient information on nutrients in the lakes where the green algae predominate, particularly from the period of their highest abundance at the end of the 1970s and the beginning of the 1980s. It is possible that the light limitation is a disturbing factor at high biomasses (transparency often falls below 0.8 m when the small green algae dominate, and below 0.5 m due to *Planktothrix agardhii*), while the availability of nutrients does not act as a limiting factor in highly eutrophic lakes. Also, self-regulation in lake phytoplankton communities is possible. As Agusti et al. (1990) confirm, the nutrient content does not affect the principal characters of a community as a whole (the non-nutrient constraint).

In the lakes studied, both blue-green and green algae can dominate in a moderately but also in a totally distorted lake ecosystem. It remains unclear whether the dominance of these groups follows the gradient of eutrophication or whether they constitute two different ways in the natural development of lakes. Our findings suggest that besides the nutrient content some other factors are essential.

In some lakes, however, the alternation of dominant species was evidently connected with the increasing and subsequently decreasing trophic state, where green algae were dominant in the period of the highest degree of trophy. Earlier statistical relations with dissolved organic matter were found in such cases (Ott, 1996).

The falling abundance and species number of desmids are a universal phenomenon in Estonian lakes, even in the bog and forest ones without an evident human impact. Heinonen (1980) reported an increased abundance and species diversity of desmids in Finnish lakes during eutrophication, although the relative abundance of this group (% of the biomass) decreased. He states that the greatest number and abundance of desmid species are observed in lakes with the phytoplankton biomass over 10 g m^{-3}, the smallest numbers occur in oligo- and ultraoligotrophic waters. Thus, eutrophied oligotrophic and semidystrophic and also soft-water eutrophic lakes should be the most favourable habitats for desmids. However, our material did not confirm this. The disappearance of desmids from plankton can be connected with an increase of the sulphate content (Fig. 7). They may be affected through the air. The same is valid also for *Gonyostomum* sp., whose increasing abundance and widening distribution are not only due to an increase of the nutrient and organic matter supply but also to some other factors

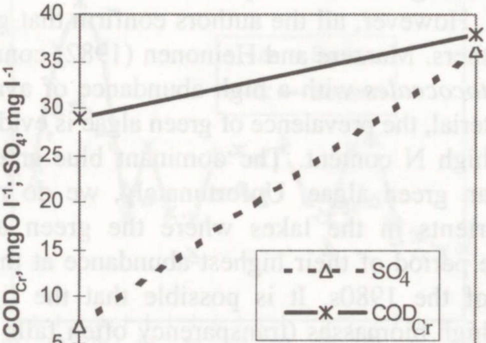

Fig. 7. Changes in chemical oxygen demand (COD$_{Cr}$) and sulphate concentration (SO$_4$) in the water.

that are connected with air pollution. The widening distribution of cryptomonads is evidently connected with the increasing organic matter content (Fig. 7), common in Estonian lake waters. The strengthening of stratification and the enlargement of hypolimnion in lakes during the last decades was one of the factors that caused the increase in the abundance of green and euglenoid algae.

4.3. Zooplankton

The maximum amount of zooplankton in the 1970s and 1980s was obviously connected with the relatively warm and poor in precipitation period in the first half of the 1970s (Figs. 8, 9) and with the maximum nutrient and pollution loads in the 1980s (Fig. 10). A big zooplankton biomass was observed also in L. Peipsi in the 1970s (Mäemets & Timm, 1990). The very high ratio of zooplankton number and biomass over this period must have been connected both with the strong pressure of fish and a high trophic state. Abiotic factors and the amount of food suitable for zooplankton (bacteria, algae) also played an important role. Usually, together with increasing eutrophy, species with a larger size are replaced by smaller ones, in some cases even the dimensions of the same species diminish (Mäemets, 1991). The number of zooplankton individuals falls abruptly in a very high trophic state (e.g. in L. Laose Valgjärv in 1988). In some hypertrophic lakes rotifers can disappear altogether (L. Ülemiste in June 1990,

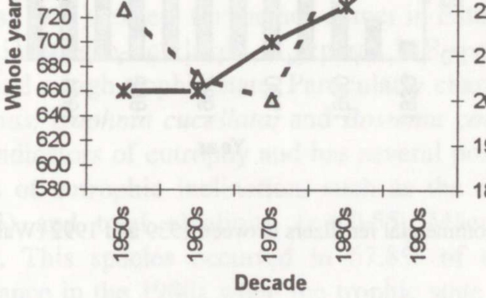

Fig. 8. Precipitation (mmHg) in 1951–91 in Estonia.

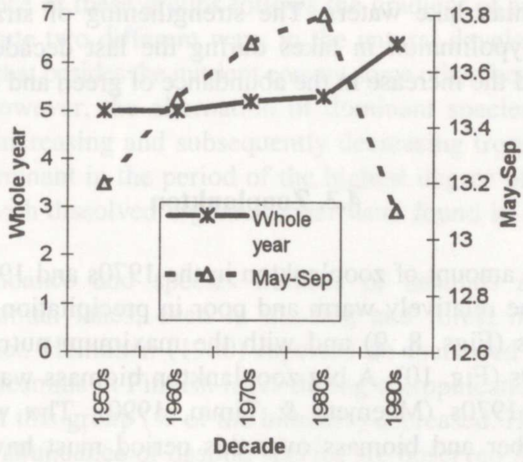

Fig. 9. Air temperature (°C) in 1951–91 in Estonia.

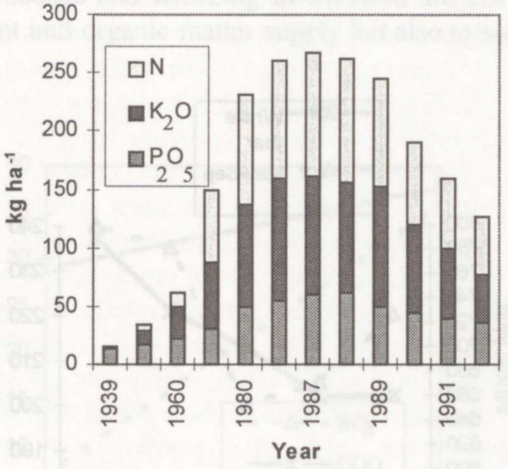

Fig. 10. Consumption of commercial fertilizers between 1939 and 1992 (Water pollution..., 1993).

L. Uljaste in July 1993, before fish kill). The average zooplankton amount and biomass ratio of the 205 lakes studied was more likely related to the dynamics of the trophic state than to the pressure of fish, as the abundance of fish fluctuates more dynamically. A joint effect of both factors is also possible, as many consumers of larger zooplankton like fry can perish altogether if the trophic level rises too high.

The role of zooplankton groups was different by decades. The dynamics of rotifers was somewhat peculiar and unexpected: in the 1980s when the trophic state of the lakes was high, the abundance of rotifers fell. The statement in the literature about an increase in the abundance of rotifers with an increasing trophic state (Haberman, 1984; a.o.) is valid only in the case of moderate eutrophication. On the other hand, the dynamics of *Chaoborus* larvae is thoroughly explicable with permanent deterioration of the oxygen regime in the hypolimnion of our lakes. It did not improve even during the decrease of the trophic state in the epilimnion in the 1990s.

Some correlations became evident between zooplankton parameters and hydrochemical characteristics. The abundance of copepods showed statistical relations with environmental parameters like pH, alkalinity, and the content of organic substances. The cladoceran group did not exhibit any correlations with ecological characteristics, but rotifers showed several statistically reliable connections both with biotic and abiotic parameters. The rotifers are antagonists to the other two zooplankton groups; the immediate affecting factors, however, remain unclear. The number of rotifer individuals was statistically connected with the amount of organic substances in our earlier material as well (with COD_{Cr} $r = 0.53$; Mäemets & Lokk, 1982).

The group of disappearing species includes mainly taxa that favour oligo- and mesotrophic waters (OM species; Mäemets, 1991). Some of them expanded their abundance and distribution in the 1990s thanks to the improvement of the state of the epilimnion of lakes although they have disappeared from part of the lakes (e.g. *Eurytemora lacustris* from L. Vagula). The group of species with an expanding distribution includes the taxa of meso- and eutrophic waters (ME species; Mäemets, 1991), except for the newcomer in Estonian fauna, *Dreissena*, who settles only in oxygen-rich lakes. In general, ME species can survive a low oxygen content and a high trophic state. Particularly characteristic of this group are *Cyclops vicinus, Daphnia cucullata,* and *Bosmina coregoni*. *D. cucullata* is one of the best indicators of eutrophy and has several positive correlations with other parameters of eutrophic inclination, such as the number of macrophyte species ($r = 0.43$) and total alkalinity ($r = 0.55$; Mäemets, 1980; Tevet & Mäemets, 1985). This species occurred in 67.8% of the lakes and had its maximum abundance in the 1980s when the trophic state of Estonian lakes was the highest (Mäemets & Ott, 1993).

Similar tendencies in the dynamics of several zooplankton species were described by Pejler (1975) in Swedish lakes: from 1921 the tendency to disappear has been revealed by *Holopedium gibberum* and obviously by *Bythotrephes longimanus, Eurytemora velox,* and *Heterocope appendiculata*; the expanding species are *Daphnia cucullata, Ceriodaphnia quadrangula, Bosmina longirostris*, and *Chydorus sphaericus*.

The zooplankton eutrophy index (ZE) reflects the ecological state of the lake. This is confirmed by a close correlation with the content of total P, N, K, and Na and some other parameters (Mäemets & Lokk, 1982). This index suggests that substantial changes took place in about 50% of the lakes during 40 years. On the basis of species composition one can resume that Estonian lakes were most heavily polluted in the 1980s: a certain improvement has become evident in the last decade due to the decreasing load of agricultural pollution. The OM species *Heterocope appendiculata* is the best example of zooplankton dynamics in Estonian lakes: its abundance was very low in the 1980s, but it is showing some increase now (Mäemets & Ott, 1993).

The general trend of our lakes has been an accelerating eutrophication, reflected in the rise of zooplankton abundance in the 1970s, in the changes of species composition, and a decrease in the diversity of crustacean fauna in the later period. Pejler (1975) described the same tendencies for zooplankton in Swedish lakes.

4.4. General influence of climatic conditions and human impact

Phytoplankton compound (FKI, Fig. 2) and ZE indices (Table 4) give information about the ecological status of a water body. Figures 8–10 show the dynamics of precipitation, air temperature (data from seven Estonian hydrometeorological stations), and the amount of fertilizers (data from the Estonian Central Board of Statistics; Water pollution..., 1993) for the same period. Generally, the ecological state seems to be affected first of all by the amount of fertilizers applied. Similarly to the dynamics of ZE and FKI, also the dynamics of air temperature from May to September is presented for the period under study. This means that we cannot distinguish the influence of fertilizers and temperature.

The dynamics of precipitation is different from that of the amounts of fertilizers and air temperature from May to September. Generally, the weather became constantly warmer with more precipitation during the investigated period. The curves of the measured plankton values, like these of phytoplankton biomass and the total count of bacteria, seem to be similar to the dynamics of precipitation (Figs. 2, 6, 8): the more precipitation, the less plankton. The same situation was noted also in L. Võrtsjärv from 1973 up to the 1990s when TC and FBM values showed a falling tendency (P. Nõges, unpublished data). Here we can take into account the effect of dilution.

Some contradiction exists between the dynamics of the amount of plankton and the values of the indices of ecological state. The highest plankton amounts were determined in the 1970s, whereas the highest ecological state values occurred in the 1980s. This lag may be due to the fact that the ecological state indices include information on aeration conditions, pH, organic compounds, stratification, light, diversity of species, biomass of the hydrobionts, etc. Generally, these parameters describe the efficiency of matter circulation and living conditions in the lake. The amount of plankton depends directly on the abiotic properties of water, like, for instance, the content of nutrient and organic compounds. Response of the ecosystem to the changed trophic conditions, expressed, for example, in the species composition, will take time. Therefore, indices of the ecological state were on the highest level in the 1980s.

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REFERENCES

Agusti, S., Duarte, C. M. & Canfield, D. E., Jr. 1990. Phytoplankton abundance in Florida lakes. Evidence for the frequent lack of nutrient limitation. *Limnol. Oceanogr.*, **35,** 1, 181–188.

Bailey-Watts, A. E., Kirika, A., May, L. & Jones, D. H. 1990. Changes in phytoplankton over various time scales in a shallow, eutrophic loch: The Loch Leven experience with special reference to the influence of flushing rate. *Freshwater Biol.*, **23**, 85–111.

Bell, R. T. & Tranvik, L. 1993. Impact of acidification and liming on the microbial ecology of lakes. *Ambio*, **22**, 5, 325–330.

Gorlenko, V. M. & Lokk, S. J. 1979. Vertical distribution and special composition of microorganisms from some stratified Estonian lakes. *Mikrobiologiya*, **2**, 351–359 (in Russian).

Haberman, J. 1984. Zooplankton of Lake Võrtsjärv in 1964–1982. In *State of Ecosystem of Lake Võrtsjärv*. Academy of Sciences of the Estonian SSR, Tartu, 65–78.

Heinonen, P. 1980. Quantity and composition of phytoplankton in Finnish inland waters. *Publ. Water Res. Inst.*, **37**. Helsinki.

Laugaste, R. & Ott, I. 1988. Changes in phytoplankton of Estonian soft-water lakes during the last 20–30 years. In *Dynamics and Ecology of Wetlands and Lakes in Estonia*. Academy of Sciences of the Estonian SSR, Tallinn, 155–166.

Lokk, S. 1982. Mikrobioloogilistest näitajatest erineva troofsustasemega järvedes. In *Eesti NSV järvede nüüdisseisund*. Eesti NSV Teaduste Akadeemia, Tartu, 65–74.

Mantere, R. & Heinonen, P. 1982. The quantity and composition of phytoplankton, particularly *Chlorophyta*, in lakes of different trophic levels. *Publ. Water Res. Inst.*, **49**. Helsinki, 58–63.

Mikheeva, T. M. 1984. Eutrofication of water bodies and domination of phytoplankton species. In *Limnologiya gornykh vodoemov. Tez. vsesoyuzn. soveshch.* Sevan, Jerevan, 170–171 (in Russian).

Morling, G. & Willen, T. 1990. Acidification and phytoplankton development in some West-Swedish lakes 1966–1983. *Limnologica* (Berlin), **20**, 2, 291–306.

Mäemets, A. 1958. About the quality composition of *Crustacean*-fauna of the summer zooplankton of Estonian lakes. *Hydrobiol. Res.* (Tartu), **1**, 104–134 (in Russian).

Mäemets, A. 1961. Eesti vesikirbuliste (Cladocera) ökoloogiast ja fenoloogiast. In *Hüdrobioloogilised uurimused*, **2**, 108–158.

Mäemets, A. A. 1966. On the abundance of bacteria in the water of Lake Peipsi-Pskov. In *Hydrobiol. Res.*, 4. Academy of Sciences of the Estonian SSR, Tallinn, 43–48 (in Russian).

Mäemets, A. 1969. On the introduction of *Daphnia cucullata* G. O. Sars (*Crustacea, Cladocera*) into Lake Veskijärv. In *Year-book of the Estonian Naturalists Society*, **60**, 58–66.

Mäemets, A. 1974. On Estonian lake types and main trends of their evolution. In *Estonian Wetlands and Their Life*. Academy of Sciences of the Estonian SSR, Tallinn, 29–62.

Mäemets, A. 1976. Lake types as basis for the limnological division of the Estonian S.S.R. In *Estonian Regional Studies*. Tallinn, 63–70.

Mäemets, A. 1977. *Eesti NSV järved ja nende kaitse.* Valgus, Tallinn.

Mäemets, A. 1980. Correlations of Estonian lakes. *Hydrobiol. Res.* (Tartu), **9**, 59–68 (in Russian).

Mäemets, A. 1991. Zooplankton. In *Sostoyanie myagkovodnykh ozer*. Estonian Academy of Sciences, Institute of Zoology and Botany, Tartu, 156–200 (in Russian).

Mäemets, Aime & Mäemets, Aare. 1976. Neeruti järved. In *Loodusuurijate Seltsi Aastaraamat*, **64**. Valgus, Tallinn, 92–136.

Mäemets, A. & Lokk, S. 1982. Eutrofeerumise otsesest ja kaudsest seosest järvede ökosüsteemi parameetritega. In *Eesti NSV järvede nüüdisseisund.* Eesti NSV Teaduste Akadeemia, Tartu, 142–150.

Mäemets, A. & Ott, I. 1993. The state of lakes. Small lakes. In *Water Pollution and Quality in Estonia. Environmental Report*, 7. Helsinki, 35–38.

Mäemets, A. & Timm, M. 1990. Peipsi zooplanktonis aastail 1909–1987 toimunud muutused. In *Peipsi järve seisund.* Eesti Teaduste Akadeemia, Tartu, 107–110.

Ojaveer, H., Lokk, S. & Nõges, T. 1993. Microbiological status of some Estonian small lakes. *Proc. Estonian Acad. Sci. Ecol.*, **3**, 2, 53–64.

Ott, I. 1987. The structure of the phytoplankton as indicator of durability in different water ecosystems. In *Tez. XXII konf. po izuch. vodoemov Pribaltiki.* Pribaltijskoe basseinovoe otdelenie ikhtiologicheskoj komissii MRKH SSSR, Vilnius, 140–141 (in Russian).

Ott, I. 1996. Relationship between organic matter and summer phytoplankton species composition. Eutrophication in planktonic food web dynamics and elemental cycling. In *International PELAG Symposium*. Finnish Environment Institute, Helsinki, 54.

Pejler, B. 1975. *On Long-Term Stability of Zooplankton Composition.* Inst. Fresh. Res., Drottningholm, Report No. 54, 107–117.

Reynolds, C. S. & Bellinger, E. G. 1992. Patterns of abundance and dominance of the phytoplankton of Rostherne Mere, England: Evidence from an 18-year data set. *Aquat. Sci.*, **54**, 1, 10–36.

Ross, J. (ed.). 1990. *Tartu kliima ja selle muutumine viimastel kümnenditel*. Tartu.

Ross, J. & Russak, V. 1991. Eesti kiirguskliima muutumine aastail 1950–1990 ja selle võimalikud ökoloogilised tagajärjed. In *Kaasaegse ökoloogia probleemid. Eesti V ökol. konv. teesid.* Tartu, 151–152.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. *Science*, **195**, 4275, 260–262.

Shapiro, J. 1984. Blue-green dominance in lakes: The role and management significance of pH and CO_2. *Int. Revue ges. Hydrobiol.*, **69**, 6, 765–780.

Talling, J. F. 1993. Comparative seasonal changes, and inter-annual variability and stability, in a 26 year record of total phytoplankton biomass in four English lake basins. *Hydrobiologia*, **268**, 65–98.

Tauson, A. 1932. Die Abhängikeit der Verbreitung von *Holopedium gibberum* Zadd. von einigen Faktoren des äusseren Mediums. *Arch. Entw.*, 123.

Tevet, J. T. & Mäemets, A. 1985. Isoquanta and structure of interrelations between lake characteristics obtained by their means. *Proc. Acad. Sci. Estonian SSR. Biol.*, **34**, 2, 94–111.

Water pollution and quality in Estonia. 1993. Environmental Report, 7. Helsinki.

MUUTUSED EESTI VÄIKEJÄRVEDE PLANKTONIS AASTAIL 1951–1993

Ingmar OTT, Reet LAUGASTE, Saida LOKK ja Aare MÄEMETS

On uuritud planktonis toimunud muutusi ja hinnatud kliimafaktorite toimet ning inimmõju järvede troofsusseisundi dünaamikale. Planktoni hulk on järvedes alates 1970. aastatest vähenenud. Hüpertroofsetes järvedes on bakterite üldarvukus kasvanud. Kihistumata järvedes on ökoloogiline režiim halvenenud: bakterite koosluste struktuur on põhjalähedases veekihis muutunud või bakterite asustustihedus kogu veesambas suurenenud. Kihistunud järvedes avaldub sama nähtus mikroaerofiilsete ja anaeroobsete bakterite suuremas levikus. Füto- ja zooplanktonis on toimunud suhteliselt ulatuslik liigilise koosseisu vahetumine, kusjuures iseloomulik on suuremõõtmeliste liikide asendumine väikestega. Planktoni koguse vähenemine on seotud sademete hulga kasvuga samal perioodil: toimib lahjendusefekt. Veekogude ökoloogiline seisund kui biogeenide eelneva pikaajalise koormuse peegeldus on olnud halvim 1980. aastatel.