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MICROBIAL STATUS OF SOME ESTONIAN SMALL LAKES

Abstract. Total count of bacteria, the incorporation of [methyl-^{3}H] thymidine into the ice-cold trichloroacetic acid insoluble material as a measure of bacterial heterotrophic activity, and the number of saprophytic bacteria, growing on fish peptonic agar, were measured during the complex investigations of 29 Estonian small lakes in summer 1990. Bacterial total number fluctuated from low to very high (from $0.8 \cdot 10^6$ to $12.2 \cdot 10^6$ cells $\cdot$ ml^{-1}), the mean value was $3.1 \cdot 10^6$ cells $\cdot$ ml^{-1}1. Bacterial heterotrophic activity varied from $2.2 \cdot 10^{-12}$ to $234.7 \cdot 10^{-12}$ (mean $23.3 \cdot 10^{-12}$) molTdR $\cdot$l^{-1}h^{-1}, the number of saprophytic bacteria ranged between 210 to 4700 (mean 940) cells $\cdot$ ml^{-1}. The total count of bacteria and their heterotrophic activity in oligotrophic and mesotrophic lakes were lower than in eutrophic and hypertrophic lakes. However, this difference was statistically significant only for the total count of bacteria (t-test, $p<0.05$). Bacterial abundance in the subsurface water was lower than in the near-bottom water layer (t-test, $p<0.05$), contrarily to the values of the bacterial heterotrophic activity. Total count of bacteria correlated with the five-day biochemical oxygen demand ($r=0.91$; $p<0.001$) in the subsurface water of eutrophic and hypertrophic lakes and with the chlorophyll *a* concentration ($r=0.81$; $p<0.001$) in the near-bottom water layer. Bacterial heterotrophic activity correlated with the total number of bacteria ($r=0.72$; $p=0.04$) in subsurface water of oligo- and mesotrophic lakes.

In 17 lakes studied repeatedly the mean bacterioplankton abundance has decreased 1.4 times and the mean number of saprophytic bacteria increased 3.1 times as compared to the 1970s and 1980s.

Key words: bacterial abundance, heterotrophic activity, small lakes.

Introduction

Bacteria are the most important heterotrophs in aquatic habitats. The overall result of bacterial heterotrophic activity is decomposition (or mineralization) of organic matter and nutrient regeneration. The organic substrates used by heterotrophic bacteria originate mostly from algae and plants. However, in waterbodies which are under substantial human impact compounds of allochthonic origin are also used by bacteria. The distribution of bacteria, and consequently the activity of mineralization and recycling processes, are mainly influenced by water temperature and oxygen regime. Measurements of bacterial abundance and activity are therefore necessary in studies on aquatic microbial ecology. On the other hand, these parameters are useful tools for estimating the trophic status of a waterbody.

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Most aquatic bacteria (more than 99%) cannot grow on nutrient agar (Colewell et al., 1985). Of the remaining total bacterial population less than 1% plays an important role inactivating pathogenic micro-organisms due to their competitive and antagonistic relations in the metabolic processes and also destructing easily utilizable organic matter as a main substrate. Saprobes, requiring high substrate concentration for growth, react very quickly to substrate concentration changes, caused by termination of plant or animal development cycle or pollution impact. The number of saprophytic bacteria and especially the ratio of bacterial total count to the number of saprophytic bacteria serve as indicators of water pollution with easily decomposing organic matter and water quality (Юрковска, 1990; Veeobjektide . . . , 1985).

The purposes of the present study were to estimate the status of Estonian small lakes by means of some microbiological characteristics, to estimate long-term changes that have taken place in the lakes during the recent 10 to 20 years, and to find out the ecological factors exerting the main influence upon the bacterial abundance and activity.

Materials and Methods

Water samples were collected from 29 Estonian small lakes (Fig. 1) during June and July 1990. All sampling was performed in the deepest part of the lakes and two water samples were taken from each lake — from subsurface and near-bottom layers. From shallow Lake Kirikumäe only the subsurface water sample was taken. To assess long-term changes having taken place in lake ecosystems, the microbiological data from the 1970s and 1980s were used. Bacterial total count (TC) was measured by carbolerythrosine staining (5% erythrosine solution in 5% phenol) with Synpor 8 membrane filters (pore size 0.23 μm). The filters were inspected at a magnification 1050 under a MBI-15 microscope in 20 random fields (Методические . . . , 1982).

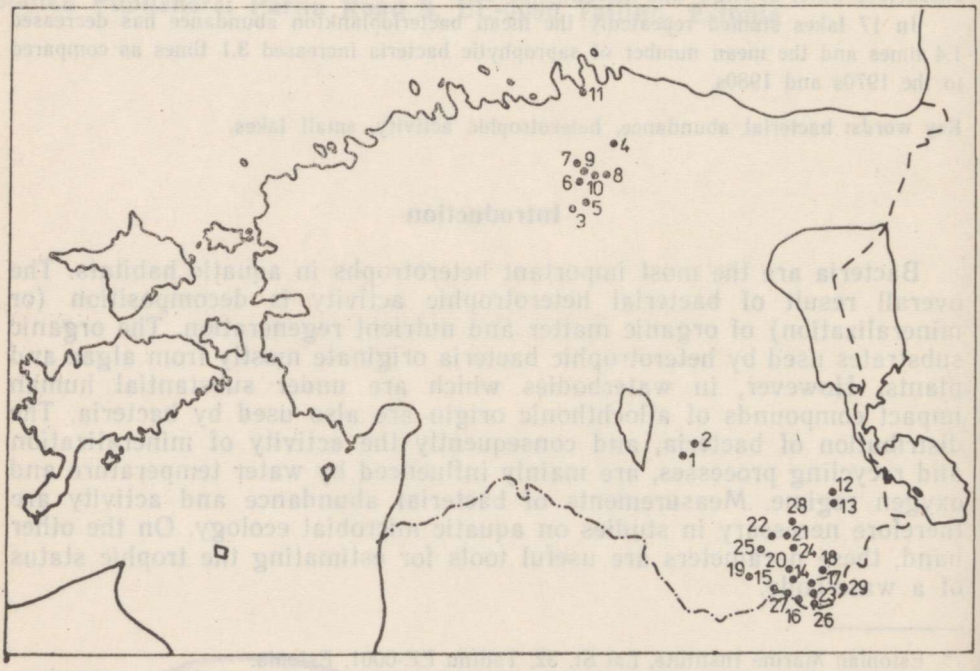

Fig. 1. Location of the studied lakes (numbers as in Table 1).

Table 1

General data on the lakes studied

No	Lake	Area, m	Maximum depth, m	Secchi depth, m	Stratification *		Trophic index**
					temp.	O_2	
1	Otepää Pikajärv	9.3	23.0	1.3	S	S	E7
2	Otepää Valgjärv	64.6	5.5	1.0—1.4	A	A	E5/E7
3	Jäneda Kalijärv	3.8	9.1	1.2	S	S	E6
4	Viitna Pikkjärv	16.3	6.2	3.6—6.0	W	W	O3
5	Ännijärv	11.1	9.0	2.4	S	S	O3/E1
6	Veinjärv	5.5	4.2	2.9—3.3	A	S	E5
7	Paukjärv	8.6	11.0	4.1—6.2	S	S	O2/O4
8	Jussi Suurjärv	20.1	5.7	2.9—3.1	S	S	E5
9	Jussi Linajärv	5.8	9.7	1.9	S	S	O3
10	Jussi Pikajärv	6.1	9.7	2.0—2.5	S	S	O3
11	Lohja	56.8	3.7	0.5	A	S	DE2
12	Nohipalu Valgjärv	6.3	11.7	3.5	S	S	O3
13	Nohipalu Mustjärv	22.0	8.9	0.4—1.0	S	S	D2
14	Ruusmäe	3.9	11.6	0.25	S	S	E7
15	Palkna	45.0	32.0	4.0—8.0	S	S	O3
16	Murati	66.6	4.3	1.0—1.7	A	A	DE4/SD4
17	Kise	48.9	5.9	2.0—3.1	W	W	O4
18	Kirikumäe	61.4	3.5	1.0—2.0	A	A	SD4
19	Palujüri	6.9	15.0	2.3—2.8	S	S	SD3
20	Plaani Külajärv	20.0	5.0	2.1—2.6	W	W	DE4/SD4
21	Vaikjärv	9.8	15.0	1.9—2.7	S	S	SD1
22	Kurgjärv	10.5	9.1	2.7—2.9	S	S	SD3
23	Pullijärv	61.7	7.1	2.4—3.0	W	W	O4
24	Vaskna	25.0	10.0	1.8—3.3	W	W	SD4
25	Vihtla	6.0	11.8	2.5—4.0	S	S	SD3
26	Hino	198.8	10.4	1.7—4.2	S	S	E4
27	Majori	15.0	11.8	1.8—2.1	S	S	E6
28	Kavadi	27.4	8.2	2.5—3.0	S	S	E1
29	Pabra	96.9	3.6	2.4—2.7	A	A	E2

* S — strong, W — weak, A — absent.

** Mäemets, 1974.

O2 — unstratified oligotrophic lake,
O3 — stratified eutrophicated oligotrophic lake,
O4 — unstratified eutrophicated oligotrophic lake,
SD1 — stratified semidystrophic lake,
SD3 — stratified eutrophicated semidystrophic lake,
SD4 — unstratified eutrophicated semidystrophic lake,
D2 — stratified dystrophic lake,
E1 — stratified softwater eutrophic lake,
E2 — unstratified softwater eutrophic lake,
E4 — unstratified hardwater eutrophic lake of mesotrophic character,
E5 — unstratified hardwater eutrophic lake,
E6 — stratified eutrophic lake,
E7 — hardwater hypertrophic lake,
DE2 — unstratified softwater dyseutrophic lake,
DE4 — unstratified hardwater dyseutrophic lake.

The number of saprophytic bacteria was determined as plate counts on fish peptonic agar (PC), inoculating 0.5 to 1.0 ml of water sample into one Petri dish. The dishes were hold at room temperature and colonies were counted on the 5th and 7th day after inoculation.

For the evaluation of the role of saprophytic bacteria in various lakes, the coefficient K (the relation of bacterial total count to the number of saprophytic bacteria) was calculated by the formula:

$$K = TC/PC.$$

Bacterial heterotrophic activity (BHA) was estimated by a modified [^{3}H]TdR method. Triplicate water samples (5 ml) were incubated with 8 nM [methyl ^{3}H] thymidine (specific activity 33.8 $Ci \cdot mmol^{-1}$, Izotop, USSR; or 44 $Ci \cdot mmol^{-1}$, Amersham, England) at *in situ* temperature for 30 minutes. The reaction was stopped by the addition of prefiltered formalin (the final concentration 1%). Formalin-killed (the final concentration 1%) blanks were incubated along with three subsamples. After incubation, samples were filtered through Millipore membrane filters (pore size 0.2 μm). Filters were rinsed five times with 1 ml of 5% ice-cold trichloroacetic acid (TCA) solution and the radioactivity retained on filters was assayed in a liquid scintillation counter RackBeta 1211 LKB Wallace (Baltic..., 1988).

Water transparency (S) was measured using a Secchi disc. In order to determine chlorophyll *a* (Chl) and pheopigments (Pheo), plankton was concentrated on Whatman glass fibre filters (GF/C). Pigments were extracted with 90% acetone and analysed spectrophotometrically (Recommendations..., 1979). The Lorenzen (1967) equations were used for calculations. In order to determine total nitrogen (N_{tot}) and total phosphorus (P_{tot}), organic compounds were mineralized with persulphate into nitrite and phosphate. Standard photometric analysis was then applied (New Baltic Manual..., 1972). Potential primary production (PP) was measured by the radiocarbon method, destruction activity (Destr) by the oxygen light and dark bottle method (Greeson et al., 1977). Oxygen concentration and biochemical oxygen demand at 20 °C for 5 days (BOD_5) were measured using a thermooximeter.

General Data on the Studied Lakes

The area (3.9—199 ha), maximum depth (3.6—32 m) stratification character, and trophic status of the investigated 29 lakes are given in Table 1. Among them Lake Nohipalu Valgjärv, which used to be oligotrophic, and strongly hypertrophic Lake Ruusmäe are considered as extremes. The general data were obtained mainly from the report compiled by Pihu (1990). The ecological classification of Estonian lakes composed by Mäemets (1974) on the basis of their trophic status was used.

Current Status of the Lakes

The TC in the investigated lakes ranged between $0.8 \cdot 10^6$ and $12.2 \cdot 10^6$ (mean $3.1 \cdot 10^6$, median $2.7 \cdot 10^6$) $cells \cdot ml^{-1}$ (Table 2). The PC varied from low to very high (from 210 to 4700; mean 940, median 650 $cells \cdot ml^{-1}$). The BHA, based on labelled thymidine incorporation rates, changed from $2.2 \cdot 10^{-12}$ to $234.7 \cdot 10^{-12}$ (mean $22.9 \cdot 10^{-12}$, median $13.7 \cdot 10^{-12}$) $molTdR \cdot l^{-1}h^{-1}$ (Table 2).

Bacterial abundance in the subsurface water layer was lower than in the near-bottom layer (2.7 and $3.6 \cdot 10^6$ cells $\cdot$ ml^{-1}, respectively). This difference is statistically significant (t-test, $p<0.05$). The average number of PC reached 676 cells $\cdot$ ml^{-1} in subsurface water and 1251 cells $\cdot$ ml^{-1} near the bottom (statistically significant difference: t-test, $p<0.05$). Such vertical distribution of the TC and of the PC (the biggest in the near-bottom water layer) is typical of mesotrophic and eutrophic lakes (Lokk, 1982). Contrary to the above-described regularity, BHA was higher near the surface than at the bottom ($27 \cdot 10^{-12}$ and $18 \cdot 10^{-12}$ molTdR $\cdot$ l^{-1}h^{-1}, respectively; statistically insignificant difference: t-test, $p>0.05$). The near-bottom BHA could be underestimated because the exogenous thymidine incorporation into cellular DNA synthesis might be inhibited due to low oxygen concentration (Bloem and Bär-Gilissen, 1989) or by low water temperature in stratified lakes (Moriarty, 1986).

To study the relation of microbiological indices and lake types, the ecological classification of lakes by Mäemets (1974) was used. The aver-

Table 2

Bacterial total count (TC, $\cdot 10^6$ cells $\cdot$ ml^{-1}), plate count (PC, cells $\cdot$ ml^{-1}), coefficient K ($\cdot 10^3$ TC/PC), and bacterial heterotrophic activity (BHA, $\cdot 10^{-12}$ molTdR $\cdot$ l^{-1}h^{-1}) in the studied lakes

Lake	TC		PC		K		BHA	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Otepää Pikajärv	4.1	4.2	300	220	14	19	20.9	15.5
Otepää Valgjärv	3.6	4.6	320	340	11	14	27.8	22.6
Jäneda Kalijärv	11.0	3.5	400	1100	28	3	13.1	6.3
Viitna Pikkjärv, N	2.1	4.5	400	780	5	6	6.4	18.2
Viitna Pikkjärv, S	1.8	12.2	490	2600	4	5	5.6	13.9
Ännijärv	1.5	4.8	540	2000	3	2	6.5	—
Veinjärv	1.2	1.5	700	810	2	2	5.8	12.6
Paukjärv	0.9	0.8	1040	1040	0.9	0.8	—	36.6
Jussi Suurjärv	1.6	4.2	1300	4700	1	0.9	4.5	15.7
Jussi Linajärv	2.8	3.9	2200	4100	1	1	21.4	12.1
Jussi Pikajärv	2.4	2.1	1800	3500	1	0.6	13.7	—
Lohja	2.0	3.3	1000	1500	2	2	234.7	—
Nohipalu Valgjärv	1.0	2.8	530	1440	2	2	—	—
Nohipalu Mustjärv	1.7	2.2	650	1640	3	1	—	—
Ruusmäe	6.7	6.8	770	1200	9	6	103:9	—
Palkna	2.2	2.0	300	440	7	5	—	—
Murati	1.9	1.9	350	600	5	3	24.1	28.2
Kise	2.1	2.1	520	660	4	3	2.2	5.2
Kirikumäe	3.6	—	390	—	9	—	21.8	—
Palujüri	2.6	2.7	730	490	4	6	16.7	7.8
Plaani Külajärv	3.1	3.0	1050	1100	3	3	20.0	13.9
Vaikjärv	2.0	3.4	400	420	5	8	8.6	4.9
Kurgjärv	2.5	3.2	410	280	6	11	11.0	9.8
Pullijärv	3.2	3.1	260	460	12	7	9.6	7.0
Vaskna	1.7	3.4	690	800	2	4	—	—
Vihtla	2.0	2.3	490	630	4	4	14.8	89.3
Hino	2.1	2.9	720	1070	3	3	10.7	11.9
Majori	3.0	4.7	550	320	5	15	40.6	4.8
Kavadi	2.1	2.7	410	800	5	3	13.7	8.2
Pabra	1.6	1.7	560	700	3	2	19.6	18.1

age TC in eutrophic and hypertrophic lakes was higher than in oligotrophic and mesotrophic lakes ($3.7 \cdot 10^6$ and $2.8 \cdot 10^6$ cells $\cdot$ ml^{-1}, respectively; t-test, $p<0.05$). A similar situation was observed in the BHA: it was more intensive in the lakes of higher trophic status ($32 \cdot 10^{-12}$ and $15 \cdot 10^{-12}$ molTdR $\cdot$ l^{-1}h^{-1}, respectively). PC did not follow this regularity. It was higher in oligotrophic and mesotrophic lakes (1002 cells $\cdot$ ml^{-1}) than in eutrophic and hypertrophic waterbodies (869 cells $\cdot$ ml^{-1}). However, the differences in BHA and PC were statistically insignificant (t-test, $p>0.05$).

According to the evaluation scale of microbiological data for the Estonian lakes (Lokk, 1982), the TC and the PC in the investigated lakes corresponded to the medium values (3—$6 \cdot 10^6$ cells $\cdot$ ml^{-1} and 200—1000 cells $\cdot$ ml^{-1}, respectively). However, some very high values were found; e.g. the TC in Lake Viitna Pikkjärv ($12.2 \cdot 10^6$ cells $\cdot$ ml^{-1}) and the PC in Lake Jussi Suurjärv (1700 cells $\cdot$ ml^{-1}).

The value of the coefficient K in the investigated lakes (Table 2) varied between $0.6 \cdot 10^3$ (in the bottom water layer of Lake Jussi Pikajärv) and $28 \cdot 10^3$ (in the subsurface water of Lake Jäneda Kalijärv), the average was $8 \cdot 10^3$. A low K value (less than $10 \cdot 10^3$) reflects a great amount of easily degradable organic matter in the waterbody (Юрковска, 1990).

Microbiological Changes in the Ecosystems of the Investigated Lakes in the Last Two Decades

The TC and PC data from 17 lakes obtained in 1973—1985 were subjected to a comparative analysis. For each lake the microbiological data for 1990 were compared with the corresponding indices obtained earlier (Table 3).

Table 3

The increase (present value divided by past value) of bacterial total count (TC) and plate count (PC) and the decrease of coefficient K (TC/PC) value in 1990 as compared with some earlier years

Lake	Years of comparison	TC increase	PC increase	K decrease
Otepää Pikajärv	1977	0.8	1.7	2.1
Otepää Valgjärv	1981	0.8	17.0	35.0
Paukjärv	1981	0.5	9.8	22.0
Jussi Linajärv	1981	1.1	1.9	3.7
Jussi Pikajärv	1981	0.3	0.7	1.9
Lohja	1977, 1985	0.4	8.8	17.9
Nohipalu Valgjärv	1977	1.6	4.0	4.8
Nohipalu Mustjärv	1983	1.0	2.3	2.3
Palkna	1974, 1983	2.0	2.8	1.4
Kise	1981	0.7	—	—
Kirikumäe	1981	1.1	1.4	2.0
Palujüri	1973	1.0	7.2	6.0
Vaikjärv	1981	1.7	6.0	3.8
Pullijärv	1973, 1981	1.4	1.7	1.3
Vaskna	1981	1.0	3.0	2.7
Hino	1974, 1981	0.3	2.0	2.4
Kavadi	1981	1.0	0.7	1.3
Average		1.0	0.7	6.9

The mean value of the TC of all 17 lakes was in 1990 1.4 times lower than that for the 1970s and 1980s ($2.4 \cdot 10^6$ and $3.7 \cdot 10^6$ cells $\cdot$ ml^{-1}, respectively). The changes were similar in surface and in bottom water layers (drop from $3.2 \cdot 10^6$ to $2.4 \cdot 10^6$ and from $4.2 \cdot 10^6$ to $2.9 \cdot 10^6$ cells $\cdot$ ml^{-1}, respectively). The decrease in the mean TC could be caused by the dilution effect. In the last 20 years the total yearly amount of precipitation has increased by 130 mm (Ross and Russak, 1991) and this has resulted in a rise of the water level in lakes.

The estimation of the changes in the TC in the lakes one by one (Table 3) revealed that TC has decreased in seven and increased in six lakes; the average value remained unchanged.

The mean PC increased 3.1 times (from 300 cells $\cdot$ ml^{-1} in the 1970s and 1980s up to 933 cells $\cdot$ ml^{-1} in 1990).

The corresponding changes in PC in the surface and bottom water layers were from 249 to 721 and from 354 to 1171 cells $\cdot$ ml^{-1}. PC decreased only in two lakes (Jussi Pikajärv and Kavadi), the greatest increase (17 times) was found in Lake Otepää Valgjärv. The mean increase of PC in the repeatedly studied lakes was 4.4 times the mean of the 1970s and 1980s (Table 3). The increase of PC could also be caused by the increase in precipitation and the inflow of easily degradable allochthonous organic matter.

The mean ratio (K) of TC to PC decreased 3.2 times during the observation period (from 16,884 to 5,342). The decrease was the smallest in lakes Pullijärv and Kavadi (1.3 times); whereas in lakes Otepää Valgjärv, Paukjärv, and Lohja this value ranged between 17 and 35 (Table 3). The great value of the average decrease of K (6.9 times) is chiefly caused by these high numbers.

Dependence of Bacterioplankton Abundance and Activity on Environmental Factors

Several environmental parameters such as water temperature, pH, oxygen, the content of Chl, Pheo, P_{tot} and N_{tot}, PP, Destr, and BOD_5 were used to estimate the main factors influencing bacterioplankton abundance and activity. None of these ecological parameters showed strong correlation with the bacterial abundance and activity when all lakes were analysed together. This could be caused by different physical-geographical conditions and human impact or other factors. The best correlations in all lakes were established between TC and Destr ($r=0.60$, $p<0.001$) and between TC and BOD_5 ($r=0.59$, $p<0.001$) in near-surface water (except Lake Lohja, where BOD_5 was not measured).

The source of carbon and energy for heterotrophic bacteria is organic matter. Therefore a good correlation was found between the bacterial abundance and the amount of oxygen required by the aerobic microbes to utilize easily degradable organic matter (BOD_5). As seen in Fig. 2 Lake Jäneda Kalijärv had an unaccountably high value of TC: $11.0 \cdot 10^6$ cells $\cdot$ ml^{-1}. Excluding this lake from the analysis, TC can be calculated by the following equation (valid in BOD_5 range 1—11 $mgO_2 \cdot l^{-1}$):

$$TC = 0.83 + 0.53BOD_5 \quad R^2 = 69\%, \quad p < 0.001.$$

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 role of bacterioplankton in the aerobic destruction of organic matter was characterized by a positive correlation between TC and Destr (Fig. 3). Our results show that the destruction processes were faster in

the lakes with higher oxygen contents (lakes Otepää Pikajärv, Jäneda Kalijärv, and Ruusmäe). Lake Ruusmäe differed from the other lakes studied in extremely active destruction and production processes in the near-surface water layer (PP was $3.6 \cdot 10^3$ mgC $\cdot m^{-3}h^{-1}$, Destr — 0.1 mg$O_2 \cdot l^{-1}h^{-1}$, BHA — $104 \cdot 10^{-12}$ molTdR $\cdot l^{-1}h^{-1}$, BOD_5 — 11.0 mg$O_2 \cdot l^{-1}$).

In the near-bottom water layer of all investigated lakes TC was determined mainly by the Chl concentration:

$$TC = 2.1 + 0.009 \cdot Chl \quad R^2 = 66\%, \; p < 0.001.$$

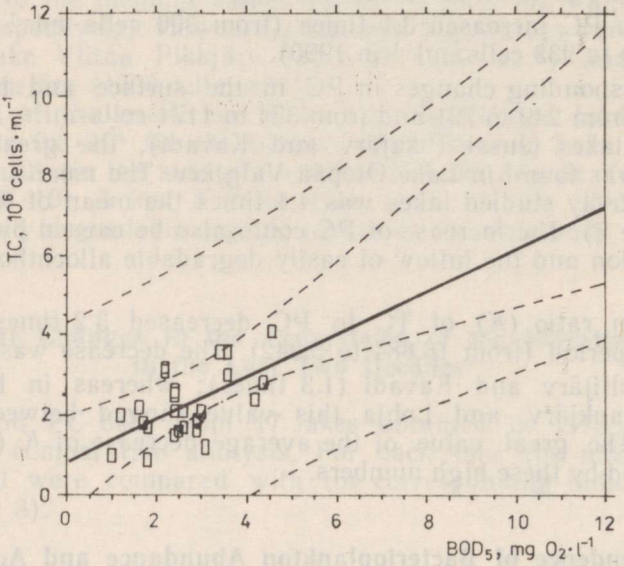

Fig. 2. Regression between the total count of bacteria (TC) and biochemical oxygen demand (BOD_5) in near-surface water of studied lakes (except lakes Lohja and Jäneda Kalijärv). Broken lines represent the 95% confidence and prediction limits.

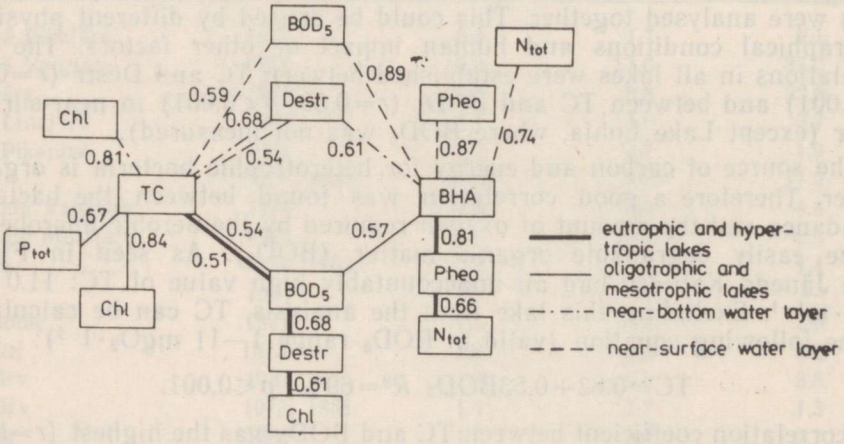

Fig. 3. Significant ($p < 0.01$) correlations between investigated parameters in the studied lakes.

The relatively high Chl concentration (93 mg · m^{-3}) in the bottom layer of Lake Viitna Pikkjärv (Fig. 4) was obviously the result of phytoplankton sinking after an earlier phytoplankton bloom. The active destruction of organic matter (0.09 mgO_2 · $l^{-1}h^{-1}$) was in progress there at the time of sampling. In addition to high TC and Chl, the amounts of P_{tot}, Pheo, and PC were great (133 mg · m^{-3}, 93 mg · m^{-3}, 2600 cells · ml^{-1}, respectively). The low value of PP (0.96 mgC · $m^{-3}h^{-1}$) compared with the high Chl concentration is characteristic of the decaying algal population.

In oligotrophic and mesotrophic lakes, the bacterial abundance was strongly influenced by P_{tot}. TC was determined by the following equation:

$$TC = 1.1 + 0.02 \cdot P_{tot} + 0.08 \cdot Chl \quad R^2 = 73\%, \quad p < 0.001.$$

Lack of inorganic phosphorus leads to the inhibition of oxidative phosphorylation. This is the prevailing reason of the decrease of bacterial respiration activity and the population growth rate at low phosphorus concentrations (Гуренович, 1988). In summer the concentration of inorganic phosphorus is negligible because bacteria and phytoplankton utilize phosphates immediately after their regeneration (Vadstein et al., 1988). The same authors note that bacteria suffer phosphorus deficiency from the end of May up to the total water convection in fall. The fact that TC was dependent also on Chl concentration gave the basis to believe that in these lakes the main carbon and energy sources for bacteria were algal metabolites and dead phytoplankton.

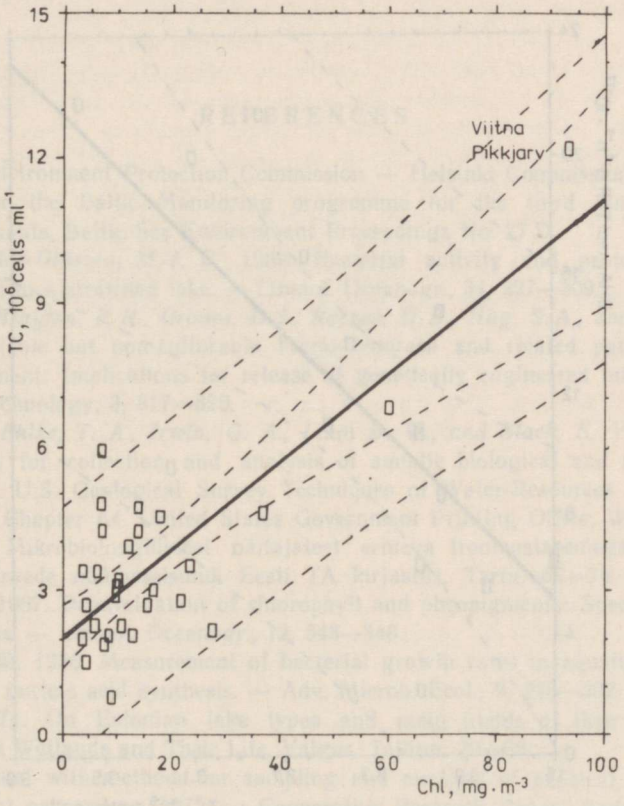

Fig. 4. Regression between the total count of bacteria (TC) and chlorophyll *a* concentration (Chl) in near-bottom water of the studied lakes. Broken lines represent the 95% confidence and prediction limits.

In the surface waters of oligotrophic and mesotrophic lakes BHA depended on TC in the range of TC from $1.5—3.6 \cdot 10^{12}$ cells $\cdot$ ml^{-1} according to the following equation:

$$BHA = (7.50 \cdot TC - 6.04) \cdot 10^{-24} \quad R^2 = 51\%, \quad p = 0.04.$$

Although the correlation is not strong, the tendency is still notable (Fig. 5). The two last equations show that in oligotrophic and mesotrophic lakes phytoplankton provides an optimum amount of nutrients for bacteria. Obviously no inhibition of bacterial activity by algal metabolites or bacterial population density can be stated.

There was no correlation between TC and their activity when all lakes were treated together ($r = 0.01$, $p = 1.0$).

The bacterial abundance and their heterotrophic activity correlated directly or indirectly with the concentration of Pheo (Fig. 3). Pheopigments appear in the bottom water layers mostly as particles of macrozooplankton faeces. In surface water chlorophyll degradation products occur mainly in microzooplankton excrements and there is also evidence of their accumulation within the algal cells (Welschmeyer and Lorenzen, 1985). The same authors point out that the importance of bacteria in chlorophyll degradation is insignificant. Consequently, the above correlation may reflect utilization of zooplankton excrements by bacteria.

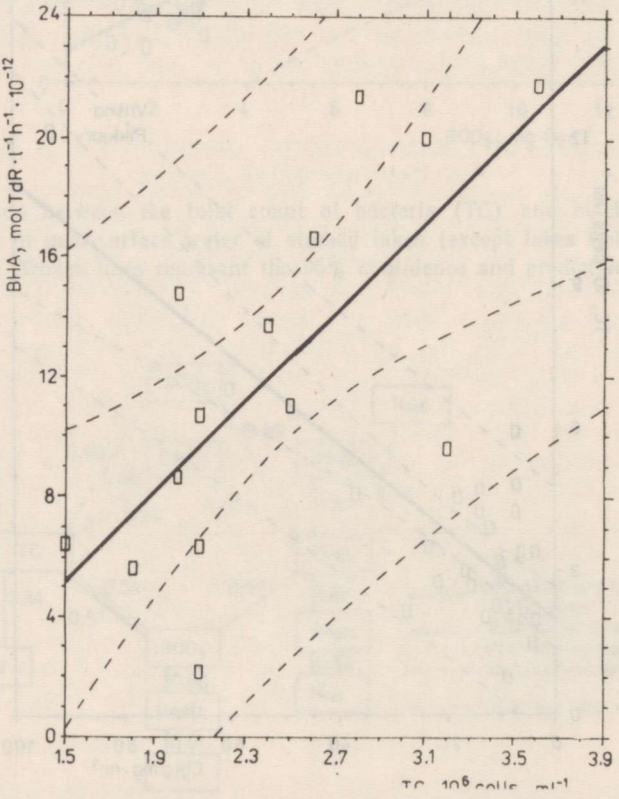

Fig. 5. Regression between bacterial heterotrophic activity (BHA) and the total count of bacteria (TC) in near-surface water of oligo- and mesotrophic lakes. Broken lines represent the 95% confidence and prediction limits.

No correlation was detected between the water temperature and the bacterial abundance and activity ($r=-0.27$, $p=0.5$ and $r=0.08$, $p=0.6$, respectively). The reason might be the monotonously warm sampling period (June and July) and the relatively small sampling depths of lakes (the sampling depths exceeded 10 m only in 5 lakes, as we did not find the deepest site of some lakes).

The BHA in near-surface water layer was correlated with N_{tot} (Fig. 3). The bacterial mineralization and destruction processes involve changes of several nitrogen compounds. Micro-organisms control the nitrogen cycle more than any other major element cycle; they are responsible for nitrification, denitrification, ammonia production, etc. For example, in the ocean 50% or so of the recycled nitrogen is mineralized by planktonic bacteria (Williams, 1981).

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