

## TENDENCIES AND RELATIONSHIPS IN THE PELAGIC ENVIRONMENT AND PLANKTON COMMUNITY OF LAKE VÖRTSJÄRV IN 1964–93

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**Abstract.** Main trends in the water level regime, hydrochemical and plankton variables in the shallow eutrophic Lake Võrtsjärv are discussed on the basis of a 30-year (1964–93) monthly database. An increase of the average depth of the lake from 2.1 to 3.2 m during this period resulted in a 7-fold decrease of bottom irradiance and in the reduction of water column irradiance by 1/3. The mainly light-limited phytoplankton responded to this by a decrease in primary production. This, in its turn, reduced the phytoplankton biomass and the pH of water. In seasonal aspect, phytoplankton growth was dependent upon the release rate of mineral nitrogen only in August and September, under the best relative light conditions due to the low water level. Phytoplankton biomass had a maximum in the first half of the 1970s. During 30 years the proportion of filamentous algae increased and the proportion of small algae, edible for zooplankton, decreased. A new species, *Limnothrix redekei* (van Goor) Meffert, appeared in phytoplankton in the 1960s and became a dominant in the 1980s, when several zooplankton species disappeared. Substrate limitation as well as the increased grazing pressure of zooplankton on bacteria accounted probably for the decreasing trend of the total number of bacteria.

**Key words:** long-term changes, plankton community, shallow lake, limiting factor.

### INTRODUCTION

Regular monthly collection of chemical and biological samples from Lake Võrtsjärv, the second largest lake in Estonia, started in the mid-1960s and has been carried on up to now. The great value of complex long-term investigations of lakes is obvious, especially in the case of a large lake like Võrtsjärv, which has

several common features with other European shallow lakes such as Lake Balaton or Neusiedler See, and reflects changes in climate as well as in human activity on a large territory.

At the beginning of the 1990s a computerized database of 30-year investigations on Lake Võrtsjärv was created. The first overviews of water chemistry, and phyto-, zoo-, and bacterioplankton have been published or prepared for publishing (Nõges, 1992; Kisand, 1994; Järvet & Nõges, 1994; Haberman, 1995a, b, in press; Haberman et al., in press; Kisand & Tammert, in press; Nõges, in press; Nõges & Järvet, in press; Nõges & Laugaste, in press; Nõges & Nõges, in press). The present paper summarizes the main trends that have been revealed in the whole plankton community and in the pelagic environment, and endeavours to outline the mechanisms controlling these changes. The authors fully realize the risk hidden in the statistical approach in judging about causal relations.

## GENERAL DESCRIPTION OF THE LAKE

Lake Võrtsjärv is a shallow, highly eutrophic lake in Central Estonia. Its area is 270 km<sup>2</sup>, mean depth 2.8 m, and maximum depth 6 m. The 3104 km<sup>2</sup> drainage area of Võrtsjärv has a major effect on the formation of the water quality, as it exceeds the surface area of the lake by a factor of 11.5 (Fig. 1). Eighteen rivers and streams collect their water mostly from intensively cultivated lands where soils have been formed on rich-in-carbonate glacial and glaci-fluvial sediments covering the Middle Devonian sandstone bedrock. The exchange of the 750 million m<sup>3</sup> water mass proceeds, on an average, once a year, with annual differences in the water exchange coefficient ranging from 0.75 to 1.4 (Jaani, 1990). The increase in the lake's water budget is mostly (73–83%) accounted for by the inflow and the decrease by the outflow (80–91%). A strong dependence of the water level on precipitation is characteristic of the hydrological regime of Võrtsjärv. The average height of the water level in years rich and poor in precipitation differs by about 2 m. The unfavourable conditions of the outflow – the small gradient of the Suur Emajõgi River and bifurcation in its upper course during flood – lead to prolonged high water periods while extensive overbank areas are flooded. Lasting low level periods in dry years result in the expansion of reed-bed areas and in the deterioration of the water quality.

In the surroundings of Võrtsjärv the mean annual amount of precipitation is 590 mm. The mean water temperature reaches its maximum of 19.8°C in July. The ice cover lasts from November to April, on an average for 135 days.

Võrtsjärv is a strongly eutrophic waterbody with an average concentration of total N of 2 g m<sup>-3</sup> and that of total P 53 mg m<sup>-3</sup>. The water is alkaline (pH 7.5–8.5) with a great buffering capacity and a high seston content. During the ice-free period, the mean transparency does not exceed 1 m.

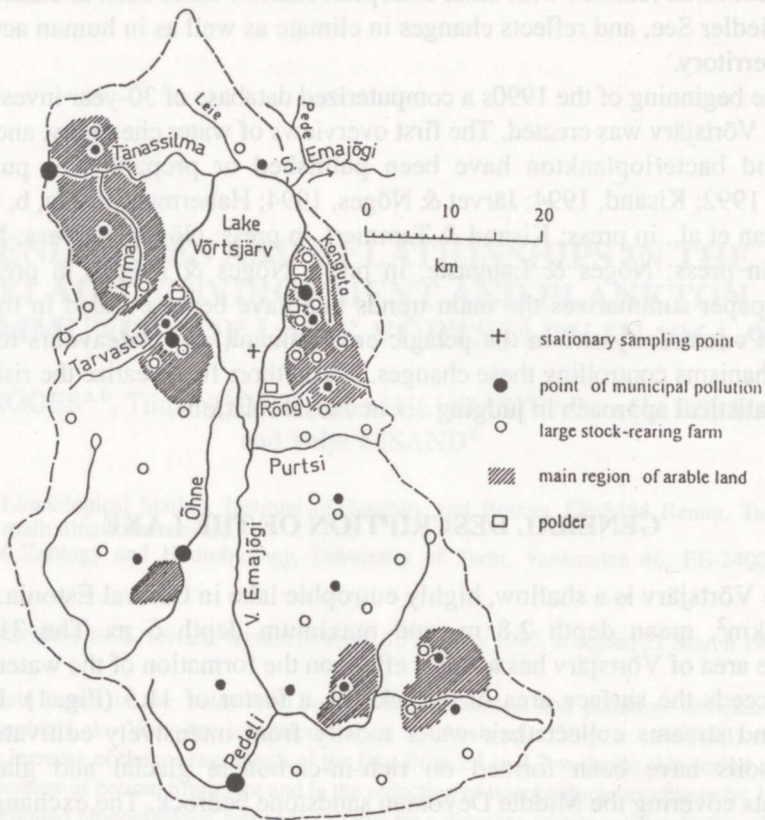


Fig. 1. Lake Vörtsjärv and its drainage area.

## MATERIAL AND METHODS

The data set used in the present paper consists of water level, water temperature, and transparency measurements and hydrochemical and plankton analyses made in 1964–93. The water level data were obtained from the hydrological station situated on the outflow. The other measurements and analyses pertain to the surface layer of the main monitoring point (Fig. 1). Routine sampling was performed once a month, in some periods more frequently, 2–6 times a month. The length of different time series was not exactly the same because many values during 1964–68 were missing. The measuring of some variables like chlorophyll *a*, total phosphorus, and total nitrogen began as late as 1982. Time series are shorter also in the case of permanganate and dichromate oxygen consumption.

The following abbreviations were used for the variables analysed:

- YEAR – year number;  
LEVEL – absolute water level, m;  
TEMP – water temperature, °C;  
S – Secchi disc transparency, m;  
O2 – concentration of dissolved oxygen, mg l<sup>-1</sup>;  
PH – pH of water;  
HCO<sub>3</sub> – concentration of hydrocarbonate HCO<sub>3</sub> ions, meq l<sup>-1</sup>;  
BOX – dichromate oxygen demand, mg O l<sup>-1</sup>;  
POX – permanganate oxygen demand, mg O l<sup>-1</sup>;  
NTOT – total nitrogen concentration, mg l<sup>-1</sup>;  
NO<sub>3</sub> – nitrate concentration, mg l<sup>-1</sup>;  
PTOT – total phosphorus concentration, mg l<sup>-1</sup>;  
PO<sub>4</sub> – phosphate concentration, mg l<sup>-1</sup>;  
BAC – biomass of diatoms, g m<sup>-3</sup>;  
CYAN – biomass of blue-green algae, g m<sup>-3</sup>;  
SUBT – biomass of *Planktolyngbya subtilis* (W. West) Anagnostidis *et* Komárek, g m<sup>-3</sup>;  
REDEK – biomass of *Limnothrix redekei* (van Goor) Meffert, g m<sup>-3</sup>;  
CHLOR – biomass of green algae, g m<sup>-3</sup>;  
CHRYS – biomass of chrysophytes, g m<sup>-3</sup>;  
EUG – biomass of euglenophytes, g m<sup>-3</sup>;  
BFP – biomass of total phytoplankton, g m<sup>-3</sup>;  
CLAD – biomass of cladocerans, g m<sup>-3</sup>;  
ROT – biomass of rotifers, g m<sup>-3</sup>;  
COP – biomass of copepods, g m<sup>-3</sup>;  
BZP – biomass of total zooplankton, g m<sup>-3</sup>;  
TNB – total number of free-living bacteria, 10<sup>6</sup> cells ml<sup>-1</sup>.

As a first step of the data analysis, average values were calculated for months that included more than one sampling. The obtained regular monthly database was used for describing most of the seasonal and long-term changes. Further, seasonal averages were calculated as follows: March, April, May – spring (sp); June, July, August – summer (su); September, October, November – autumn (au); December, January, February – winter. For each year two winters were analysed: the preceding winter (wi) including December of the previous year and the following winter (fowi) including January and February of the following year. These abbreviations were used for distinguishing between variables of different seasons, e.g., suS – summer Secchi disk transparency. In this way, seasonality was removed and variability essentially reduced. For correlation analysis seasonal blocks were joined into pairs in the following way: wi–sp, wi–su, sp–su, sp–au, su–au, su–fowi, au–fowi. Correlations with the year number enabled to reveal variables with a linear trend. As a rule, only correlations with >99% significance (exceptionally >95%) were taken into account.

## RESULTS

### Long-term trends

The most consistent linear trends that occurred in the 30-year time series could be followed during several seasons (Table 1). A continuous increase in the water level became evident in all four seasons. The spring level was characterized by the strongest linear trend (correlation coefficient with the year number  $r = 0.784$ ). The trend line for monthly time series showed a 1.5 m increase in the average water level (Fig. 2) during 30 years.

Table 1

Long-term linear trends in the seasonal blocks of variables

Variable	$r^*$	$p^{**}$	Fitting line
suCHLOR	-0.642	<0.01	2.48 - 0.0783 YEAR
auCHLOR	-0.641	<0.01	3.33 - 0.103 YEAR
wiCHRY	-0.536	<0.01	0.852 - 0.0307 YEAR
wiHCO3	-0.544	<0.01	4.03 - 0.0223 YEAR
spLEVEL	0.784	<0.01	-75.9 + 0.0555 YEAR
suLEVEL	0.622	<0.01	-29.9 + 0.0321 YEAR
auLEVEL	0.629	<0.01	-73.6 + 0.0541 YEAR
wiLEVEL	0.725	<0.01	-103.7 + 0.0694 YEAR
wiNO3	0.497	0.03	0.457 + 0.0343 YEAR
suPO4	0.610	0.02	2.05 + 0.168 YEAR
suPH	-0.793	<0.01	8.70 - 0.0181 YEAR
auPH	-0.600	<0.01	8.33 - 0.0109 YEAR
auPOX	0.582	<0.01	8.57 + 0.199 YEAR
wiPOX	0.787	<0.01	7.55 + 0.199 YEAR
suREDEK	0.647	<0.01	-1.09 + 0.191 YEAR
auREDEK	0.611	<0.01	-1.27 + 0.181 YEAR
wiREDEK	0.601	<0.01	-0.425 + 0.0468 YEAR
auS	0.515	0.01	0.576 + 0.00991 YEAR
wiS	-0.595	<0.01	1.86 - 0.0204 YEAR
spTNB	-0.515	<0.01	5.70 - 0.0904 YEAR
suTNB	-0.721	<0.01	7.63 - 0.154 YEAR
auTNB	-0.738	<0.01	7.74 - 0.163 YEAR

\* correlation coefficient;

\*\* significance level.

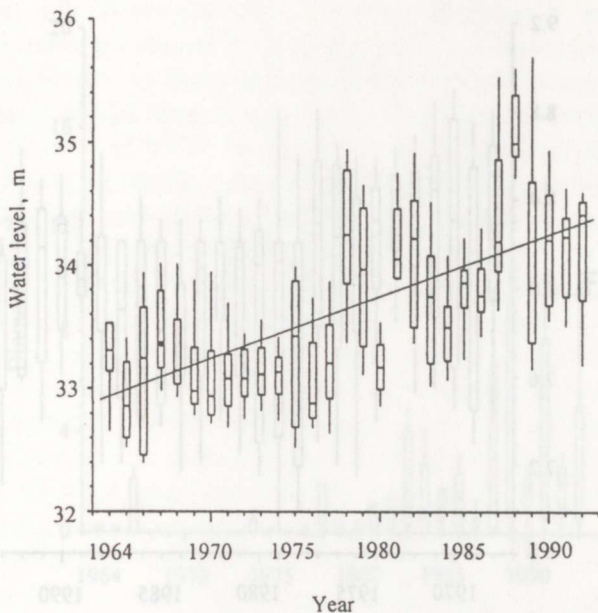


Fig. 2. Increase of the water level of Vörtsjärv (median, quartiles, minimum, and maximum).

Autumn and winter water transparency had opposite trends. Probably, due to the decreasing BFP, auS grew from the average 58 cm of the 1970s to 88 cm in the 1990s. Several mild winters at the end of the 1980s and the early 1990s, with less snow on the ice, promoted phytoplankton growth in winter, which resulted in a decline of wiS.

The permanganate oxygen consumption increased in the autumn and winter series. However, the dichromate oxygen consumption remained almost constant.

A continuous decrease in pH values could be observed in the summer and autumn series. The whole pH time series (Fig. 3) demonstrated a rather smooth decline of the yearly maxima and a large variability of the yearly minima. Cross-correlation of monthly phytoplankton biomass and pH values revealed a one-month lag of the former (Fig. 4). Winter nitrates and summer phosphates demonstrated a slight increase, giving evidence of continuous eutrophication.

Among phytoplankton variables the increase of the biomass of *Limnithrix redekei* was the most striking change (Fig. 5). This species competed successfully with *Planktolyngbya subtilis* (W. West) Anagnostidis et Komárek, a dominating species of blue-green algae in the lake. Mainly due to the abundance of *P. subtilis*, the total biomass of phytoplankton reached its maximum in the middle of the 1970s, with summer maxima up to  $100 \text{ g m}^{-3}$  (Fig. 6). This high level period was followed by a sharp decrease at the end of the decade. During the 1980s and

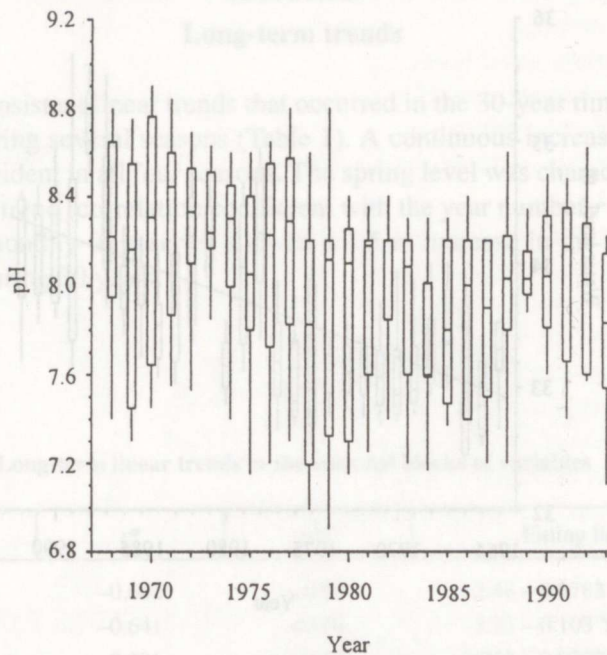


Fig. 3. Long-term changes in pH.

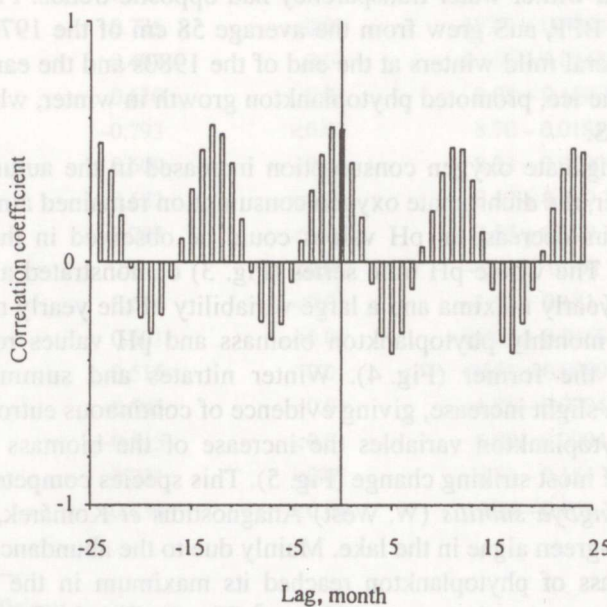


Fig. 4. Cross-correlation between monthly phytoplankton biomass and pH.

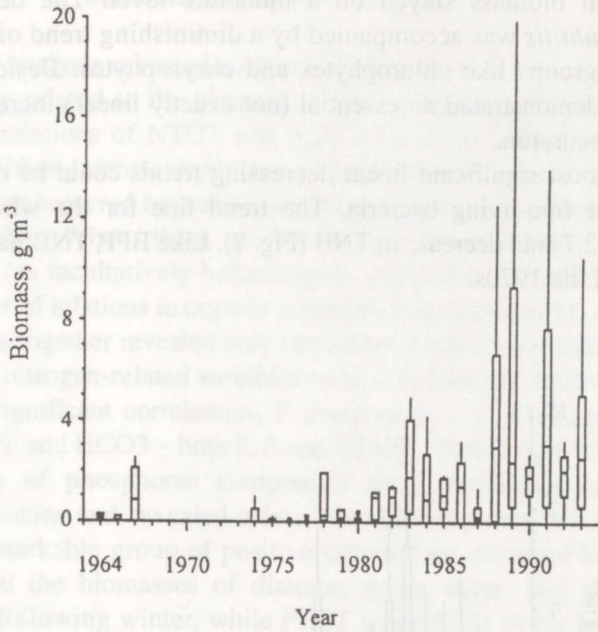


Fig. 5. Long-term changes in the biomass of *Limnithrix redekei*.

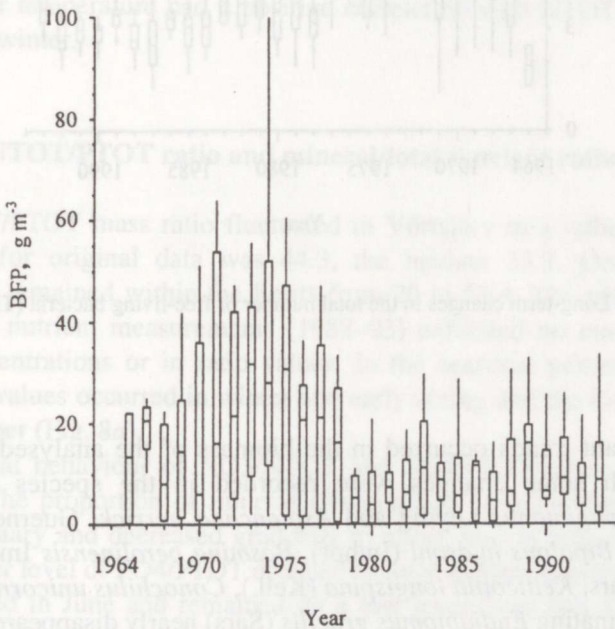


Fig. 6. Long-term changes in total phytoplankton biomass (BFP).



1990s, the total biomass stayed on a moderate level. The decrease of the biomass of *P. subtilis* was accompanied by a diminishing trend of several minor phytoplankton groups like chlorophytes and chrysophytes. Besides *L. redekei*, euglenophytes demonstrated an essential (not exactly linear) increase during the period under discussion.

One of the most significant linear decreasing trends could be observed in the total number of free-living bacteria. The trend line for the whole data series demonstrated a 2.7-fold decrease in TNB (Fig. 7). Like BFP, TNB had its maximum in the middle of the 1970s.

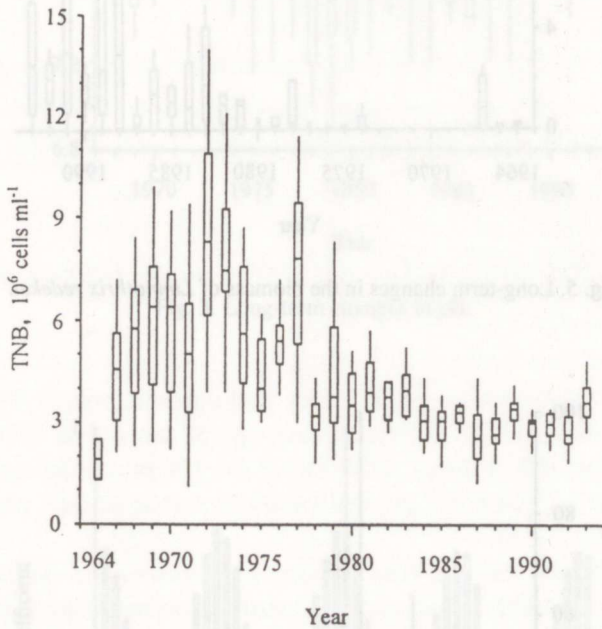


Fig. 7. Long-term changes in the total number of free-living bacteria (TNB).

No significant trends occurred in the biomass of the analysed zooplankton groups, though some changes were recorded in the species composition: *Bythotrephes longimanus* Leydig and *Asplanchna herricki* Guerne disappeared entirely, while *Bipalpus hudsoni* (Imhof), *Bosmina berolinensis* Imhof, *Bosmina obtusirostris* Sars, *Kellicottia longispina* (Kell.), *Conochilus unicornis* Rouss, and the earlier dominating *Eudiaptomus gracilis* (Sars) nearly disappeared.

## Seasonal correlations with nutrients

Correlation analysis revealed a clear tendency for nitrogen, especially NTOT, to be positively related to the biomass of blue-green algae (Table 2). Of the 45 significant correlations of NTOT and NO<sub>3</sub> 14 were found either with the total biomass of the blue-greens or with one of the dominant species. Another group of positive relations occurred between nitrogen and the content of organic substances (POX or BOX). When three positive correlations between nitrogen and euglenophytes (as facultatively heterotrophic algae) are also added to this group, the total number of relations to organic compounds increases to 11. All other phytoplankton groups together revealed only two rather weak correlations with suNTOT. The remaining nitrogen-related variables were distributed as follows: zooplankton variables – 5 significant correlations, P compounds – 4, N compounds of other seasons – 3, BFP and HCO<sub>3</sub> – both 2, S and TEMP – both 1 significant correlation.

Correlations of phosphorus compounds were distributed among a larger number of variables and revealed a less pronounced pattern of tendencies than nitrogen. A remarkable group of positive correlations occurred between autumn phosphorus and the biomasses of diatoms, green algae, and chrysophytes of autumn or the following winter, while PTOT was related to the biomasses of the same season and PO<sub>4</sub> to those of the following season. The summer biomass of *L. redekei*, on the contrary, was positively correlated with suPO<sub>4</sub>.

Phosphates were negatively correlated with pH in summer and autumn. Total phosphorus had a negative correlation with water transparency in autumn. Summer water temperature had a positive correlation with NTOT and PTOT of the following winter.

## NTOT/PTOT ratio and mineral/total nutrient ratios

The NTOT/PTOT mass ratio fluctuated in Vörtsjärvi in a rather wide range. The average for original data was 44.3, the median 33.3. One half of the measurements remained within the limits from 20 to 53.4. The rather short time series of total nutrient measurements (1982–93) exhibited no remarkable trend either in concentrations or in ratio values. In the seasonal pattern, the highest NTOT/PTOT values occurred in winter and early spring and the lowest values in July and October (Fig. 8a).

The seasonal behaviour of NO<sub>3</sub>/NTOT and PO<sub>4</sub>/PTOT ratios was different (Fig. 8b, c). The proportion of mineral nitrogen had its maximum (40–75% of NTOT) in January and decreased gradually to about zero in August–September. The high winter level of PO<sub>4</sub>/PTOT dropped sharply in May, shortly after the ice-break, increased in June and remained on a low level from July to September–October.

Table 2

## Seasonal correlations with nutrients

Season	NTOT			NO3		
	Variable	<i>r</i>	<i>p</i>	Variable	<i>r</i>	<i>p</i>
wi	spCYAN	0.926	<0.01	spPTOT	-0.857	0.02
	spBFP	0.900	<0.01	wiREDEK	0.702	0.03
	spREDEK	0.874	0.01	spREDEK	0.668	0.03
	spCOP	0.794	0.01	wiS	-0.628	0.04
	spSUBT	0.792	0.01			
	spNTOT	0.758	0.02			
	spBZP	0.749	0.02			
sp	wiNTOT	0.758	0.02	suPTOT	0.911	0.02
	spCYAN	0.727	0.02	spPTOT	-0.854	0.03
	spBOX	0.709	0.03	auNO3	-0.706	0.02
su	fowiPOX	0.915	0.01	suBOX	0.994	<0.01
	auEUG	0.781	<0.01	spBOX	0.962	<0.01
	auPOX	0.780	0.05	auNO3	0.950	<0.01
	suCLAD	-0.689	<0.01	fowiEUG	0.931	<0.01
	auBAC	0.685	<0.01	spCLAD	0.802	<0.01
	suSUBT	0.663	<0.01	spSUBT	0.735	0.02
	auCHRY3	0.662	<0.01			
au	spCYAN	0.794	<0.01	suNO3	0.950	<0.01
	auPO4	0.783	0.02	spBOX	0.901	0.02
	spREDEK	0.755	<0.01	suBOX	0.844	0.03
	spSUBT	0.648	<0.01	fowiEUG	0.738	<0.01
	spBFP	0.640	<0.01	spNO3	-0.706	0.02
fowi	suPOX	0.902	0.01	auREDEK	0.720	<0.01
	suHCO3	0.846	<0.01			
	auCYAN	0.707	0.01			
	suTEMP	0.687	0.01			
	suCYAN	0.670	0.02			
	suROT	0.629	0.03			
	auHCO3	0.621	0.03			

Table 2 continued

Season	PTOT			PO4		
	Variable	<i>r</i>	<i>p</i>	Variable	<i>r</i>	<i>p</i>
wi	spO2	0.744	<0.01			
	wiSUBT	-0.720	0.01			
sp	wiNO3	-0.857	0.02	suPO4	0.867	0.02
	spNO3	-0.854	0.03			
su	spNO3	0.911	0.02	spPO4	0.867	0.02
	auPO4	0.706	0.04	auHCO3	-0.801	<0.01
	fowiS	-0.626	0.02	fowiPO4	0.795	0.03
				suPH	-0.753	<0.01
				suREDEK	0.744	<0.01
				suPOX	0.724	0.05
				spPH	-0.710	<0.01
				YEAR	0.610	0.02
				fowiCLAD	0.610	0.03
au	auBAC	0.754	<0.01	fowiPTOT	0.943	<0.01
	auS	-0.749	<0.01	fowiCHLOR	0.790	<0.01
	auCHLOR	0.628	0.02	suREDEK	0.785	<0.01
	auTNB	0.624	0.02	auNTOT	0.783	0.02
	auCHRYS	0.622	0.02	fowiBAC	0.759	<0.01
				spBFP	0.719	<0.01
				spCOP	0.717	<0.01
				suPTOT	0.706	0.04
				auPH	-0.619	0.02
fowi	auPO4	0.943	<0.01	suPO4	0.795	0.03
	suTEMP	0.627	0.01	auPOX	0.741	0.02

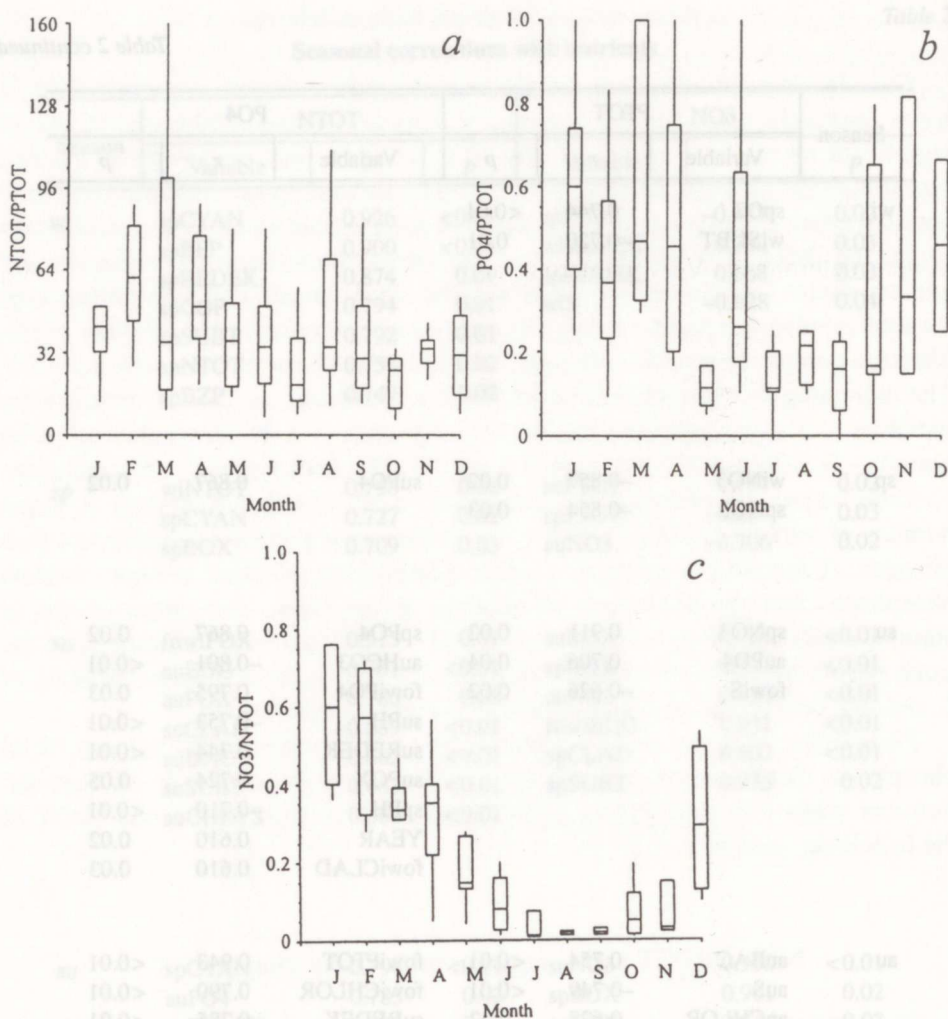


Fig. 8. Seasonal dynamics of nutrient ratios. *a*, total nutrients ratio; *b*, *c*, mineral to total nutrients ratios.

### Underwater light field

The percentage of surface irradiance reaching the bottom of the lake ( $I_b$ ) during the ice-free period was used as a measure of underwater light conditions:

$$I_b = 100 \text{ EXP}(-k_e z_b), \quad (1)$$

where the extinction coefficient ( $k_e$ ) was calculated from Secchi transparency and the average depth of the lake ( $z_b$ ) from the water level using the bathymetric curve of the lake. According to light attenuation measurements in Vörtsjärvi in 1989

$$k_e S = 1.48 \pm 0.05 (\pm SE). \quad (2)$$

The relationship between the water level and the average depth of the lake was precisely described by the linear model:

$$z_b = 0.741 \text{ LEVEL} - 22.29 \quad (r = 0.99; p < 0.001). \quad (3)$$

Surface temperature above 1 °C was used for sorting out the data pertaining to the ice-free period. In spite of the long-term increasing trend of water transparency in summer and autumn, the relative bottom irradiance decreased from about 2.8% in the middle of the 1960s to 0.4–0.5% in the 1990s (Fig. 9). During the ice-free period the relative bottom irradiance was the lowest in May (due to high water level coinciding with large algal biomass) and increased towards the end of the year (Fig. 10).

As the water is continuously mixed, the average water column irradiance can be calculated according to Mallin & Paerl (1992):

$$I_{\text{mix}} = I_0[1 - \text{EXP}(-k_e z)]/k_e z \quad (4)$$

by replacing the mixing depth  $z$  by the average depth of the lake  $z_b$  and taking 100% for  $I_0$ . During 30 years the relative  $I_{\text{mix}}$  decreased from 28 to 19%, i.e. by about one third.

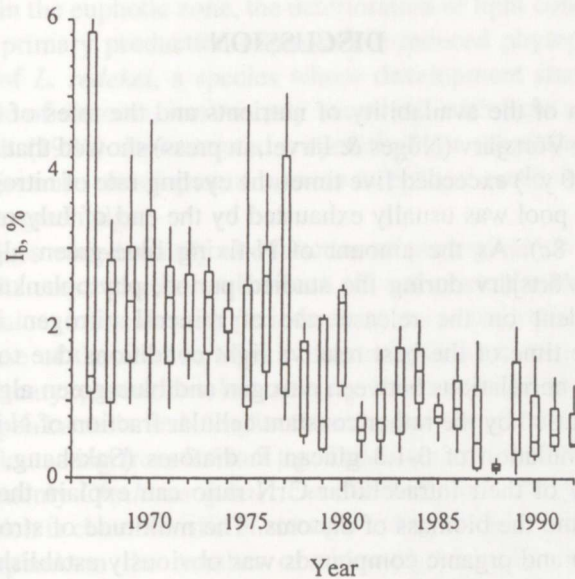


Fig. 9. Long-term changes in relative bottom irradiance ( $I_b$ ).

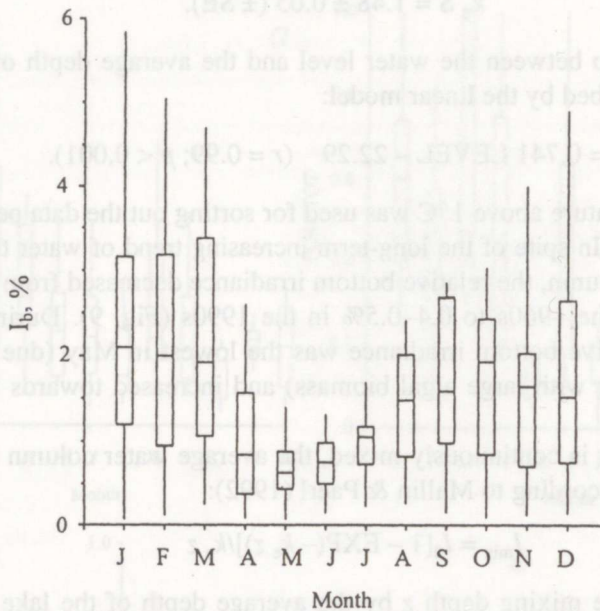


Fig. 10. Seasonal dynamics of relative bottom irradiance ( $I_b$ ).

## DISCUSSION

A comparison of the availability of nutrients and the rates of their uptake by phytoplankton in Vörtsjärv (Nöges & Järvet, in press) showed that the cycling rate of phosphorus ( $40 \text{ y}^{-1}$ ) exceeded five times the cycling rate of nitrogen ( $8 \text{ y}^{-1}$ ). The mineral nitrogen pool was usually exhausted by the end of July or the beginning of August (Fig. 8c). As the amount of N-fixing blue-green algae was rather unimportant in Vörtsjärv during the studied period, phytoplankton growth was probably dependent on the release rate of mineral nitrogen in August and September at the time of the best relative light conditions due to the low water level. The strong correlations between nitrogen and blue-green algae in Vörtsjärv were probably caused by the rather constant cellular fraction of N in this group of algae. The accumulation of  $\beta$ -1.3 glucan in diatoms (Sakshaug, 1980) and the higher variability of their intracellular C:N ratio can explain the disconnection between NTOT and the biomass of diatoms. The multitude of strong correlations between nitrogen and organic compounds was obviously established through the link of blue-green algae as well.

The hypothesis of the possible phosphorus limitation was checked by means of the model of Vollenweider (1976) relating the concentrations of chlorophyll *a* and total phosphorus. In phosphorus-limited conditions this model usually gives highly

predictive results (Harris, 1986) and, vice versa, it is hopeless to search for a relation between phytoplankton and phosphorus if phosphorus is available in excess (Schindler, 1978). Our data revealed no relation of chlorophyll *a* and total phytoplankton biomass with either mineral or total phosphorus. The rapid consumption of phosphates after the ice-break and a very low concentration during summer do not prove phosphorus limitation either, as the dominating blue-green algae are able to accumulate surplus phosphorus in the form of polyphosphates (Zaiss, 1978). In a phosphorus enrichment experiment (Lehman & Sandgren, 1982) *Oscillatoria* sp. and *P. subtilis* were able to double their cellular phosphorus pool in two minutes. In the conditions of equal initial nutrient supply these small procaryotes exceeded eucaryotes in their efficiency to transform nutrients to biomass.

Several circumstances support the hypothesis of the prevalence of light limitation in phytoplankton growth in Vörtsjärv. The increasing height of the water level was the single independent environmental factor demonstrating a clear trend during the period of investigation. Other environmental factors being rather constant, this smooth continuous trend offered a unique possibility to follow changes in the ecosystem. Mathematically, changes in the mixing depth and in the light extinction coefficient influence water column irradiance equally, as both of them stand in the exponent. At low water transparency the light extinction coefficient is very sensitive to changes in the Secchi depth (hyperbolic relation). In spite of this the 1.5 m increase in the height of the water level in shallow turbid Vörtsjärv had a much stronger influence on light conditions than the improvement of water transparency. Although almost the whole water column in Vörtsjärv remained within the euphotic zone, the deterioration of light conditions resulted in a decrease of primary production expressed in reduced phytoplankton biomass. The invasion of *L. redekei*, a species whose development starts in early spring under the shade of diatoms, is obviously connected with light conditions as well. Nicklisch et al. (1981) demonstrated a specific light adaptation of this species, which allows its mass development in more turbid and cooler water as compared with other blue-green algae.

The pH values varied mainly as a function of phytoplankton growth. The one-month lag in the cross correlation between pH and phytoplankton biomass shows that high pH values coincide with periods of intensive phytoplankton growth.

The decrease of the total number of bacterioplankton may be caused by the decline of primary production but also by the increased grazing pressure of zooplankton upon bacteria. In Vörtsjärv the mean weight of zooplankton individuals is very small fluctuating from 0.4 to 2 µg. This is connected with dominating small cladocerans, mainly *Chydorus sphaericus* (Müller), and a rather great abundance of rotifers, which is characteristic of strongly eutrophic lakes (Haberman, 1995b). Among phytoplankton the number of chlorophytes, chrysophytes, and small diatoms, i.e. edible forms for zooplankton, has undergone a remarkable decrease and these species have been replaced mainly by filamentous *L. redekei*. Considering the species composition of phyto- and zooplankton a high grazing pressure on phytoplankton cannot be expected.



## CONCLUSIONS

The decrease in phytoplankton biomass, total number of bacteria, and water pH against the background of the clearly increasing trend of water level and a rather constant or slightly growing load of nutrients ( $\text{wiNO}_3$ ,  $\text{suPO}_4$ ) can be explained by changes in underwater light field. Both the mixing depth and the Secchi depth, which affect diametrically water column irradiance, increased during 30 years. Though at low water transparency the light extinction coefficient is very sensitive to changes in the Secchi depth, the water level was the leading factor that determined the light field of the water column. In continuously mixed Võrtsjärv the mixing depth is equal to the lake depth during most of the time. The 1.5 m increase in the average height of the water level resulted in 1.1 m increase in the average lake depth while the bottom irradiance dropped 7-fold and the water column irradiance by 1/3. The light-limited phytoplankton community responded to this deterioration of light conditions by a decrease in primary production which, in its turn, reduced the phytoplankton biomass and pH of water. The availability of mineral nitrogen controlled phytoplankton growth in August and September when the light conditions in the water column improved. Changes in the phytoplankton species composition led to a growth of the proportion of filamentous algae and a decrease in the proportion of small algae edible for zooplankton. Probably, the decreasing trend of the total number of bacteria reflected, besides substrate limitation, also the increased grazing pressure of zooplankton on bacteria.

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## REFERENCES

- Haberman, J. 1995a. Dominant rotifers of Võrtsjärv (Estonia). *Hydrobiologia*, **313/314**, 313–317.
- Haberman, J. 1995b. Estimation of the trophic state of Lake Võrtsjärv on the basis of rotifers (Rotatoria). *Proc. Acad. Sci. Estonia. Biol.*, **44**, 3/4, 92–105.
- Haberman, J. Zooplankton of L. Võrtsjärv. *Limnologia* (in press).
- Haberman, J., Nõges, P., Pihu, E., Nõges, T., Kangur, K. & Kisand, V. Characterization of L. Võrtsjärv. *Limnologia* (in press).
- Harris, G. P. 1986. *Phytoplankton Ecology: Structure, Function and Fluctuation*. Chapman & Hall, London.
- Jaani, A. 1990. Võrtsjärve veerežiim ja -bilanss. *Eesti Loodus*, **11**, 743–747.
- Järvet, A. & Nõges, P. 1994. Võrtsjärve osa maastiku ainerings. In *Eesti jõgede ja järvede seisund ning kaitse* (Järvekülg, A., ed.). Teaduste Akadeemia Kirjastus, Tallinn, 16–31.
- Kisand, V. 1994. Comparison of different approaches to estimating heterotrophic bacterial production:  $^3\text{H}$ -thymidine, -leucine and -adenine incorporation techniques,  $^{14}\text{CO}_2$  dark assimilation and  $^{14}\text{C}$ -glucose uptake activity. *Limnologia*, **24**, 4, 351–358.

- Kisand, V. & Tammert, H. Bacterioplankton of L. Võrtsjärv in 1982–1991. *Limnologia* (in press).
- Lehman, J. T. & Sandgren, C. D. 1982. Phosphorus dynamics of the procaryotic nanoplankton in Michigan Lake. *Limnol. Oceanogr.*, **27**, 5, 828–838.
- Mallin, M. A. & Paerl, H. W. 1992. Effects of variable irradiance on phytoplankton productivity in shallow estuaries. *Limnol. Oceanogr.*, **37**, 1, 54–62.
- Nicklisch, A., Conrad, B. & Kohl, J.-G. 1981. Growth kinetics of *Oscillatoria redekei* van Goor as a basis to understand its mass development in eutrophic lakes. *Verh. Int. Ver. Limnol.*, **21**, 3, 1427–1431.
- Nõges, P. 1992. Changes in the ionic composition of L. Võrtsjärv (Estonian Republic). *Limnologia*, **22**, 2, 115–120.
- Nõges, P. & Järvet, A. The role of L. Võrtsjärv in the matter circulation of the landscape. *Limnologia* (in press).
- Nõges, P. & Laugaste, R. Seasonal and long-term changes in phytoplankton of L. Võrtsjärv. *Limnologia* (in press).
- Nõges, T. Cladoceran grazing in L. Võrtsjärv. *Limnologia* (in press).
- Nõges, T. & Nõges, P. Primary production of L. Võrtsjärv. *Limnologia* (in press).
- Sakshaug, E. 1980. Problems in the methodology of studying phytoplankton. In *The Physiological Ecology of Phytoplankton. Studies on Ecology*, 7 (Morris, J., ed.). Blackwell Scientific Publications, 57–91.
- Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. *Limnol. Oceanogr.*, **23**, 3, 478–486.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.*, **33**, 53–83.
- Zaiss, U. 1978. Daily rhythm of regulation of polyphosphate metabolism in an algal bloom of *Oscillatoria redekei*. *Verh. Int. Ver. Limnol.*, **20**, 4, 2298–2301.

## VÕRTSJÄRVE PLANKTONIS AASTATEL 1964–1993 ILMNENUD TENDENTSID JA NENDE SEOS KESKKONNATINGIMUSTEGA

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On analüüsitud aastatel 1964–1993 Võrtsjärve veetasemes, vee kvaliteedis ja planktonis ilmnenuid trende. Järve keskmise sügavuse kasv 2,1-lt 3,2 meetrini sel perioodil vähendas järve põhja jõudva valguskiirguse hulka seitsmekordselt ja veesamba keskmist valgustatust ühe kolmandiku võrra. Peamiselt valguse poolt limiteeritud fütoplanktoni produktsioon langes, mis omakorda vähendas selle biomassi ja alandas vee pH-d. Sesoonselt oli fütoplanktoni kasv vaid augustis ja septembris sõltuv mineraalse N vabanemise kiirusest, sest sel ajal valgusolud madala veeseisu tõttu paranesid. Uuritud 30 aasta jooksul suurenes niitjate vetikate osakaal ja kahanes väikeste, zooplankterite toiduks sobivate vetikate oma. 1960. aastatel järve ilmunud sinivetikas *Limnothrix redekei* (van Goor) Meffert kujunes 1980. aastatel üheks fütoplanktoni dominandiks. Mitmed zooplanktoni liigid kadusid järvest. Bakterite üldarvukuse langustendents oli ilmselt tingitud vetikate kui substraadi hulga vähenemisest ja zooplanktoni suurenenud bakterisöömast.